The Ecology and Conservation of the Southern Damselfly (*Coenagrion mercuriale*)

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Thesis submitted in accordance with the requirements of the
University of Liverpool for the degree of Doctor in Philosophy

October 2001

Abstract

This thesis presents an autecological study of the Southern Damselfly (*Coenagrion mercuriale*), a rare insect that is on the northern edge of its range in Britain. The primary aims of this study were to examine habitat use (at both broad and small scales) and to investigate other aspects of development and behaviour in *C. mercuriale* with a view to devising appropriate management practices for the species. *Coenagrion mercuriale* was found to be restricted in its national and global distribution and was estimated to have undergone more than a 30% decline in its British distribution since 1985. It is a stenotopic species being highly sensitive to a number of habitat factors at both broad and small scales of habitat use. A requirement for a thermally advantageous microclimate was reflected in broad scale habitat use (e.g. use of shallow, sun-exposed, permanently flowing waterbodies indicated by perennial, herbaceous, aquatic vegetation) and in habitat use for oviposition and emergence by *C. mercuriale*. This species was found to have a semi-voltine life cycle in Britain, with a shorter larval growth period and flight period than in mainland European populations. Seasonal regulation is probably achieved in Britain by a facultative autumn diapause in the penultimate larval instar. In field experiments, mature adults of *C. mercuriale* exhibited a relatively low rate of emigration and travelled relatively short distances over non-habitat. However, examination of the distances between extant sites suggest that such rates of dispersal may be sufficient to promote founding and persistence of local populations within four large clusters of populations in Britain. Weather conditions, namely temperature were found to effect daily emergence, activity (including reproductive activity) and mature adult survival. Thus, in common with other thermophillic insects, *C. mercuriale* was found to be limited by temperature in many respects on the edge of its range. The requirement for a thermally advantageous microclimate restricts this species to an early successional stage in both its biotopes and a range of management practices are suggested for maintenance of such stages on *C. mercuriale sites in Britain. Since rates of dispersal* seemed highly dependent on landscape structure, management to facilitate movement between sites across non-habitat was also suggested.

Acknowledgements

I would like to thank the Environment Agency, English Nature and the Countryside Council for Wales for funding this PhD and members of the UK Southern Damselfly Steering Group, past and present, for their advice and encouragement. In particular I would like to thank Tim Sykes for additional support during writing up, Mike Jenkins for venturing out onto a wintry, windswept Mynydd Preseli on several occasions and for identifying insects, and Martin Drake and Adrian Fowles for providing records, bibliographies and such like.

The following people helped me to locate dispersing damselflies, discern tiny runnels in the mire or filled in lengthy questionnaires: Norman Baldock, Simon Bates, Steve and Anne Coker, John Campbell, Les Colley, Sean Cooch, Stephania Davani, Alan Hold, Zoe James, Jessie Marcham, David Painter, Evelyn Prenderghast, Emma Rothero, Phil Stuckey, Matt Sutton, Howard Taylor, Simon Weymouth, the 1998 New Forest dispersal day attendees. Derek Jenkins, Dave Winsland and Steve Coker shared their expert knowledge of the Southern Damselfly.

The Forestry Commission, Clinton Devon Estates and the RSPB and the Countryside Council for Wales granted access to Upper Crockford, Aylesbeare and Mynydd Preseli respectively for fieldwork. Thanks to Pete Gotham, Toby Taylor and Leslie Kerry for their enthusiasm and assistance during my work on Aylesbeare Common and for putting me up in the volunteer's cottage. Thanks to those people in the Hampshire EA office that provided assistance during my 1999 summer field season. I would like to thank especially those people that really got stuck into the bog with me during fieldwork including Sarah Hawkes, Ali Strange, Joe Stevens, Charlotte Walker and Pete – especially to Sarah who provided 70% rum and top tunes on the mandolin.

Thanks to Joanna Hughes and Pauline Morrow for their essential help with GIS and deciphering ArcView and to Nigel Webb and Rob Rose at the Institute of Terrestrial Ecology in Wareham for hosting me for a week's work on their Dorset GIS. Thanks to Sean Cooch at the Forestry Commision for providing GIS data for the New Forest.

Within the University of Liverpool, I would like to thank my supervisor, Dave Thompson, for his continued input through the PhD. Pavel Toropov, Debbie Stevens and Sally Collinge provided help with water chemistry (and endured bucket loads of broken glassware). Julian Collins, Rob Marrs, Ian Gill, John Eaton, Ian Harvey and Mike Begon have provided advice and Sandra Telfer gave invaluable help with program MARK. Within population biology, I would especially like to thank Steve Sait for discussing ecology with me, for recommending references and providing helpful comments on chapters and ideas.

Thanks to those people that that make Liverpool and the Nicholson building as fun as it can be; to Nic for taking me climbing, for providing faecal anecdotes and classic inventions such as the clothes horse emergence trap, for always being a great mate and for being the only other person that's regularly as drunk as me; to Olivier for long discussions (!), for being amazingly generous with his time and knowledge and for great crêpes; to Chris and Esther for making me laugh, taking me dancing and walking and also for being great mates, especially lately. Big thanks too to Ted who supported me in many ways through most of my PhD, took me cycling and introduced me to the wonderful world of technical outdoor clothing. Cheers to fellow writer-uppers Paul, Chadden and Laura for sharing the strange type of insanity that ensues when one spends far too much of one's time in the Nicholson Building and to Nick P for help with formatting in the early hours and for that wicked salad with the cherry tomatoes and green beans. Thanks to Rach and Steve H for providing gags and to Adrian, Alex G, Kate, Sarah Y (and Phil), Sara G, Suzanne, Becky, Bex, Kris, Jim, Phil, Jianbin, Ross, Russell, Rob, Lil, Matt, Mary and all the other post-grads and post-docs that have enriched the Liverpool PhD experience. I would like to thanks those who rowed and raced with me in the University boat club for providing the ideal environment in which to forget all about damselflies for a bit. Thanks to Alice, Ben and Alex for providing advie from afar.

Most of all I would like to thank my family without whose support this thesis may not have been completed. Cheers to Lisa and Joe for enduring the Christmas of 1999 and for distracting me with discourses on 'The Matrix', 'Spaced' and the relative merits of DVDs versus CDs. Thanks to Dad for coming on fieldwork, showing me some mean tricks with a pond net, enlightening me as to the wonders of triangulation, for permitting me a 'domain' in your office, for fixing the departmental car and for providing the much needed pragmatist's eye view. Thanks to Mum for providing a 'haven' in Gloucester and for always being there on the end of the telephone and to both of you for having confidence in me.

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Chapter 1 Introduction

This thesis presents an autecological study of the Southern Damselfly, *Coenagrion mercuriale* (Charpentier, 1840). This chapter explains the justification for and context of the study within insect conservation and gives a brief species description, before providing an overview of the rest of the thesis.

1.1 Extinction and conservation of insects

Insects make up around 56% of described species and an estimated 64% of all species in the world (Groombridge 1992) and perform a disproportionate number of functional roles within ecosystems (Speight *et al.* 1999) including agricultural ecosystems (e.g. pollination of crops, biological control Pyle *et al.* 1981). Despite these facts, conservation effort has, until recently, been directed mainly towards wholescale ecosystems, vertebrates and plants (New *et al.* 1995). The vast majority of insect species remain undescribed (May 1988; Franklin 1993), especially in tropical regions, and relatively few insect extinctions have been documented. Given their small size, poikilothermy (i.e. they lack a means to maintain a constant body temperature independent of fluctuations in ambient conditions) and rapid dynamics, insects are particularly susceptible to environmental change (New *et al.* 1995) and are likely to be undergoing high rates of extinction (Samways 1996). In Britain, where the insect fauna are relatively well described, 40 species of terrestrial invertebrates (mainly insects and spiders) have gone extinct in the last 100 years (Hambler & Speight 1996). The most important cause of insect extinction is the habitat destruction and fragmentation of natural biotopes (e.g. Thomas 1991) due to causes such as urbanisation, agricultural conversion (including deforestation), drainage and pollution (Pyle *et al.* 1981).

Thus in practice most insects are protected by the protection of their biotopes. Very few insect species are individually protected, even if they are listed in Red Data Books and the setting aside of specific reserves for specific insects is almost non-existent. (Samways 1994). This approach has been supported by the identification of hot spots of biodiversity (Myers *et al.* 2000) and by investigations of the effect of different habitat factors on species richness of various insect taxa. (e.g. Boggs & Murphy 1997). However, conservation of a particular plant community (Usher & Jefferson 1991) or biotope will not necessarily lead to conservation of all consumer species. Habitat fragmentation produces nonrandom extinction of biotopes and of species with different attributes such as mobility (Thomas 2000), geographical range (Gaston 1994) and habitat specificity (Thomas & Morris 1995). Thus some populations, species or biotopes are worthy of special conservation effort (see assessments of rarity by Rabinowitz *et al.* 1986; Schoener 1987; Gaston 1994). The extent to which this is true of odonates and their biotopes and of populations on the edge of a species' range is discussed next.

1.2 Conservation of wetlands and odonates

Wetlands have been subject, more than most biotopes (Thomas 1991), to fundamental destruction due to processes such as drainage (leading to lowering of water tables and loss of temporary ponds), pollution, eutrophication, and inappropriate management (Foster 1991; Thomas & Morris 1995). This is likely to have been accompanied by population extinction or reduction of aquatic insect species including odonates, since they are restricted to water in their egg and larval stages and use open water areas for breeding (Corbet 1980).

Odonates are generalist carnivores, often constituting the top predators in freshwater ecosystems (Corbet 1962), they still require particular shelter and roosting areas as adults and aquatic habitat for the larvae (Moore 1991, section 1.5) and thus may be affected by biotope fragmentation to a similar degree as specialist insect herbivores such as lepidopterans (Samways 1993). Within Europe, Van Tol & Verdonk (1988) reviewed the status of 164 indigenous European odonate species and found that 61 were considered endangered, vulnerable or rare (under IUCN red data book categories). Decline or extinction of odonates in Europe was particularly noticed among species of lakes, peat bogs, mesotrophic marshlands and rivers. In addition, 22% of resident British odonates are listed in British Red Data Books (Thomas & Morris 1995), a percentage comparable to that found for Orthoptera (20%) and Lepidotera (31%) in the same British review.

Studies of the responses of odonate species richness to alteration in habitat factors or the provision of artificial waterbodies (Samways 1989; Samways 1992; Steytler & Samways 1995; Samways & Steytler 1996) have revealed that odonates, as with other organisms, can be placed along a continuum of biotope tolerance from eurytopy to stenotopy. Stenotopic species are those that are confined to one or a few biotopes whilst eurytopic species are found across a range of biotopes. Stenotopic species will be relatively more vulnerable to biotope loss or fragmentation (Samways 1994) and will thus be worthy of more conservation effort (Moore 1991). Stenotopic odonates are those which are highly sensitive to a number of factors such as sunlight, shade, water flow and vegetation structure (Steytler & Samways 1995). whilst eurytopic species can colonise newly formed, sparsely vegetated lentic conditions common in artificial waterbodies (Samways 1989).

1.3 Risk of extinction in edge of range versus core populations

Species of a variety of taxa are generally less dense and more variable in space and time in populations on the edge of their ranges versus the core (Brown *et al.* 1995; Brooks 2000; Channell & Lomolino 2000). Thus they are often more prone to extinction on range edges (Brooks 2000; Channell & Lomolino 2000). Insects are poikilothermic and need to raise their body temperatures above a threshold before activity becomes possible (see May 1976 for odonate examples). Thus, they thermoregulate by selection of appropriate microclimates (Willott, 1997). Thus small differences in mean temperature can have a large effect on habitat availability for ectotherms in temperate regions (Thomas 1991) and species often occupy narrower niches within biotopes towards the northern edges of their ranges (Thomas *et al.* 1999). Since many insects reach their northern latitudes in Britain (e.g. butterflies Thomas & Morris 1995) and may be more vulnerable to extinction on their range edges, this may partially account for the comparatively small invertebrate fauna here (22000 species of insect and several thousand other invertebrates) containing relatively few endemic species.

Thermophilic insect taxa will be particularly adversely affected by narrowing of niches at northern range edges. Of extant dragonfly species 70% live in the tropics and sub tropics and only 30% are distributed in the rest of the world indicating that dragonflies are indeed primarily thermophilic insects (Sternberg 1994; Krishnaraj & Pritchard 1995). Their distribution, seasonality and inter-habitat variation is strongly restricted by temperature and other climatic factors and these responses seem to be species-specific (May 1978). Intraspecific comparisons of the functioning of core and edge of range populations are particularly pertinent in such species (Thomas *et al.* 1999).

1.4 Resource types required by odonates

Given that management for a single species can be complex and plans are often expensive to execute, the needs of species must be clearly defined through detailed knowledge of the species biology (New *et al.* 1995). Before carrying out an autecological study of *C. mercuriale* it was necessary to consider more generally the types of resources normally required by odonates in their habitat.

It has been estimated that around 80% of all animal species have a complex life cycle i.e. one that includes metamorphosis (Werner 1988). As stated above, odonates are almost exclusively aquatic in their larval (and egg) stages (Corbet 1980) whilst adults are terrestrial. Niche separation of adults and larva, probably a form of intraspecific competition avoidance, is widespread within holometabolous insects but only occurs within 3 of the 24 orders of hemimetabolous insects (i.e. Ephemeroptera, Plecoptera, and Odonata Sternberg 1994). Such developmental polymorphism is of great significance in conservation biology since survival depends on the optimal survival of all developmental stages. Each successive stage depends on the number of survivors from the previous stage (i.e. is a linear phenomenon Samways 1994) and it in necessary to ensure protected habitats contain the resources required by all developmental stages of a rare species.

Although abundance patterns as larvae are related to physical water conditions (Samways 1993) odonates are associated with plants at every ontogenetic stage (Buchwald 1992). In the larval stage, aquatic plants are used for cover from predators and for feeding. In the adult stage, aquatic plants are used as emergence supports and for oviposition (in zygopterans) and bankside plants are used for mating and thermoregulation (basking). Surrounding vegetation is used for roosting (especially during maturation), shelter and for feeding throughout adult life (Corbet 1980; Buchwald 1992). For insects in general, Samways (1994) suggests that the concept of the 'plantscape' is more useful than that of habitat structure per se, since plant-insect interactions (especially herbivory) are the dominant biotic interaction in their life cycles and because macrophytes play a major role in determining habitat structure. Although this is true of odonates, even though they are generalist predators rather than herbivores, relatively few biocenolgical studies have been carried out on them (Buchwald 1992). Thus an autecological study of a rare odonate should consider a range of resources, including vegetation factors and as well as physical water conditions, and also landscape patterns at a larger spatial scale (Samways 1993). Autecological studies have been carried out elsewhere in the European range of *C. mercuriale* (Buchwald 1983; Buchwald *et al.* 1989; Buchwald 1994; Roske 1995) but, given the need for intraspecfic comparisons of the functioning of core and edge of range populations (section 1.3), such a study is pertinent in Britain.

1.5 Justification for individual species protection of *Coenagrion mercuriale*

Coenagrion mercuriale enjoys individual species protection within Europe as a whole and several European countries (including Britain) have taken complementary legislative measures (Table 1.1) for protection at a national or regional level (Van Tol & Verdonk 1988; Grand 1996b). In Britain, due to such measures, very few populations of *C. mercuriale* (e.g. River Test) occur outside Special Sites of Scientific Interest (SSSI) or Special Areas for Conservation (SAC). This species is also unique among odonates in the level of protection afforded to it with only one other odonate listed on the Wildlife and Countryside Act (*Aeshna isosceles*) and no others listed on the EC Species and Habitats Directive. The Biodiversity Convention, signed by Britain at the Rio Earth Summit, in June 1992, required that national programmes for the conservation of biological diversity were developed. In 1994, the UK Biodiversity Action Plan was produced (HMSO 1994), that initially selected and provided action plans for 14 key habitats and 116 key species of top conservation priority. *Coenagrion mercuriale* was among this list and, in 1995, a species action plan was produced for this species that highlighted the need for further research into the ecological requirements of this species in Britain (5.5.1 *of plan HMSO 1995*). The current study was commissioned to fulfil this need.

This odonate species is thought to be worthy of such protection since it is restricted to a few biotopes that have undergone fragmentation (such as wet heathlands, chalkstreams, water meadow brooks and ditches). It is rheophilic (an intolerant of lentic conditions found in artificial water bodies) and is on the northern edge of its range in Britain.

Table 1.1 Protection measures for *C. mercuriale*

Legislation or convention.	Level
1. listed on the Bonn Convention for the conservation of Migratory Species of Wild Animals	International
2. listed on Appendix II of the Berne Convention, Convention on the Conservation of European Wildlife and Natural Habitats (1979) which outlaws the collection or possession of listed species.	International
3. listed on Annex II of the European Community Habitat and Species Directive (1992) that requires that special areas of conservation (SACs) be designated for animal and plant species of community interest.	Europe
4. listed on Schedule 5 of the Wildlife and Countryside act (1981) - protects against damage and killing of individuals and damage or destruction of habitat, protects biotopes in localities designated Sites of Special Scientific Interest (SSSIs).	Britain
5. listed as rare (category 3) in the British Red Data Book and also features on the red lists of other countries in Europe (Grand 1996a).	Britain & Europe
6. subject of a UK Biodiversity Action Plan (HMSO 1995)	Britain

1.6 Species description and identification

Coenagrion mercuriale is one of five members of the genus *Coenagrion* currently to be found in Britain. This genus, together with *Enallagma cyathigerum*, constitute the 'blue damselflies' which are all blue and black in colouration and of which *C. mercuriale* is the smallest. *Coenagrion mercuriale* has a sub-species in North Africa, *C. m. hermeticum* – (Selys, 1872) and one in Italy, *C. m. castellanii* (Robert 1948). Males can usually be distinguished from other British blue damselflies by the 'mercury mark' on the 2nd abdominal segment. However, this mark shows considerable variation within and between populations such that the anal appendages and black spines along abdominal segments 3-5 constitute more reliable characters (Hammond 1983; Askew 1988). There are two female forms or morphs. The more frequent heterochrome form is olive green laterally with small pale marks anteriorly, on segments 3-7, and on the head. There are blue intersegmental rings on segments 7-10. In the homeochrome or andromorph form, the pale colour is more extensive and the rest of the body is blue like the male. The female may be distinguished from *Coenagrion puella* and *Enallagma cyathigerum* by the pale markings described above, and from *Coenagrion pulchellum* by the straight hind margin of the pronotum (Hammond 1983; Askew 1988). Additional characters for both sexes include a short, lozenge shaped pterostigma, and large, rounded, post-ocular spots.

1.7 Thesis overview

In Chapter 2, the distribution, status (including population sizes) and rate of decline of British *C. mercuriale* populations are examined using biological records. Proximate habitat features, associated with the occurrence, decline or expansion of *C. mercuriale* populations are identified (including physical, chemical and vegetation features), to build up a coarse scale habitat profile for this species in Britain. The possible ultimate factors determining coarse scale habitat use in this species are discussed. Habitat use is compared to other odonates and between core European and British populations to permit speculation on whether the niche for this species narrows on the edge of its range.

Chapters 3 and 4 look at aspects of development and seasonal regulation in *C. mercuriale* in Britain. Chapter 3 examines the form and synchrony of the emergence curve in a British population where *C. mercuriale* co-exists with *Ceriagrion tenellum* - another species that is on the northern edge of its range in Britain. The relative role of season and climatic factors in determining daily emergence are determined as is mortality at emergence. In Chapter 4, larval growth pattern is investigated in a single population of *C. mercuriale* and the location of diapause is related to the form of the emergence curve found in Chapter 4. More generally, voltinism and growth in *C. mercuriale* in Britain is compared to that found in core populations and also placed within the context of the Odonata. Qualitative observations are made on habitat use in the larval stage.

In Chapter 5, proximate micro-habitat features used by the adult at emergence and oviposition are examined, to determine whether requirements during these life stages affect population occurrence or abundance at a broad scale. Since *C. mercuriale* is non-territorial and oviposition occurs mainly in tandem, oviposition site quality is likely to have an over-riding influence on oviposition habitat use whereas in territorial species, the location and behaviour of conspecifics will have a greater effect.

Lifetime mating success is examined in a small, isolated population of *C. mercuriale* in Chapter 6, with particular focus how the relative effects of stochastic weather events, natural selection and sexual selection may shift in an edge of range population. A range of reproductive behaviour is also described. Survival is examined, using capture-mark-recapture models that take account of variation in recapture probability, again to determine the relative roles of weather versus phenotype.

As stated above, the likelihood of extinction due to habitat fragmentation depends on species attributes such as mobility, geographical range and habitat specificity. The latter two attributes are dealt with in Chapter 2 for *C. mercuriale* whilst in Chapter 7, dispersal is investigated in this species, again using mark-release-recapture data. Both within and between population movements are considered and the effects of phenotype and landscape structure on dispersal are examined. The likelihood of colonisation and exchange between populations is discussed given the current configuration of British sites.

Chapter 8 draws together the range of broad and small scale information on habitat use and dispersal and provides a series of management recommendations and site condition assessments for this species in Britain. The functioning of these edge of range populations versus core populations of this species are compared and the role of climate in determining habitat use, survival and activity in *C. mercuriale* is discussed. Fruitful areas for future research are highlighted and suggestions for better monitoring of this species in the future are given.

Chapter 2 Status, habitat use and management of *Coenagrion mercuriale* in Britain

2.1 Introduction

Habitat is an autecological concept which emphasises the interaction between a species and the physical structure of its surrounding environment whilst biotope refers to the physical local area where a species lives (Samways 1994). Estimates of habitat availability and connectivity are most accurate if based on the distribution of individual species' habitat patches rather than biotope islands (Thomas & Hanski 1997). For organisms to persist they must select habitat that meets the ecological needs of all the stages of their life cycle. With regards to conservation of insects it is important to protect their habitats as well as the insects themselves (Collins & Thomas 1991; Usher & Jefferson 1991). *Coenagrion mercuriale* benefits from individual species protection since it is thought to fulfil several of the criteria used to assess rarity. Assessment of rarity is of practical importance in deciding where to direct conservation effort (Usher 1986). Categories of rarity can be defined (Rabinowitz *et al.* 1986; Schoener 1987) according to attributes of a species including its geographical range, the size of its populations and the degree to which it is restricted to a particular biotope. In this chapter, these attributes will be investigated for *C. mercuriale* in Britain by reviewing biological records, site descriptions, monitoring documents and field studies for British populations *of C. mercuriale.* Such attributes are of ecological importance because habitat fragmentation produces non-random extinction of populations and species characterised by different levels of dispersal (Thomas 2000), habitat specificity (Thomas & Morris 1995) and those with small geographical ranges (Gaston 1994).

In particular, determining the distribution of species is essential for making decisions on their conservation management (Samways 1994). Here biological records are analysed to describe the rate of decline over time in this species in comparison to other insect species and to highlight problems in interpretation of biological records for rare species. At finer scales, most insects are small with small home ranges, especially insects of particular conservation concern and thus the documents are reviewed to determine what biotope types *C. mercuriale* uses in Britain and what habitat is used within these biotopes.

In Europe, *C. mercuriale* occupies three different biotopes (Buchwald 1994; Sternberg *et al.* 1999). In the core of its distribution it mostly occupies meadow brooks and ditches, on the alluvial planes of the Rhône in France and in Bavaria and Baden Württemburg in Germany. Secondly, it occupies headwaters of major rivers (marshy flatlands) such as the Upper Rhine in Germany, and the Rhône and Durance in France (Deliry & Grand, 1998). On the edge of its range (in the Alpine region, Bavaria in Germany), it is found on runnels in pre-alpine calcareous spring marshes (Buchwald 1983; Buchwald *et al.* 1989). The specificity of its habitat requirements seems to increase in edge-of-range, alpine populations with regards to the type of waterbody occupied and the vegetation structure (Buchwald 1994). It is interesting to consider whether such regional stenotopy occurs in Britain.

Samways (1994) suggests that, for insects, the concept of the 'plantscape' is more useful than that of habitat structure per se, since plant-insect interactions are the dominant biotic interaction in their life cycles and because macrophytes play a major role in determining habitat structure. Buchwald (1992) describes how since vegetation is used at all stages of the odonate life cycle (e.g. providing cover for larvae, perches at emergence and breeding at substrate for oviposition), macrophytes are likely to feature highly among the proximate cues used for habitat selection. For example, *Orthetrum coerulescens* and *Ceriagrion tenellum*, showed a strong preference for particular plant communities and vegetation during selection of suitable breeding habitat (Buchwald 1992). Despite the importance of vegetation, few biocenological studies have been carried out on odonates. Thus, features of vegetation are emphasised in the discussion of this species' habitat although physical and chemical features are also investigated.

Habitat use is most directly investigated by the construction of resource selection functions to predict the probability of an animal using an area depending on the quality and abundance of resources within it (Boyce 1999). Such an approach requires large amounts of data and was not appropriate here given the current state of knowledge of this species. Thus requirements of *C. mercuriale* are inferred indirectly from (1) features that often occurred where populations were found; (2) features that, when altered had positive or negative impact on population numbers or persistence; (3) features that when altered produced a contraction or expansion in the range of the species within a site. These types of features are emphasised and compared to the habitat requirements of this species in Europe – in the core of its range and in other edge-of-range populations (such as the German alpine populations).

2.2 Organisation of review

2.2.1 Analysis of biological records

Biological records up to 1999 were collated from a variety of national (databases by Steve Cham and Adrian Fowles) and regional sources as follows; Devon and Dartmoor (Kerry 1994; Smallshire 1995; Smallshire 1998), Dorset (Winsland 1994b; Prendergast 1996; Sutcliffe 1998 Dorset Environmental Records Centre, RSPB), New Forest (Stevens & Thurner 1999 Institute of Freshwater Ecology, Forestry Commission; Strange 1999), Oxford (J. Campbell pers comm.). Of the 1697 records obtained, 531 were duplicates and were discarded. The remaining 1166 records were distributed between 552 different grid references, 69 were at a 10km grid square resolution (15 grid references), 125 were at a 1km grid square resolution (59 grid references) and 972 are at a 100m grid square resolution (478 grid references).

2.2.2 Review of site documents

Knowledge of the distribution of *C. mercuriale* is preliminary. Its presence has been recorded for the first time in many 100 metre (100m) grid squares recently, especially in regions such as Pembrokeshire (section 2.3.2). Thus it is difficult to determine precisely the number of separate British populations of *C. mercuriale* (Table 2.1). Site descriptions and monitoring documents are not available for every *C. mercuriale* population. As with most species and habitat data in Britain (*cf* Griffiths *et al.* 1999), the lack of standard recording methodology has resulted in different types of information being recorded in different sites, making joint analyses difficult. Attempts to standardise the information available across sites by way of site questionnaires (14 returned - see Appendix 1 for sample questionnaire) and the use of existing Geographical Information Systems were unsuccessful.

Documents contained information on 76 extant sites (Table 2.1). For Dorset, Devon, Gower, the New Forest and Oxfordshire, information was available for probably all extant populations. For Pembrokeshire, only a small fraction of extant populations were covered in documents and for Anglesey only 1 of 2 extant populations was described (though these both occur on Cors Erddreiniog). For all areas, but particularly Dartmoor and Pembrokeshire, there is potential for discovery of further populations in the future.

Information was retrieved from documents on a number of biotope and habitat features including stream type and dimensions, geology, biotope type, vegetation communities and architecture, plant species presence and management practices (grazing, burning, scrub clearance and water course alteration). Where information on colony location was sufficiently precise, altitude and slope of sites were calculated using contours on 1:25000 Ordnance Survey maps. On Tables in section 2.3, '-' indicates that information was not available for a particular site or region.

Table 2.1 No. of populations covered by documents in each region.

Region	Number of populations covered in documents	Number of different 100m grid squares in which *C. mercuriale* has been recorded since 1990	No. of discrete populations thought to occur in region
Oxfordshire	2	1 (mainly 1k records)	2
Dartmoor	2	2	2
Devon	2	4	2
Dorset	6	16	6
New Forest	36	59	36
Itchen and Test	15	40	20+?
Anglesey	1	8	2 (1 found in 2000)
Pembrokeshire & St. Davids	10	187	20-40
Gower	2	6	2
Total	76	324	92 – 150?

2.2.3 Water chemistry survey

2.2.3.1 Study Area

In April and May 1998, 91 water samples were taken from 53 extant and 7 extinct sites across the British distribution of *C. mercuriale*. Samples were taken from sources of flushes and from streams sections that *C. mercuriale* was known to utilise. Acid-washed 1-litre bottles were rinsed with stream water at the point of sampling and then filled with stream water. 1ml of mercuric chloride solution was added (i.e. ratio of 1ml: 1 litre) to preserve the sample and bottles were stored in the dark until chemical analysis took place (*cf* Bondorf *et al.* 1981). Conductivity and pH were measured in the field using a Whatman pH meter (model 3051). Nitrate, ammonia, soluble reactive phosphate, total soluble phosphate and total phosphate were measured in the laboratory using colourimetry (e.g. Mackareth 1963). Soluble unreactive phosphate and particulate phosphate were calculated from values for other types of phosphate, following the methods of Mackareth (1963). Since these samples provide only a 'snapshot' of chemical conditions on sites, monthly water chemical samples (mean interval between samples = 39.0 ± 4.4 days) were taken from Glan-yr-afon Uchaf, Pembrokeshire between 18th October 1999 and 3rd October 2000. These were analysed by the Environment Agency. Monthly measurements of stream depth and width are presented in Chapter 4. A datasonde (Hydrolab Datasonde 3 Water Quality Logger) was placed in the stream between 3rd December-12th February 1999 to record temperature, pH and conductivity at half-hourly intervals.

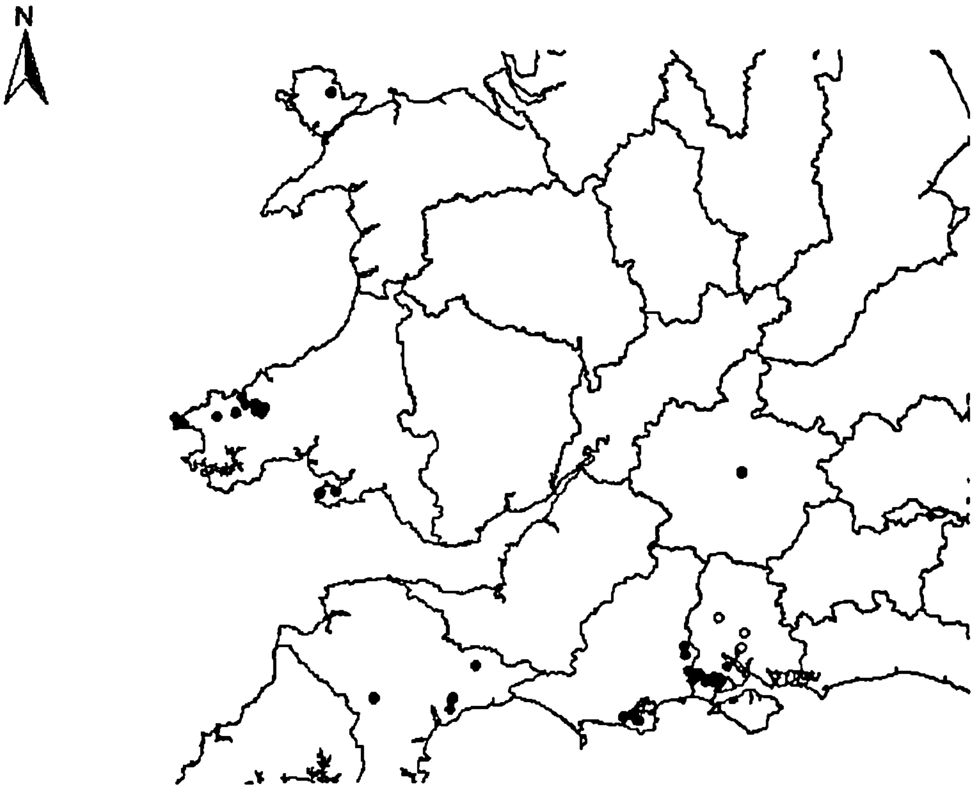


Fig. 2.1 Location of heathland (closed circles) and chalkstream (open circles) sampling sites for the 1998 and 1999 water chemistry survey.

2.3 Results

2.3.1 Distribution of *C. mercuriale*

C. mercuriale is restricted in distribution at both a global and national level. It is limited to the south and west of Europe (Fig. 2.2) and has populations of unknown status in northern Africa (Grand 1996b). Populations in Italy and northern Africa consist of different sub-species (*C. m. castellani* and *C. m. hermeticum* respectively) to other European populations (Askew 1988; Van Tol & Verdonk 1988). It has disappeared or is on the edge of extinction in seven European countries along the northern boundaries of its distribution (Belgium, Holland, Luxembourg, Slovenia, Romania, Poland, Austria) and is declining in three others (Britain, Germany, Switzerland) (Grand 1996).

Fig. 2.2 Global distribution of *C. mercuriale* – (taken from Askew 1988).

Coenagrion mercuriale is on the northern edge of its range in Britain and has a discontinuous distribution, restricted mainly to the south and west of the country (see Figs. 2.3-2.5 for maps of the UK distribution at 10km, 1km and 100km resolutions, Figs. 2.6 a and b show 100m resolution maps for the New Forest and Pembrokeshire in more detail). Major strongholds of populations are found on heathlands in the New Forest in Hampshire and the Preseli mountains in Pembrokeshire with scattered populations in Devon, Dartmoor, Dorset, Gower and Anglesey and Oxfordshire (Figs. 2.4, 2.5, Table 2.1). There are large centres of population on chalkstreams along the Itchen and Test Valley which have been discovered relatively recently (Mayo & Welstead 1983; Stevens & Thurner 1999; Strange 1999). Examination of when *C. mercuriale* was last recorded at each 10km grid reference (symbols on Fig. 2.3) suggests that substantial contractions may have occurred in its British distribution this century (though accuracy of old records is difficult to confirm). These references indicate that the species was previously found in Cornwall (Trevorgan's, St. Buryan) and was more widely distributed in Devon, Dorset (Clayhidon, Glanvilles Woolton, Hense Moor, Luppitt, Godlingston Heath) and Pembrokeshire (Llanrhystud, Letterston). Thus although *C. mercuriale* has been recorded in 35 10km squares since 1975 (Fig. 2.3) only 28 of these have been re-recorded since 1990. The rate of this decline is quantified in more detail in section 2.3.2.

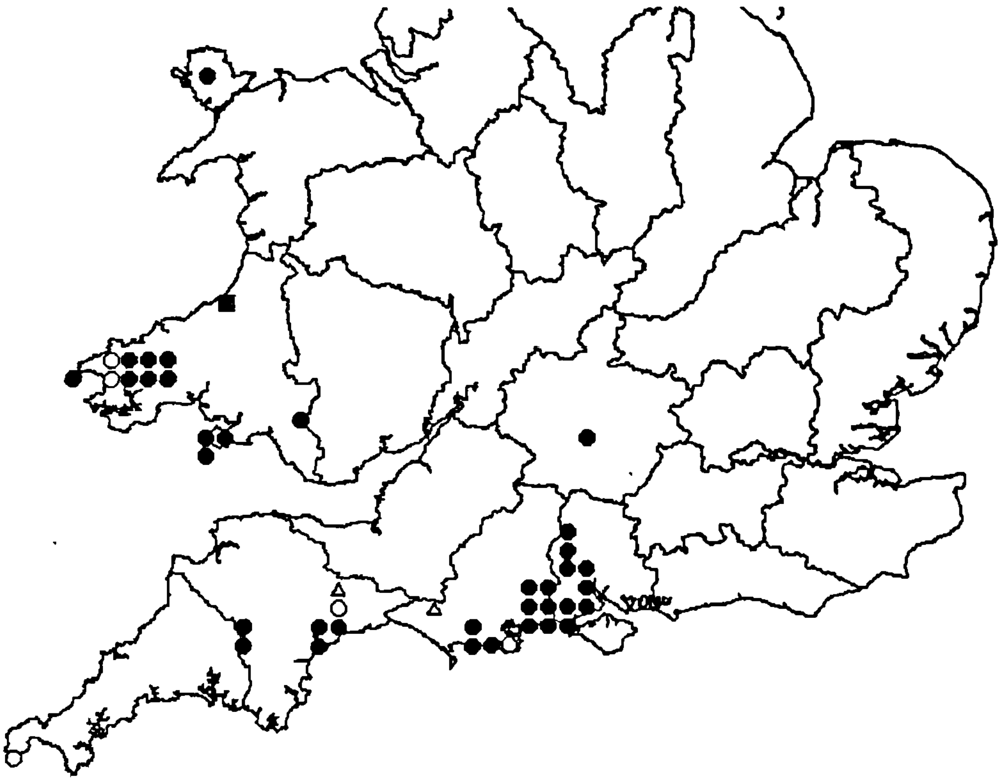


Fig. 2.3 Distribution of *C. mercuriale* in the UK at a 10km grid reference resolution. Symbols indicate the 25 year period in which *C. mercuriale* was last recorded at a particular grid reference according to the following key; Closed circles – 1975-1999, open circles – 1950-1974, grey squares – 1925-1949, open triangles – 1900-1924.

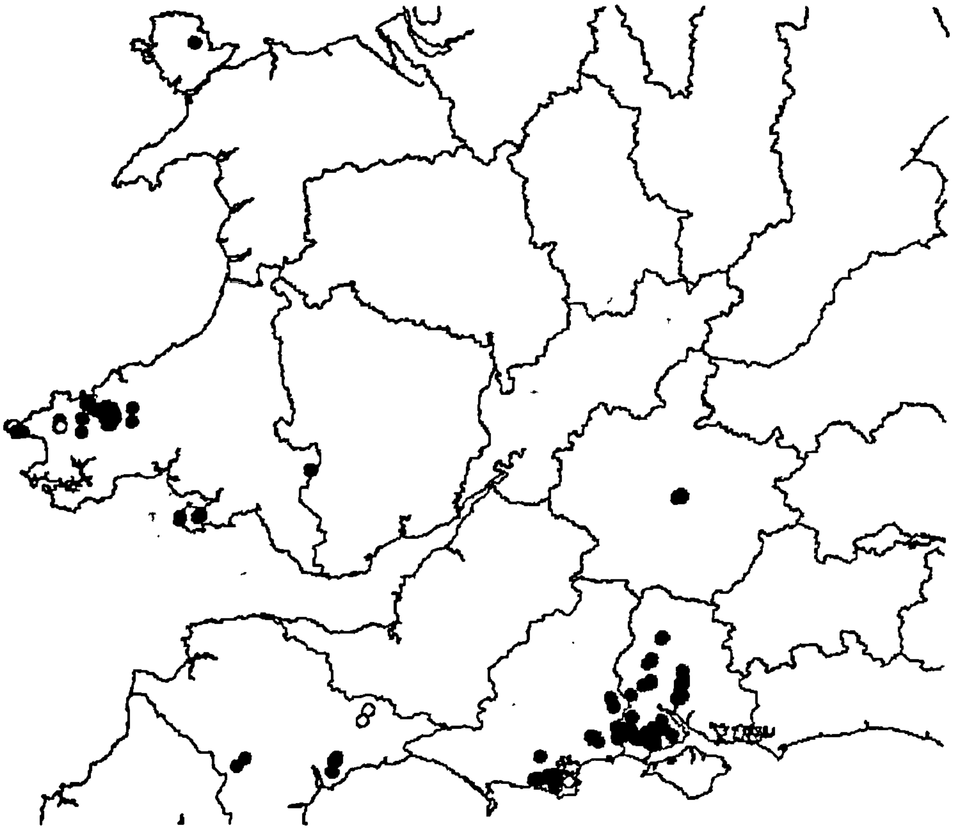


Fig. 2.4 Distribution of *C. mercuriale* in the UK at a 1km grid reference resolution. Symbols as for Fig. 2.1.

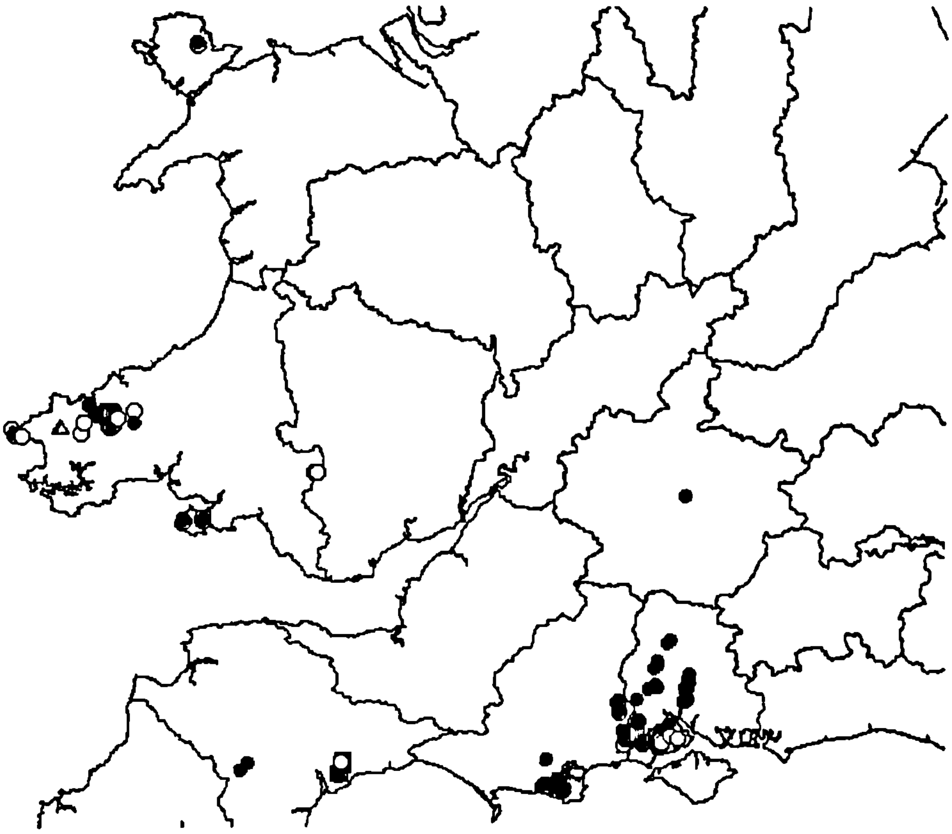


Fig. 2.5 Distribution of *C. mercuriale* in the UK at a 100m grid reference resolution. Symbols indicate the decade in which *C. mercuriale* was last recorded at a particular grid reference according to the following key; Closed circles – 1990-1999, open circles – 1980-1989, grey squares – 1970-1979, open triangles – 1960-1969, dotted circles – pre-1960 records.

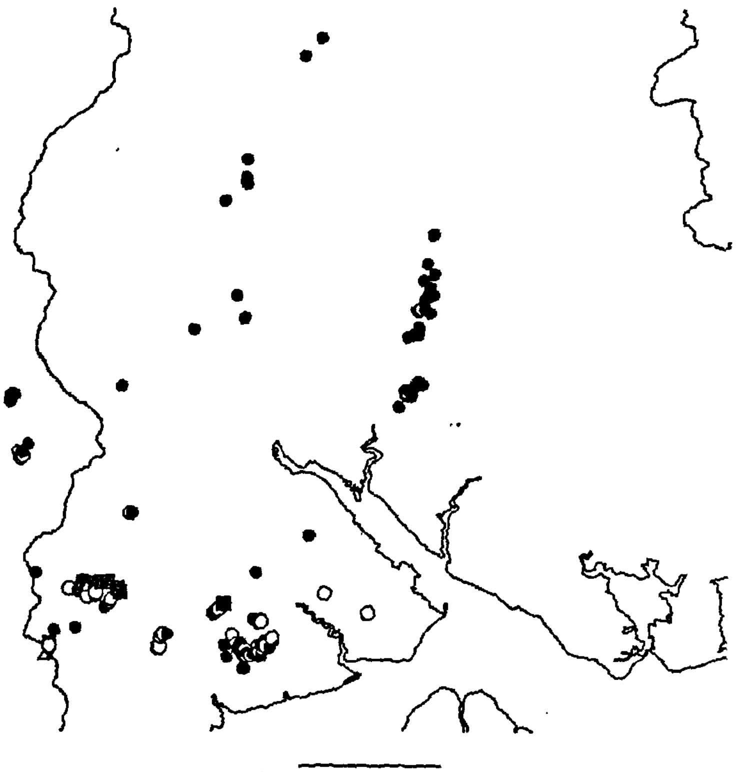


Fig. 2.6a Distribution of *C. mercuriale* in Hampshire at a 100m grid reference resolution (see legend of Fig. 2.5 for symbols). Scale bar represents 10km.

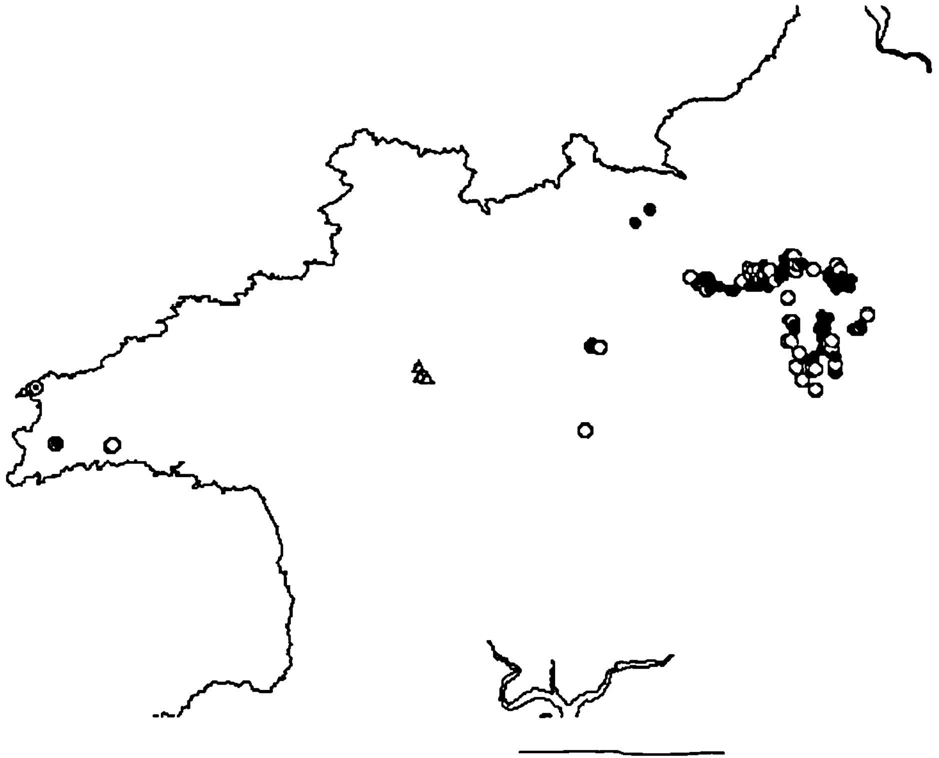


Fig. 2.6b Distribution of *C. mercuriale* in Pembrokeshire (Mynydd Preseli) at a 100m grid reference resolution (see legend of Fig. 2.5 for symbols). Scale bar represents 10km.

Previous authors have suggested that Britain contains a substantial proportion of the global population of *C. mercuriale* (up to 25% - Kerry 1997) and the degree of representivity is one criterion sometimes used to assess the relative importance of areas for conservation (e.g. Brown *et al.* 2000). Although biological records are not sufficiently accurate to allow the number of discrete populations of *C. mercuriale* in Britain to be determined at present, this figure must lie between 100 and 150 populations (Table 2.2). In Europe, *C. mercuriale* has been recorded in 260 sites in Germany (156 in Baden-Wurtemburg (Sternberg *et al.* 1999) and 102 in Bavaria (Kuhn 1998), over 400 sites in France (Grand 1996) and is said to be widespread in Spain (Grand 1996). However, although Britain does not contain 25% of the global population of *C. mercuriale*, there is some indication that the population sizes here are substantial compared to those in Germany. Population sizes have been obtained for few if any *C. mercuriale* sites, but maximum daily counts of adults (of counts obtained since 1994) were available in documents for 61 sites and the frequency distribution of these is shown in Fig. 2.7. Maximum counts of more than 50 adults were recorded in 49% of British sites. There is only anecdotal evidence of how sporadic maximum adult counts correspond to annual population sizes. In Aylesbeare Common, Devon in 1998, 217 adults were observed over the 1998 field season but the maximum daily count was 75 (with an average daily count of 10 males - Chapter 5). At Upper Crockford in 1997, the maximum daily count was 269 (62 on average) but 3000 adults were marked through the season (Chapter 7). Thus annual population sizes could be at least ten times larger than maximum adult counts and many British populations could contain hundreds of individuals in relatively short stretches of stream or mire. In contrast, 80% of sites in Baden-Württemburg, in Germany contained less than 10 individuals per 100m and no sites contained more than 50 per 100m (Roske 1995).

The length of stream occupied by *C. mercuriale* has not been ascertained in most sites but ranges from 25 to 700m where available (section 2.3.4.). Adult and larval populations have a very localised distribution within potential stream habitat (Corbet 1957; Knights 1983; Evans 1989). For example, data from the questionnaires show that the amount of habitat actually used by *C. mercuriale* adults ranges from 26-100% of the potential stream habitat present on site. Similarly in calcareous spring mires, *C. mercuriale* is restricted to 20-100m lengths of stream habitat (Kuhn 1998). This species may be more patchily distributed across its biotopes on the edge-of-its ranges due to narrow habitat requirements there.

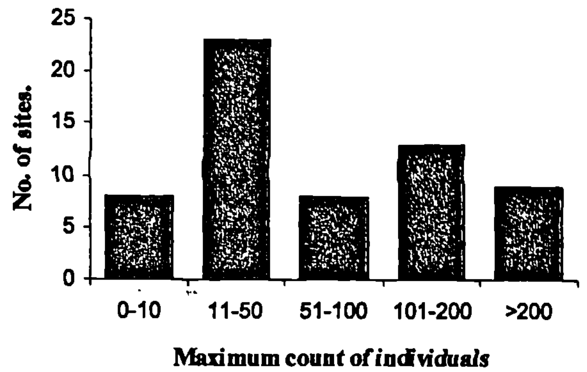


Fig. 2.7 Maximum counts of individuals in *C. mercuriale* sites in Britain (n=61).

2.3.2 Rate of decline of *C. mercuriale*

There has been a dramatic increase in recording effort for this species through time, particularly since 1980 (Fig. 2.8) and there has been an increase in the resolution at which records have been taken (Fig. 2.9). Up until 1940, this species was not recorded at a higher resolution than a 10km grid square. If the number of grid squares in which *C. mercuriale* was recorded as present in each year is considered (regardless of the number of visits in that year), these too show a sharp increase through time (Fig. 2.10 shows this graphically at a 100m grid square resolution). This increase in occupancy is not due to a range expansion but is due to the increase in recording effort through time as shown by the large proportion of newly recorded grid squares even in recent years (Fig. 2.10.). Merritt (1996) found a similarly dramatic increase in recording effort through time in a well-recorded species, *Ischnura elegans*.

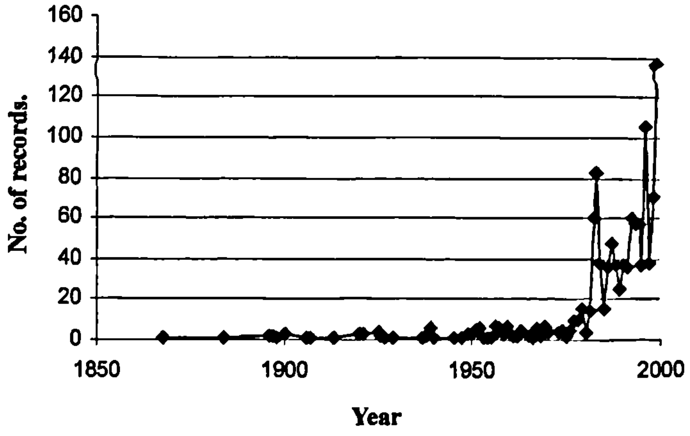


Fig. 2.8 Total number of records of *C. mercuriale* in each year.

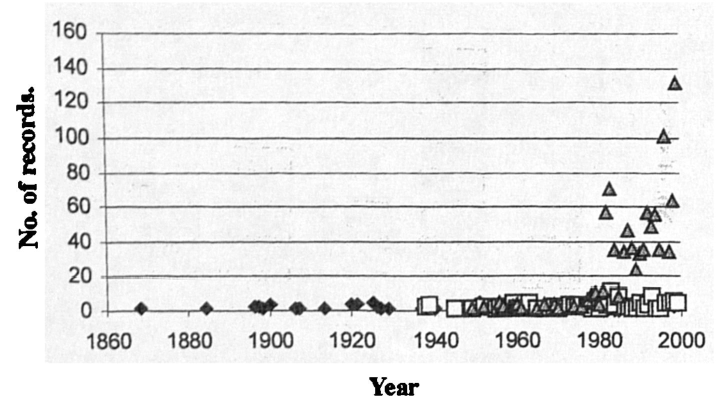


Fig. 2.9 Number of 10km (closed squares), 1km (open squares) and 100m (grey triangles) grid square records of *C. mercuriale* in each year.

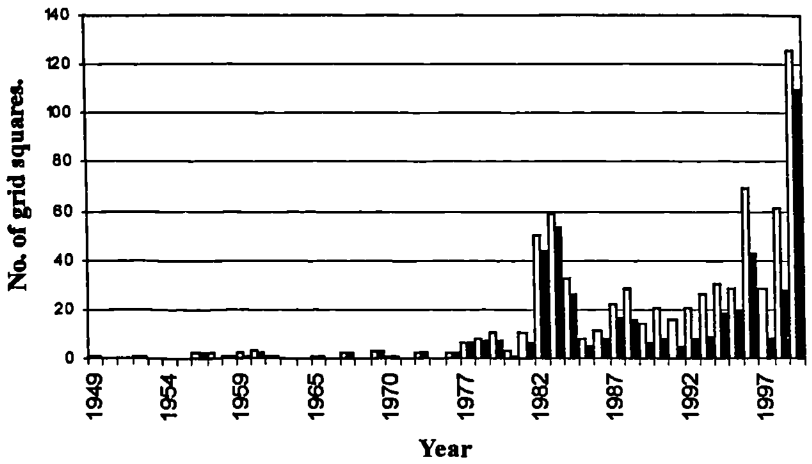


Fig. 2.10 Total number of 100m grid squares occupied by *C. mercuriale* each year (open bars) and the number of squares in which this species was newly recorded in each year (closed bars).

There is also considerable regional variation in recording effort (up to 1999) of *C. mercuriale* at both a 1km and a 100m grid square resolution (Table 2.2). For example, in Anglesey, since the species is found on only one site in this region, a large amount of effort has been invested in recording it in one 1km grid square. To calculate the rate of decline (percentage decline, D since time t) for *C. mercuriale* whilst accounting for this regional and temporal variation in recording effort, the following formula was used for each region (*cf* Thomas & Abery 1995).

$D = 100 \times (1 - a/b)$

Where *a* is the number of grid squares in which *C. mercuriale* was recorded between time *t* and 1999 and *b* is the total number of grid squares recorded. 1985 was designated as *t* since 15 years probably constitutes a sufficient time span to assess whether an extinction has occurred in a particular grid square and also to compensate for the surge in recording effort in the 1980s. In addition, the analysis was performed with all squares (D_{all} assuming that any colony that exists after time *t* also occurred before time *t*) but also omitting those squares newly recorded since 1985 (D_{corr}). This was performed at the 100m, 1km and 10km grid square resolutions. The total rate of decline in Britain at each resolution is summarised in Table 2.3 and regional analyses are shown in Table 2.4.

Table 2.2 No. of grid squares, total number of records and number of records per square across each region (from Ordnance Survey regions) at a 1m and 100m resolution.

OS Region code	Region name	No. of 1km grid squares	No. of records	No. of records per square	No. of 100m grid squares	No. of records	No. of records per square
12	St David's	9	33	3.6	11	28	2.6
20	Dartmoor	2	8	4.0	2	8	4.0
21	Pembrokeshire	7	35	5.0	16	26	1.6
22	Pembrokeshire	42	366	8.7	237	336	1.4
23	Anglesey	1	35	35.0	7	29	4.1
30	Devon & Dorset	23	185	8.0	43	155	3.6
31	Devon	2	5	2.5	0	0	0.0
40	Hampshire	16	240	15.0	48	225	4.7
41	Hampshire & Oxfordshire	54	190	3.5	114	165	1.5
	Total	156	1097	7.03	478	972	2.03

C. mercuriale has undergone at least a 38% rate of decline at the 1km grid square resolution since 1985 and thus fulfills the criterion for classification as vulnerable on the IUCN red list (i.e. a reduction in distribution of at least 20% over the last 10 years IUCN 2001). Although detailed distribution maps are not available for much of Europe, a comparable decline has occurred in Baden-Wurttemberg, Germany, where 41% of populations (58 out of 141) have disappeared since 1983 (Roske 1995). Six figure grid references are often given for the centre of the site and do not indicate the extent of the site. A site may be represented by more than one grid reference at a 100m resolution not due to the extent of the site but because the perception of the colony location has changed. Thus although a much higher rate of decline was found at the 100m grid square resolution references, these do not indicate extent or number of populations. More generally, the informativeness of such grid reference data without site related information (Griffiths *et al.* 1999) is limited.

The data presented in these first two sections raise the question of what limits the distribution of *C. mercuriale* to the south and west of Britain and why it is discontinuous and declining. As described in Chapter 1, odonates are thermophilic (Sternberg 1994; Krishnaraj & Pritchard 1995), being of tropical origin, and their distributions are strongly restricted by climatic factors - especially temperature (May 1978). Within Britain, biological records reveal an increase in species richness within both odonates and orthoperans along a north to south gradient (Griffiths *et al.* 1999). With regards to *C. mercuriale*, this species' restriction to south and western areas is also observed in Germany (Buchwald 1994). The edge of its distribution in Britain has been said to follow the 2.2°C February minimum isotherm (Chelmick 1980 - although this suggestion preceded the discovery of the Anglesey colonies) and the species is found in oceanic areas with a relatively mild climate. Within the New Forest (Fig. 2.6a), Winsland (1985) pointed out the greater incidence of colonies on the southern heaths than on the northern ones. This species' requirement for high temperature is reflected in its associations with particular waterbodies and plant communities (sections 2.3.4 and 2.3.6).

Table 2.3 Percentage decline of *C. mercuriale* in Britain since 1985 at 10km, 1km and 100m grid square resolutions.

Resolution	a	No. recorded since 1985	b	D_{all}	D_{corr}
10km	28	9	43	34.9	44.1
1km	115	49	156	26.3	38.3
100m	353	303	478	26.2	71.4

Table 2.4 Analysis of percentage decline in *C. mercuriale* distribution (divided by region) at 10km, 1km and 100m grid square levels.

		10 km grid square					1km grid square					100m grid square				
Region code	Region name	a	No. 1st recorded in/after 1985	*b*	D_{all}	D_{corr}	*a*	No. 1st recorded in/after 1985	*b*	D_{all}	D_{corr}	*a*	No. 1st recorded in/after 1985	*b*	D_{all}	D_{corr}
10	Cornwall	1	0	1	100	100	-	-	-	-	-	-	-	-	-	-
12	St David's	1	0	3	66.7	66.7	2	0	9	77.7	77.7	5	3	11	54.5	75
20	Dartmoor	2	2	2	0	0	2	29	2	0	0	2	2	2	0	0
21	Pembrokeshire	3	0	3	0	0	5	1	7	28.6	33.3	10	8	16	37.5	75
22	Pembrokeshire	4	1	8	50	57.1	32	11	42	23.8	32.3	190	169	237	19.8	69.1
23	Anglesey	1	1	1	0	0	1	0	1	0	0	6	4	7	14.3	33.3
30	Devon & Dorset	5	2	6	16.6	25	15	6	23	34.8	47.1	26	22	43	39.5	81
31	Devon	0	0	4	100	100	-	-	-	-	-	-	-	-	-	-
40	Hampshire	2	0	12	50	50	13	4	16	18.7	25	31	26	48	35.4	82.1
41	Hampshire & Oxfordshire	11	4	3	8.3	12.5	45	25	54	16.7	31	83	69	114	27.2	68.8
	Total	28	9	43	34.9	44.1	115	49	156	26.3	38.3	353	303	478	26.2	71.4

Thermal requirements of this species cannot explain the discontinuity of its distribution or the pattern of recent decline that may be due in part to fragmentation at the level of its biotopes. This species breeds in two biotopes in Britain - small streams on heathlands and old water meadow ditch systems on chalkstreams – both of which have undergone considerable fragmentation in the last century. Moore (1962) estimated that heathlands had declined in area by 67% in South West Britain between 1811 and 1960 due to factors such as afforestation, sand and gravel extraction and reclamation for agriculture. Webb (1993) estimates an 85% decline over the past 150 years. Chalkstreams have suffered a similar decline due to abstraction for irrigation, dredging and channelisation, domestic and industrial pollution and changes in grazing regimes (Ladle 1991; HMSO 1995). However, the decline of *C. mercuriale* is likely to be due to factors operating at the habitat rather than the biotope level. For example, in Dorset, *C. mercuriale* occupies a very small fraction of available heathland (Fig. 2.11) suggesting that this species is stenotopic i.e. has very specific habitat requirements within heathland and chalkstream waterbodies. It is these specific habitat preferences that are the subject of the next sections.

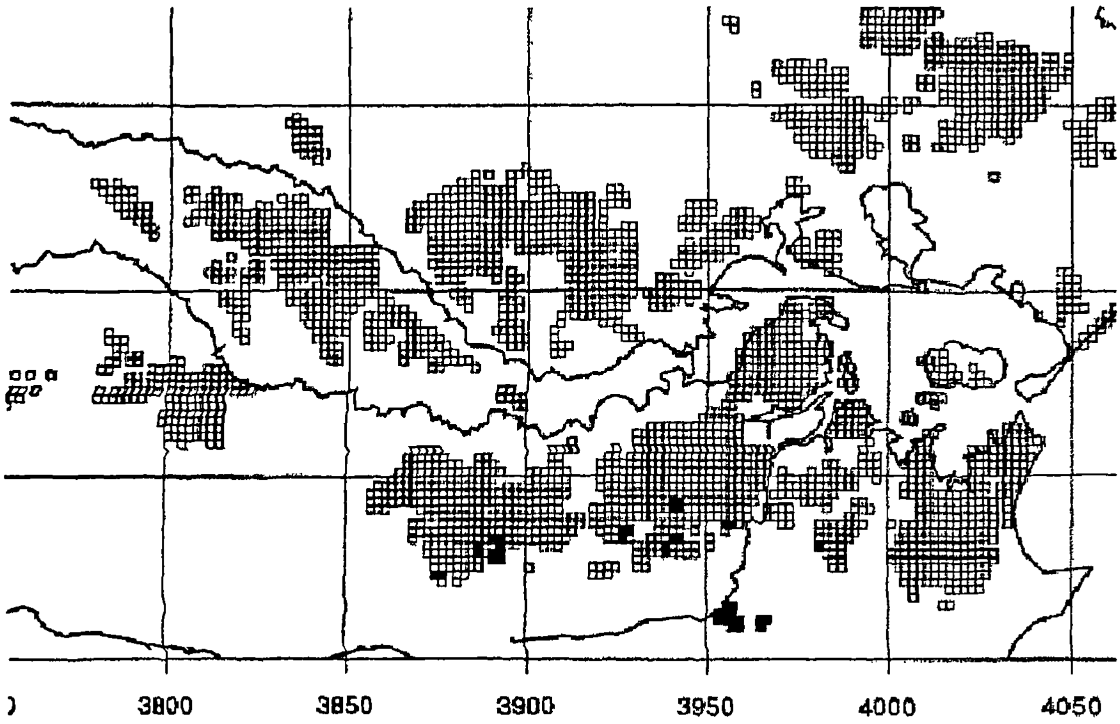


Fig. 2.11 The distribution of *C. mercuriale* (closed squares) in South – East Dorset in relation to the distribution of heathland (open squares). Large squares are 5km by 5km squares. This figure was produced by Rob Rose, using the Dorset Heathland Survey, at the Institute of Terrestrial Ecology, Wareham.

2.3.3. Topography and geology

Although *C. mercuriale* may be found at altitudes of up to 270m above sea level (a.s.l.) in Britain (Fig. 2.12), it is mainly found at low altitudes. 82% of sites occur at or below 90m a.s.l. and the majority of these are found between 16 and 45m a.s.l. In Central Europe, this species is found at moderate altitudes. In France, most sites occur below 400m (maximum 1058 – Deliry & Grand, 1998) In Germany, most sites on meadow brooks and ditches were found between 400 and 500m a.s.l. whilst those on alpine spring marshes were found between 500 and 920m a.s.l. (Kuhn 1998). Where the species is found at higher altitudes, it occupies runnels on slopes that receive a high degree of exposure to the sun (Kuhn 1998). The species can survive at high altitudes of up to 1500m in Spain (Ancelin *et al.* 1986, cited in Grand 1996), 1600m in Switzerland (Maibach & Meier 1987) and above 1900m in Morocco (Jacquemin 1994). The fact that this species is restricted to low altitudes on the northern edge of its range in Britain but is able to occupy higher altitudes further south in its distribution again suggests that this species has specific thermal requirements. In other edge-of-range populations, in the alpine range in Germany, the species can occupy higher altitudes since cooler temperatures at higher altitudes may be offset by thermal constancy of the springs feeding these marshes (section 2.3.4) or by selection of habitats exposed to the sun (section 2.3.6). Most sites are found on very gently sloping ground. 64% of sites have a slope of less than 5% (Fig. 2.13) and only 3% have a slope of greater than 10%. *Coenagrion mercuriale* may be restricted to shallow slopes due to requirements for slow flow (section.2.3.4). Unfortunately, data were not available on aspect of slopes occupied by *C. mercuriale* in Britain.

Rock types influence topography, chemical composition of substrate and water, the amount of sediment entering the stream and the physical composition of the substrate (Haslam 1978). Most heathland streams occupied by *C. mercuriale* are fed by calcareous recently formed, soft deposits (after Paleozoic and Pre-cambrian) of clay, limestone or sandstone overlaid with acidic peat or gravel deposits (Table 2.5). Water meadow ditch systems on chalk (soft limestone) streams are fed from chalk reserves. In Germany, limestone is found under those meadow streams and spring marshes occupied by *C. mercuriale* (Buchwald 1994; Sternberg *et al.* 1999). It is also found under many water bodies occupied in France (D' Aguilar *et al.* 1985; Grand 1996a). These soft rocks are particularly susceptible to weathering (Allan 1995) especially where most flow is sub-surface (i.e. near springs) and the effect of these processes on water chemistry is discussed in section 2.3.7. The effect of the porosity of chalk on flow regime is discussed in section 2.3.4.

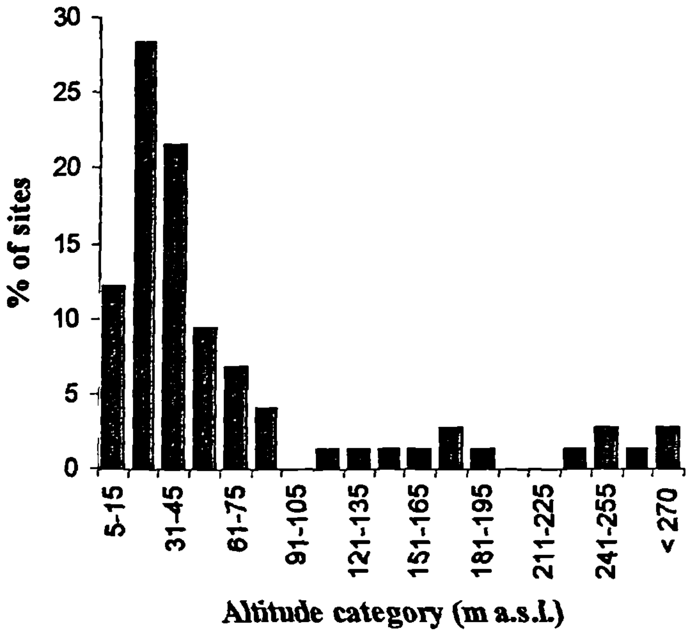


Fig. 2.12 Percentage frequency distribution of sites (*n*=74) across different altitude categories.

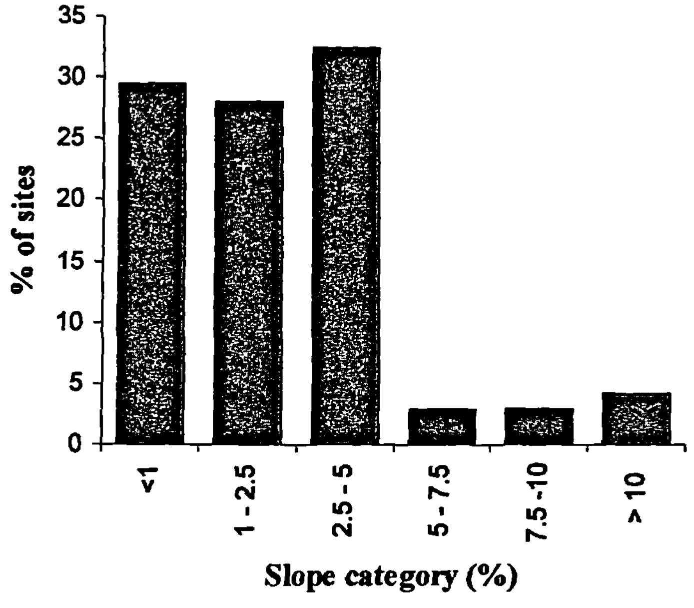


Fig. 2.13 Percentage frequency distribution of sites (*n*=71) across different slope categories (where – 2.5 means up to but not including 2.5).

Table 2.5 Range of altitude, slope and geology found in *C. mercuriale* sites in each region.

Region	Range of altitudes m a.s.l.	Range of slopes (%)	Geology
Oxfordshire	69-80	0-4%	Springs originate from Corallian limestone over laid with calcareous fen and peat formations (Paul 1998).
Dorset	25-55	0-4%	Sand over clay silt soils over acid peatland (Merritt 1983; James & Wiggers 2000).
Devon	85-115	0-13%	Springs originate from calcareous sandstone overlaid with acidic pebblebed (Knights 1983; Kerry 1994).
Dartmoor	245-285	3-5%	-
New Forest	10-70	0-10%	Springs originate from clay marls under acidic gravel deposits (Winsland 1985).
Anglesey	75-80	3%	Springs originate from carboniferous limestone (Colley 1983).
Pembrokeshire & St. Davids	35-270	0-16%	Clay deposits over laid with peat (Coker & Fox 1985; Evans 1989).
Gower	65-100	2-9%	Gravel deposits over laid with peat (Merritt 1983; Evans 1989).
Itchen & Test Valley	10-25	0-4%	Chalk reserves originating in gravel (Mayo & Welstead 1983).

2.3.4. Watercourse type and dimensions.

Watercourses across most heathland sites in Britain consist of very shallow (<40cm), narrow (usually < 5m wide), slow flowing flushes and runnels (Table 2.6) that are discontinuous in nature (except in some New Forest streams). Watercourses occupied on chalkstream water meadow ditch systems are larger and more discrete than the heathland streams (ranging from 0.75-10m in width – Table 2.6). In Germany there is similar variation between biotopes in the type of waterbodies occupied by *C. mercuriale* (Buchwald 1994). On pre-alpine spring marshes, shallow runnels occupied by *C. mercuriale* range from 2-20cm in width and flow very slowly over peat or limestone mud. Meadow brooks and ditches usually range from 0.2 to 1.6m in width (but up to 6m in small rivers) and from 1-40cm in depth (Sternberg *et al.* 1999) and have a gravel substrate (Kuhn 1998).

Table 2.6 Watercourse type and dimensions on C. *mercuriale* sites in each region.

Region	Watercourse type, water source, flow rate, and substrate	Range of water depth in region (m)	Range of peat/silt depth in region (m)	Range of stream width in region (m)	Range of approximate length of stream available
Oxfordshire	Both sites have shallow, spring-fed runnels with sluggish flow over peat. In addition, Dry Sandford Pit has open pools.	-	-	-	-
Dorset	Most sites have shallow, spring-fed runnels with slow (sluggish) flow over clay soil overlaid with silt. The Povingdon site also receives water from the outflow of a clay pit.	0-0.1	0.01-0.46	0 – 2 in 5 sites but up to 10m wide on Norden Heath	70 (Corfe Common West)- 660 (Povingdon)
Devon	Shallow, narrow, slow-flowing spring fed flushes and runnels over small pebbles overlaid with peat. Aylesbeare has man-made pools.	0.04-0.10	-	0.25-0.50	60 (Colaton Raleigh) – 100 (Aylesbeare Common)
Dartmoor	Shallow, narrow, slow flowing spring-fed flushes and runnels over peat (with pools on Tor View Moor).	0.01-0.03	0.06-0.16	0-1	225 (Tor View Moor)
New Forest	Shallow, narrow, medium to slow flowing spring-fed streams and runnels (a few receive groundwater) over gravel overlaid with peat. Some sites contain discontinuous areas of flushes or mire (13/36) but most watercourses are more discrete than those in other heathland sites.	0.02-0.43	0.02-0.30	0.2-20 (most 1m or less)	25 (Acres Down) – 700 (Roundhill)

Table 2.6 continued.

Region	Watercourse type, water source, flow rate, and substrate	Range of water depth in region (m)	Range of peat/silt depth in region (m)	Range of stream width in region (m)	Range of approximate length of stream available
Anglesey	Shallow, narrow, spring-fed, slow-flowing flushes, runnels and small pools over peat.	-	-	-	-
Pembrokeshire & St. Davids	Shallow, narrow, slow flowing, spring fed flushes and runnels over clay overlaid with peat.	0.10-0.37	0-0.78	0.5-2	-
Gower	Both sites have shallow, slow flowing, narrow, spring-fed runnels over gravel over laid with shallow peat	0.15-0.40	-	0.2-1	-
Itchen & Test Valley	Water meadow ditches, medium flowing fed by chalkstream carriers (some by springs) over gravel overlaid by silt. These watercourses are generally wider and more discrete than heathland watercourses occupied by *C. mercuriale*.	max.1.5	-	0.75-10	-

Although *C. mercuriale* occupies small water bodies across Europe, waterbodies that occur on meadows are often larger than those found on heathlands or calcareous mires and may offer larger areas of habitat, supporting larger populations of this species. For example, in Bavaria, populations on spring mires tend to consist of less than 100 adults whilst those on meadow brooks and canals can number several hundred (Kuhn 1998). Similarly, although chalkstream populations have not been studied as extensively in Britain, it is possible these meadow waterbodies provide larger areas of habitat and support larger populatuions for *C. mercuriale* than heathland waterbodies.

C. mercuriale appears to have a requirement for slow to moderate flow. In Britain, larval populations are associated with areas of slow shallow flow (Waun Fawr - Evans 1989; Povingdon Heath - James & Wiggers 2000), further indicating that small, slow flowing waterbodies are required by *C. mercuriale*. Adult populations have been noted to avoid narrow boggy runnels with no depth at Millersford Bottom West and at Highbridge, Russell's Meadow avoid areas with zero flow (Stevens & Thurner 1999). On chalkstreams, adult populations were concentrated on channels where water velocities ranged between 7.5 and 20 cm/s (Strange 1999) whilst at Glan-yr-afon Uchaf, a heathland site, flow ranged from 2 to 15 cm/s in areas of larval population (Chapter 4). Even if flow in the main channel is moderate, flow may be slower in shallow stream margins or where vegetation is dense (Strange 1999). Currents of around 10cm/s (maximum of 35 m/s), allowing for minimum concentration of between 2.5-3.0 mg/litre of oxygen (section 2.3.7), were cited as one of four important factors determining *C. mercuriale* distribution in Baden Württemburg, Germany (Buchwald 1994). Currents of 0-15 cm/s were found on the edges of meadow brooks occupied by *C. mercuriale* in the Upper Rhine (Sternberg *et al.* 1999).

Small, exposed streams have large diel temperature regimes with a rate of temperature increase of up to 3.3 °C per hour. In contrast, the maximum rate of temperature increase in rivers is around 1.17°C per hour (Ward 1982). The fact that shallow water habitats will heat up quickly in summer has been postulated as a reason for this species' restriction to shallow water bodies (Buchwald 1994; Sternberg *et al.* 1999). Such high temperatures may allow larval development, emergence and oviposition to proceed more rapidly (Chapters 3, 4 and 5).

A consequence of this species' restriction to small, slow flowing water bodies is that its populations are subject to a relatively high degree of fluctuation in water level (Chapter 4) and chemical composition. (Section 2.3.7). Watercourses are spring-fed on heathland sites (augmented by groundwater or clay pit outflows – Table 2.6) and are fed by chalkstream carriers (sometimes augmented by springs) on watermeadow ditch systems (Table 2.6). This has lead to the suggestion that *C. mercuriale* requires a permanent water supply on all its British sites (Mayo & Welstead 1983; Jenkins 1997). Permanent conduction of water and proximity to springs or groundwater are cited as two important factors in determining habitat suitability for *C. mercuriale* on meadow brooks and ditches in Germany (Baden Württemburg Buchwald 1994) and France (Deliry & Grand, 1998) and on calcareous spring mires in Germany (Buchwald 1994). As well as assuring the permanence of water flow in shallow waterbodies, springs maintain a higher than average temperature in winter (4-10 °C in watercourses in Baden Württemburg, Buchwald 1989), and are more constant in temperature throughout the year, preventing freezing over or drying up of watercourses. Similarly chalkstreams fed by groundwater or springs have a regular annual hydrograph (Berrie 1992). Since chalk is highly porous, the passage of water through rock is slow (compared to limestone that contains large fissures) such that irregularities in rainfall are smoothed out and the water temperature is stabilised at around 11°C all year (Crisp *et al.* 1982, cited in Berrie 1992). It is significant that *Ischnura pumilio,* another species that is on the northern edge of its range in Britain and has a southern distribution here (Corbet *et al.* 1960), is also restricted to spring fed watercourses or those near outflows from mineral extraction works (Fox 1994).

Consistent with this, in Britain larval populations are found within sites in those portions of waterbodies that receive permanent flow (Evans 1989; Skidmore 1996; Hold 1997). In Itchen Valley Country Park for example, *C. mercuriale* populations are found near weirs (that regulate flow from carriers) or springs. On chalkstream sites, the occurrence of *Rorippa nasturtium aquaticum* and *Ranunculus* sp (Tables 2.12-2.13) were indicative of relatively high winter and spring water temperatures respectively. Many of the NVC communities associated with *C. mercuriale* are found in permanently wet conditions e.g. M14, M16c, M21a, M13b, M10c, M9 and M29 (Rodwell 1991 Table 2.8) and some are associated with a February temperature minima of at least a degree above freezing (e.g. M29, M13b, M25a). The use, by *C. mercuriale,* of the presence of particular plant species as cues to indicate the permanence of the water supply is discussed in section 2.3.6.

Table 2.7 Number of extant British *C. mercuriale* sites threatened by different factors.

Threat	Due to -	
Reduced water availability		22
	Canalisation or artificial drainage	6
	Siltation or headward erosion	5
	Excessive scrub and tree growth	3
	Poaching of shallow runnels	1
	Peat cutting	1
Reduced water quality		4
	Nutrient run-off	4
Overgrowth of streams		34
	Channel vegetation	7
	Bankside vegetation	27

Threats to *C. mercuriale* habitat due to reduction in temporal or spatial availability of water were noted on a substantial proportion of extant British sites (Table 2.7). The main causes of reductions in water availability were canalisation or artificial drainage and siltation or headward erosion.

Where populations have been monitored, there is anecdotal evidence that reductions in water availability have had negative impacts on the population range and adundance of *C. mercuriale* within a site. Extinction of populations recorded at Cosmore Common, Dorset in 1837 has been attributed to drainage (Prendergast 1996) as has the decline at Afon Brynberian (due to the creation of an artifical watercourse in 1983 (Skidmore 1996)). The overall decline of European populations of *C. mercuriale* since the 1950's (Grand 1996b) has also been attributed to drainage. There has been a substantial reduction in population size (a maximum count of one individual was recorded in 1990 –Stevens & Thurner 1999) on Blackwell Common, New Forest, due to a drought in the late 1980's (Jenkins *et al.* 1996). At Horsebush Bottom, although adult populations have been found using the stream for breeding in late summer (Jenkins 2001) the lack of a permanent water supply (and annual frequency of drying up) prevents local recruitment to the population. In Outflow mire, part of Povingdon Heath, in Dorset, a reduction in population size since 1995 can be attributed to the gradual accumulation of silt from the clay pit outflow such that smaller streams were cut off from flow and have dried out (Winsland 1994b; James & Wiggers 2000). In Millersford Bottom East, the population has decreased on a previously well populated area of mire across which a drainage channel has been cut such that water no longer flowed through the whole mire system (Stevens & Thurner 1999). Ditches occupied by *C. mercuriale* in Baden Württemburg (Buchwald 1989) and in calcareous spring marshes (Buchwald 1994), the watercourses never (or only partially) dried out or froze up and drying out resulted in the loss of adult populations.

In addition, there is anecdotal evidence that *C. mercuriale* will expand its range and population size on British sites in response to an increase in water availability. As described above (Table 2.6) the flooding of an area of acid peatland by a clay pit outflow on Povingdon created an area of mire next to an existing colony which was then colonised by *C. mercuriale* (Prendergast 1996). On Aylesbeare Common, Devon, shallow pools, dug at intervals along the runnels in 1993 and 1994 (Kerry 1994), were rapidly colonised by *C. mercuriale* (by 1998 – pers obs., Kerry, 2000). These examples suggest that *C. mercuriale* would respond positively to the creation of new areas of suitable watercourse adjacent to existing colonies. For example, in two sites where streams are too deep and wide, Creech Heath (Sutcliffe 1998) and Afon Brynberian (Skidmore 1996), the use of weirs to (re)create shallower flush systems have been recommended and on the former site, removal of alder stumps to create small pools.

Historically, changes in the management of water meadow ditch systems have threatened the existence of the ditches themselves (Sheail 1971) probably limiting the current distribution and continuity of *C. mercuriale* in its chalkstream biotope. Water meadows are distinct from flood meadows because they can be flooded by farmers (using weirs and hatches) to ensure a continual water supply. This irrigation system, used in the mid 16th to the 19th century, increased hay production and the number of stock that could be maintained on meadows (Sheail 1971). This system declined after the mid 19th century due to a lack of labour and low demand for hay such that ditches are no longer irrigated or grazed intensively.

In addition to specific requirements for watercourse depth and width, *C. mercuriale* populations appear to be associated with watercourses with shallow bank profiles in Britain. Most heathland sites consist of mires or runnels near spring sources (i.e. first order) and the bank rises only a few centimetres above the water level. On those heathland sites where the stream occurs in deeper gulleys (e.g. Lower Peaked Hill, Cefn Bryn (gulleys 0.5-1.5m deep and 2-4m wide, Rock Hills, Millersford Bottom West) adults tend to be concentrated in areas where the banks are lowest (Stevens & Thurner 1999 pers. obs.). Although the water meadow ditch systems have higher banks than those found in heathland sites, adults still appear to favour ditches with shallower banks (Strange 1999). This preference for shallow banks probably arises since they cast less shade on the water surface, and allow grazing animals to have access to marginal aquatic vegetation (section 2.3.6). In addition, when banks are elevated due to the creation of bank spoil (from hand drainage/dredging operations) encroachment of bog myrtle *(Myrica gale)* can occur as seen in Upper Crockford (D.Winsland pers.comm. 1997).

The watercourses in British sites occupied by *C. mercuriale* usually have an inorganic substrate such as clay or gravel (Table 2.6) overlaid with an organic peat or silt that ranges from 0-78cm in depth. On heathland sites larval populations are densest in areas of stream with shallow peat (not exceeding 30cm in depth (Knights 1983; Evans 1989)), whilst, at Itchen Valley Country Park, they were associated with the silt deposits at the edge of ditches (Hold 1997). Adult populations are also not associated with stream sections that have a gravel substrate (Rock Hills –Stevens & Thurner 1999). Although meadow brooks and ditches in Germany have gravel substrates, all have a 10-30cm layer of mud at their edges (Sternberg *et al.* 1999). On calcareous spring marshes, a substrate of peat or limestone mud is found (Kuhn 1998). Whilst there has been some suggestion that early instar larvae live in these shallow organic deposits (Corbet 1957) these are not supported by findings in Chapter 4. Such organic deposits are likely to be correlated with vegetation structure and flow regime required by this species or may heat up quickly in summer due to their dark colouration.

2.3.5. Habitat types found on and around streams.

Whilst sites containing *C. mercuriale* in Britain can be broadly divided into those occurring on heathland or on chalkstream water meadow ditch systems, it is neccesary to consider which habitat types the species is associated with, within these broad biotope definitions. For example, the term 'heathland' refers to the whole habitat complex found in heath dominated rough grazings and can include grassland and mire (Sanderson 1998). From documents, 113 records of habitat type through which the breeding stream flowed (broadly based on phase I habitat survey divisions) and in the area surrounding the stream were reviewed for 50 sites. National vegetation classifications (NVC's) were also scored where available.

The prevalence of different types of habitat in the immediate area of the watercourse and in its surrounding across all sites is shown in Fig. 2.14. The most common habitat type in the immediate vicinity of watercourses was valley mire (burned in a few sites) with many streams flowing through wet heath and carr/scrub. Acid and other types of grassland were found on some streams, particularly those on water meadow ditch systems. Acidic grassland and carr/scrub were the most prevalent habitat types surrounding watercourses but different types of heath, in the transition from acid dry heath to wet heath were also found.

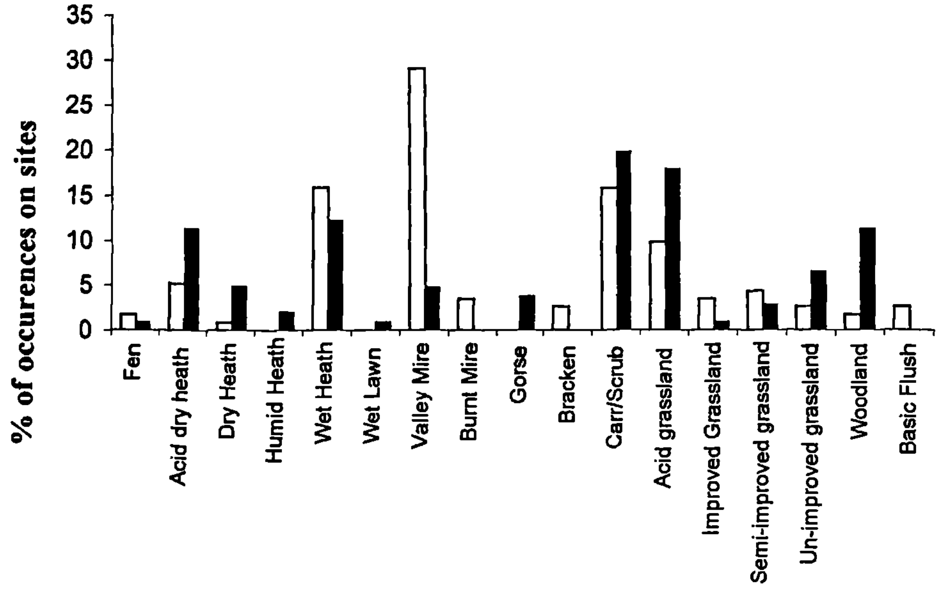


Fig. 2.14. Percentage occurrence of different types of habitat in the immediate vicinity of (open bars) and surrounding watercourses (closed bars) on British *C. mercuriale* sites (n=113).

Table 2.8 describes the habitat and community types found in each region. Relatively few watercourses run through or are surrounded by improved or semi-improved grassland. This accounts for the fact that only four sites were perceived to be threatened by nutrient run-off from agricultural land (Dartmoor sites, Hartland Moor, and Rhossili Down – Table 2.7). Streams next to improved grassland may not be favoured by *C. mercuriale* since grazing stock will prefer this nutrient improved food supply rather than grazing stream vegetation (Evans 1989).

In contrast, in meadow brooks and ditches in Baden Württemburg, Germany, most sites are near intensively used agricultural areas (Roske 1995). Here, the type and condition of adjacent agricultural land determines the suitability of the area for *C. mercuriale* (Buchwald et al. 1989), with uncut wet meadow (with *Juncus acutiflorus*) used most often followed by uncut *improved meadow, fresh cut improved meadow* and fallow field in order of decreasing suitability. While the degree of improvement influences the nutrient richness of the water (section 2.3.7), the extent of cutting influences the habitat structure and in turn the microclimate and prey availability (section 2.3.6). Similarly, *Orthetrum coerulescens*, a lotic species that often co-occurs with *C. mercuriale*, prefers extensive wet meadow but will colonise farming land (Buchwald 1994).

Table 2.8 Habitat types and NVC communities found on British C. *mercuriale* sites.

Region	Habitat type	NVC Communities
Oxford	Calcareous/ poor fenland in both sites, one of which is a flooded sandpit.	-
Dorset	Wet heathland/valley mire in most sites but one contains areas of poor fen. These sites are surrounded by dry heath, carr/scrub and unimproved grassland.	-
Devon	Wet heathland/valley mire in both sites, atleast one of has areas of basic flush. They are surrounded by acid dry heath.	M14 found both on and around streams
Dartmoor	Wet heathland in both sites surrounded by carr/scrub and a mixture of acidic, improved and unimproved grassland. The habitat is sometimes described as Rhos pasture.	M16c and M25a were prevalent on streams with some M29 and M21a. M25a was again prevalent around streams.
New Forest	Most streams flow through valley mire (21/29) and some through wet heathland (6/29) On four sites, streams flowed through burned mire. 25 sites were surrounded by a type of heath from the transition between wet heath and acid dry heath but carr (13/29) and acidic grassland (16/29) were also prevalent.	M21a and M29 were the most prevalent communities on streams with some M14. A variety of communities were found around streams including S23, M9, S5, S4, S7, S14, MG8, MG9.
Anglesey	Calcareous fenland with valley mire surrounded by moderately acidic grassland.	M13b and MG8 were found on the stream surrounded by M24b.
Pembrokeshire	Wet heathland/soligenous valley mire with carr/scrub, acid, improved, semi-improved and unimproved grassland noted surrounding streams	M6c and M10 were found on streams surrounded by M23.
Gower	Wet heathland/valley mire or boggy pasture surrounded by acid dry heath or unimproved grassland.	M15, M16c, M25a and H4 were found on streams.
Itchen & Test Valley	Water meadow ditch systems on chalkstreams where ditches flow through and are surrounded by improved, semi- improved and umimproved grassland. Carr/scrub also surrounded half these sites.	M9, MG11, and S23 were most prevalent on streams with some OV8, OV26, M22, S5 and S7. S23, S5, M9 were again prevalent around streams with some S4, MG8, MG9, S7 and S14.

2.3.6. Plant species, plant communities and vegetation structure on stream and banksides

The most prevalent plant species found near streams and surrounding streams are shown in Tables 2.9-2.10 together with the number of times they were present and formed a main component of the vegetation. Table 2.11 summarises the plant species composition by region. *Coenagrion mercuriale* is not associated with a particular plant species or set of plant species across its range although *Hypericum elodes* and *Potamogeton polygonifolius* were found in the majority of heathland sites and *Glyceria maxima* was frequent in chalkstream sites. In addition, *C. mercuriale* has been directly associated with plant species on different sites at different stages of its life cycle. The larval stage has been associated with *Potamogeton polygonifolius, Equisetum fluviatale, Callitriche* sp. *Glyceria fluitans, Juncus* sp. (James & Wiggers 2000). Breeding adults have been associated with *Rorripa nasturtium-aquaticum* agg., *Glyceria maxima* and *Apium nodiflorum* (Stevens & Thurner 1999; Strange 1999) and with *Equisetum fluviatale, Juncus* sp. and *Potamogeton polygonifolius* (Woodman 1999). However, none of these associations is consistent across sites and it appears that particular plant species are not required for particular life stages. In light of this, information on the prevalence of particular plant species is only useful when considering what particular plant species indicate about chemical and structural features of the habitat. Similarly, *C. mercuriale* is associated with a range of NVC community types (Table 2.8) with a range of habitat preferences (Rodwell 1991). Thus structural and chemical features of the habitat will be discussed in the next two sections drawing on information about plant species and communities as appropriate.

In Britain, *C. mercuriale* requires open watercourses with sparse marginal or bankside vegetation. Of 11 sites where openness was discussed specifically in documents, 8 were described as open (Kerry 1994; Hold 1997; Smallshire 1998 Evans 1989; Stevens & Thurner 1999; Strange 1999). Bankside vegetation heights were less than 75 cm in 5 out of 6 sites. Breeding adults are found in open areas (Stevens & Thurner 1999; Strange 1999; Woodman 1999 – 10 sites; James & Wiggers 2000), with short to medium edge vegetation (3-10cm Evans 1989) or where *Juncus* and *Molinia* tussocks are low (Stevens & Thurner 1999; James & Wiggers 2000). In 1992, as the central ditch on Nant Isaf, Cors Erddreiniog increased in rankness (mainly due to *Juncus subnodulosus* and *Schoenus nigricans)* the adult population moved to the tufaceous seepages that fed the ditch (Colley 1993). On heathlands, larvae were associated with open, clear runnels with abundant aquatic vegetation (Evans 1989; Skidmore 1996; James & Wiggers 2000) and, on a chalkstream site, with light shading (Hold 1997). Several of the plant species found to be prevalent on sites are usually associated with open or unshaded conditions including *Potamogeton polygonifolius, Drosera rotundifolia, Anagallis tenellum* (Kerry 1999) on heathlands and *Ranunculus* sp., *Rorripa nasturtium-aquaticum agg. Veronica* sp. and *Glyceria maxima* (Haslam 1978) on chalkstreams. On chalkstreams, the preferred community type, S23, is only found on unshaded watermargins (Strange 1999).

Table 2.9 Number of times the most prevalent plant species were present on streams on heathland and chalkstream sites (number of times they formed a main component of the vegetation in brackets).

Heathland sites n=53 Plant species	No. of presences	Chalkstream sites n=13 Plant species	No. of presences
Hypericum elodes	33 (27)	*Glyceria maxima*	12 (7)
Potamogeton polygonifolius	33 (26)	*Phalaris arundinacea*	10 (2)
Carex sp.	26 (4)	*Mentha aquatica*	7 (3)
Ranunculus flammula	16 (6)	*Rorripa nasturtium-aquaticum agg.*	7 (5)
Juncus sp.	15 (13)	*Iris pseudocarus*	6 (0)
Myrica gale	14 (9)	*Veronica beccabunga*	6 (3)
Apium nodiflorum	12 (6)	*Apium nodiflorum*	5 (5)
Juncus acutiflorus	10 (5)	*Veronica anagallis aquaticum*	5 (3)
Narthecium ossifragum	9 (4)	*Carex acutiformis*	4 (2)
Sphagnum sp.	9 (5)	*Juncus articulatus*	3 (0)
Drosera rotundifolia	8 (5)	*Ranunculus pencillatus sp.*	3 (0)
Menyanthes trifoliata	8 (6)	*Ranunculus flammula*	2 (2)
Molinia caerulea	8 (5)	*Sparganium erecta*	2 (0)
Anagallis tenellim	7 (1)	*Glyceria fluitans*	2 (1)
Equisetum fluviatale	7 (2)	*Agrostis stolonifera*	2 (0)
Mentha aquatica	7 (2)	*Epilobium hirsutum*	2 (0)
Eriophorum angustifolium	6 (1)	*Lythrum salicaria*	2 (0)
Juncus effusus	6 (4)	*Alopercurus praetensis*	2 (0)
Carex echinata	5 (1)	*Rumex hydrolapathum*	2 (0)
Sparganium erecta	5 (0)		

Table 2.10 Number of times the most prevalent plant species were present surrounding streams on heathland and chalkstream sites (number of times they formed a main component of the vegetation in parentheses).

Heathland sites n=53 Plant species	No. of presences	Chalkstream sites n=13 Plant species	No. of presences
Molinia caerulea	*17 (12)*	*Iris pseudocarus*	*4*
Sphagnum sp.	16 (7)	*Phalaris communis*	3
Myrica gale	11 (10)	*Carex acutiformis*	2
Erica tetralix	7 (3)	*Phalaris arundinacea*	2
Juncus acutiflorus	7 (3)	*Carex panicea*	1
Equisetum fluviatale	6 (3)	*Cirsium dissectum*	1
Juncus effusus	6 (6)	*Callitriche* sp.	1
Ulex galli	6 (0)	*Filipendia ulmaria*	1
Calluna vulgaris	5 (2)	*Typha latifolia*	1
Carex sp.	5 (2)	*Cirsium arvense*	1
Narthecium ossifragum	5 (1)	*Deschampsia cespitosis*	1
Agrostis stolonifera	4 (1)	*Rorripa nasturtium-aquaticum agg.*	1
Drosera rotundifolia	4 (1)	*Sparganium erecta*	1
Mentha aquatica	4 (2)	*Urtica dioica*	1
Potentilla erecta	4 (0)		
Rubus sp.	4 (0)		

Table 2.11 Commonest plant species in watercourses and on banksides in each region (frequency of occurrence on sites given in parentheses for regions with large numbers of sites).

Region	Plant species which form main or frequent components of the vegetation in the watercourse	Plant species which form main or frequent components of the vegetation in the on the bankside
Oxford	*Apium nodiflorum, Drosera rotundifolia, Narthecium ossifragum* with *Carex* sp. present.	
Dorset	*Potamogeton polygonifolius (6), Juncus* sp. (*J. inflexus (2), J. acutiflorus (1)*) *Sphagnum* sp. *(4). Mentha aquatica (4), Carex* sp. *Hypericum elodes (3), Equisetum fluviatale* (3) and *Hydrocotyle vulgaris (3). Apium nodiflorum* present.	*Myrica gale (2), Molinia caerulea (4), Sphagnum* sp. *Juncus* sp. (*J. acutiflorus (1), J. effusus (1)), Menyanthes trifoliata(1), Equisetum fluviatale (2). Carex* sp. (3).
Devon	*J. acutiflorus, J. effusus, Potamogeton polygonifolius, Schoenus nigricans, Sphagnum* sp. *Eriophorum angustifolium, Pinguicula lusitanica, Anagallis tenella, Rhynchospora alba, Scirpus cespitosus. Narthecium ossifragum* present.	*Schoenus nigricans, Molinia caerulea, J. acutiflorus, J. conglomeratus, Drosera rotundifolia, Sphagnum* sp.. (*S. papillosum, S. subnitens, S. tenellum, S. auriculatum*) tussocks of *Calluna vulgaris, Erica tetralix* and *Ulex gallii.*
Dartmoor	*Potamogeton polygonifolius, Eleocharis multicaulis with Hypericum elodes, J. bulbosus, J.acutiflorus, Apium nodiflorum, Carex flacca, Drosera rotundifolia, Narthecium ossifragum, Sphagnum* sp., *Pinguicula lusitanica* present.	*Molinia caerulea, Myrica gale. J. acutiflorus, Sphagnum* sp.. with *Pinguicula lusitanica, Succinsa praetensis and Ulex gallii* present.
New Forest	*Hypericum elodes* (25), *Potamogeton polygonifolius* (24), *Myrica gale* (12), *Juncus* sp. (7), *Ranunculus flammula* (12), *Carex* sp. (*C. rostrata, C. panicea, C.echinata*), *Narthecium ossifragum* (5), *Sphagnum* sp. (5), *Anagallis tenella* (6), *Menyanthes trifoliata* (5) *Drosera* sp. (5).	*Erica tetralix* (6), *Myrica gale* (6), *Molinia caerulea* (4), *hagnum* sp. (6) (*S. papillosum, S. palustre*), *Juncus* sp. (*J. acutiflorus* (3), *J. bufonius* (3), *J. effusus* (3), *Carex* sp. (including *C. echinata* (2), *C. panicea* (2) *C. flacca* (1), *C. nigra* (1)), *Drosera rotundifolia* (4), *Ulex gallii* (4),
Anglesey	*Anagallis tenella, Briza media, Schoenus nigricans, Triglochin palustris, Juncus subnodulosus, Chara* sp.	-
Pembrokeshire	*Potamogeton polygonifolius* (6), *Juncus* sp. (7) (*J.acutiflorus* (4), *J. effusus* (3)), *Hypericum elodes* (3), with *Eriophorum angustifolium, Eleocharis palustris, Carex* sp. (*C. demissa, C.nigra,* and *C. panicea*), *Lotus pediculatus* present.	*Juncus* sp.(7) (*J. effusus* (3), *J. acutiflorus* (2), *J. articulatus* (1), *J. bufonius* (1)), *Sphagnum* sp.(3) (*S. recurvum, S. palustre*), *Myrica gale* (2), *Molinia caerulea* (2), *Agrostis* (2).
Gower	*Potamogeton polygonifolius, Juncus* sp. (*J. bulbosus, J. acutiflorus, J. inflexus*), *Apium nodiflorum, Berula erecta, Drosera rotundifolia, Equisetum fluviatale, Eleocharis multicaulis, Hypericum elodes, Narthecium ossifragum* and *Sphagnum* sp.	*Molinia caerulea, Myrica gale, Erica ciliaris, E. cinerea, calluna vulgaris,* with *Juncus* sp., *Carex* sp. present.
Itchen & Test Valley	*Glyceria maxima* (12), *Mentha aquatica* (7), *Apium nodiflorum* (5), *Rorippa nasturtium aquaticum* (7), *Phalaris arundinacea* (10) *Veronica* sp. (6) (*V. beccabunga* (6), *V. anagallis aq.*(5)), *Carex acutiformis* (4), *Iris pseudacorus* (6) with *Glyceria fluitans, Juncus* sp. (*J. articulatus, J. inflexus, J. subnodulosus*), *Ranunculus pencillatus* present..	*Iris pseudacorus* (6), *Phragmites communis* (3) *Carex* sp. (*C. acutiformis* (2), *C. panicea* (2)), *Phalaris arundinacea* (2), C *sium* sp.. (*C. dissectum* (1), C. *arvense* (1))

Overgrowth of streams was recorded as a significant threat to habitat for *C. mercuriale* in 34 sites – further indicating the importance of open stream areas. In 7 of these sites it was the runnel itself that was choked with vegetation whilst in the remainder the overhanging/bankside vegetation was too dense. In 14 cases the source of dense growth was merely referred to as 'scrub', 6 sites were shaded by *Myrica gale,* 7 by *Juncus* species (including *J.acutiflorus*, *J. subnodulosus* and *J. effusus*), 7 by *Molinia caerulea* (when it formed tall tussocks), 2 by *Schoenus nigricans,* 1 by *Sparganium erectum* and 4 by trees (including Birch and Sallow). On 23 sites some removal of scrub or trees has taken place (sometimes on an annual basis) recently to open up watercourses and on 22 sites further such removal has been suggested. In a few sites, some clearance of watercourse vegetation has been carried out, particularly in chalkstream ditches such as those at Itchen Valley Country Park (Strange 1999). In several sites, scrub removal has resulted in an increase in population size or an expansion in range of *C. mercuriale.* Following removal of willow, birch and pine scrub on Creech Heath, the population moved from above the waterfall to below - to an area which previously contained *no C. mercuriale* (population count below the waterfall increased from 0 to 164 in consecutive years Sutcliffe 1998).

However, the most detailed record of such a change is found on Aylesbeare Common (Kerry 1994; Kerry 1999) where initially channels were overgown with dense tussocks of *Molinia* and *Schoenus nigricans.* A heavy season of winter grazing in 1990 was followed by annual light summer grazing between May and October (with intensity varying from 24 Lu/ha/yr (1999) to 32 Lu/ha/yr (1997). This produced shorter, less tussocky vegetation with less overgrowth of *Molinia caerulea.* There was a more open structure and an increase in *Cirsium dissectum* (Kerry 1999) and aquatic vegetation such as *Anagallis tenellum, Drosera rotundifolia, Pinguicula lusitanica, Potamogeton polygonifolius.* The population on this site has increased from 12 in 1986 (with maximum counts numbering less than 4 for years between 4 1977-1990) to a maximum daily count of 120 (1999). The species expanded still further into the south of the site following clearance of woodland in 1997 (Kerry 1999).

Table 2.12 shows the range of grazing regimes employed on British sites occupied by *C. mercuriale.* All but a few of these sites are grazed to some extent and sites in strongholds such as the New Forest and Mynydd Preseli have moderate to heavy grazing regimes (though the exact intensities of grazing on these unenclosed commons are difficult to ascertain). Population extinctions have been attributed to reductions in grazing regime. At St. David's Head, Pembrokeshire, grazing ceased in the 1950's and although regular burns continued, plants indicating an open pond habitat with short poached vegetation were lost (Lloyd-Evans, 1956 cited in Evans 1989) and the population of *C. mercuriale* disappeared. *C. mercuriale* also disappeared from the lower sector of Waun Isaf where, when grazing ceased, vegetation became rank and species poor, dominated by *Molinia* and rough herbage (Evans 1989). Cessation of any grazing regime also produced the population extinction at Venn Ottery Common in Devon (Kerry 1994). In 6 of 24 sites for which information was available, it was perceived that an increase in grazing intensity was required (Table 2.11). Grazing not only produces open stream areas favoured by *C. mercuriale* but also influences the structure and composition of bankside and edge vegetation as described later.

Table 2.12 Grazing regimes found in British *C. mercuriale* sites

Region	Site name	Intensity	No. of animals /area or no. of livestock units (LU)	Type of Stock	Time of year
Oxford	-Cothill Fen -Dry Sandford Pit	ungrazed ungrazed		-	-
Dorset	-Norden Heath -Creech Heath* -Povingdon* -Hartland Moor -Corfe Common East -Corfe Common West	ungrazed ungrazed very light light lightly lightly	- - - - -3H, 6C / 3 Ha -25 H, 50C on 50 Ha	- - -C, D - -C, H -C, H	- - - - -H all year, C Apr-Oct -H all year, C Jun-Oct
Devon	-Aylesbeare Common -Colaton Raleigh	both light (after heavy winter grazing in 1990)	- -	-C (Devon) -C (Devon)	-May-Oct -May-Oct
Dartmoor	-Tor View Moor* -Moortown Bottom*	light light	1-0 C / 3.5 Ha	-C (Fresian)	-Jul
New Forest (Unenclosed crownland)	-29 sites	range from light to well grazed but most are well grazed (S.Cooch. pers. comm)	-	-New Forest Stock – mainly P with C, D	-All year
Anglesey	-Cors Errdreiniog	lightly grazed	-	-C, P, S	-C Jul-Aug, P Nov-May, S Sep-Nov
Pembroke-shire (Unenclosed commonland)	-Whole area of Mynydd Preseli e.g. Waun Fawr Rhos Fach† Glan-yr-afon Uchaf Brynberian	heavy heavy heavy heavy heavy	- - - - -	-Intense S, few C, P -S, P -S -S -C, S, H	- - -S summer, P all year - all year - all year
St David's	-Ffynnon Clegyr Boia* -Pont Clegyr*	light moderate	- -	-C -C	-intermittent -
Gower	-Rhossili Down -Cefn Bryn	moderate moderate-heavy	-0.5 Lu -	-Mainly S, few C, P -C (some S, H?)	-May-Jul -
Itchen & Test Valley	-South of Clarendon Way -Itchen Valley Country Park -West of Willow Farm	light light moderate-heavy	- -1Glu/Ha -	-C, H -C (less than 1 year) -C	- -Apr-Oct -

Key to stock types. H=horses, C=cattle, P=pony, D=Deer, S=sheep. Months abbreviated to first three letters. * = current grazing regime is insufficient, † = current grazinf regime excessive.

Exposure to the sun was found in every site occupied by *C. mercuriale* on meadow brooks and ditches in Germany (Buchwald 1994) with 70% being unshaded and 20% only partially shaded. In calcareous spring marshes, sections with concentrations of *C. mercuriale* were unshaded or only partly shaded (Kuhn 1998). The average vegetation height was less than 1m, with a height of 20-40cm being optimal for *C. mercuriale* in calcareous spring marshes (Sternberg *et al.* 1999). Vegetation height in meadow brooks and ditches was always less than 60cm. Exposure is partly required because shallow larval habitat will warm up quickly and to provide radiated areas (and access to them) for adult breeding behaviour (see above). Also light is required for the growth of an adequate cover of submerged and emergent vegetation as indicated by the light-requiring species listed above for British *C. mercuriale* sites.

In Britain, *C. mercuriale* also seems to prefer streams that are generally well vegetated in the larval (Evans 1989; Skidmore 1996; James & Wiggers 2000) and adult stages (Stevens & Thurner 1999, pers obs). Indeed, breeding adults avoid sparsely vegetated watercourses such as those with gravel substrates (e.g. Hatchet Moor -Stevens & Thurner 1999 pers obs) or with burnt gorse overhanging runnels (3 sites-Stevens & Thurner 1999, pers obs). From questionnaire data, the mean percentage cover of submergent vegetation in areas where adult *C. mercuriale* were found in Britain was 29.3 ± 7.0 (n=14 questionnaires, range 0-75%) and that of emergent vegetation was 42.0 ± 5.4 (n=14 questionnaires range 8-75%). On chalkstream sites, ditches with concentrations of *C. mercuriale* had a wide shallow berm with a broad fringe of emergent vegetation (Strange 1999). Buchwald (1994) divides vegetation of running waters into two portions – hydrophyte referring to submerged or floating vegetation and helophyte referring to emergent vegetation that grows in shallow water on stream edges. Thelen (1992) found larvae predominantly using submerged vegetation all year round in meadow brooks and ditches, indicating the neccessity of some degree of cover of hydophyte vegetation for larval development. This author also found larvae were concentrated where there was emergent as well as submerged vegetation (including *Nasturtium officionalis* and *Phalaris arundinacea).* In Germany, there appears to be regional variation in preference for vegetation cover. In meadow brooks and ditches, 1-20% cover is preferred in the Upper Rhine Valley, 10-40% in the lower Alpine regions (Sternberg *et al.* 1999) and 20-60% in Bavaria (Kuhn 1998) while 50-90% is found in calcareous spring mires with *C. mercuriale* (Buchwald 1989). Buchwald (1994) found no direct correlation between the cover of submerged or aquatic vegetaion and abundance of adult *C. mercuriale* in meadow ditches in Germany. However, most *C. mercuriale* were found in areas of 40% cover, with none found in areas of less than 10% cover. The fact that, in narrow streams and ditches, overgrowth of the helophyte portion may only allow development of small fragments of hydrophyte vegetation (Buchwald 1994) may account for so many British populations being threatened by overgrowth of vegetation.

Thus some extent of submerged and emergent vegetation is a structural requirement for *C. mercuriale*, probably providing cover for larval stages (and sufficient oxygen – section 2.3.7), oviposition substrate and perching sites for adults. However the species composition of the vegetation may also indicate other habitat features required by *C. mercuriale.* Plants that indicate exposure to sun have already been mentioned. With regards to structural habitat features, some species found on chalkstreams trap silt and are thus clump-forming (*Veronica* sp., *Rorripa nasturtium-*

aquaticum agg., *Apium nodiflorum*)(Haslam 1978) and enhance the build up of a fringe of emergent vegetation as well as slowing the flow of water. On heathlands, areas of abundant aquatic vegetation were promoted by *Sphagnum* sp. and other mosses. These were under-recorded in documents, but were found on most sites and formed mats that support vascular plant species. In addition, the two most common species, *Hypericum elodes* and *Potamogeton polygonifolius*, often form dense, floating mats on shallow, narrow runnels in valley mires (e.g. in M29 in the New Forest).

In Germany, a high proportion of vegetation is made up of herbs (30-70% in the Upper Rhine sites and 50-100% in the Alpine sites) with frequent grasses and sedges (Buchwald 1989). In contrast to the finding of a range of communities on sites occupied by *C. mercuriale* in Britain, Buchwald (1994) found that 6 particular *Phragmites* communities were associated with the species on meadow brooks and ditches in Germany. These all contained herbaceous species (including *Berula erecta, Nasturtium officinale, Myostis scorpidiodes, Veronica anagallis aquatica, Veronica beccabunga, Glyceria fluitans*) with a similar 'nasturtiid' growth form i.e. stands of a low to moderate height with extensive branching and leaves. On British sites, species that were prevalent on streams were short, semi-emergent or submergent herbs rather than tall emergents and including those listed above as well as *Hypericum elodes, Apium nodiflorum, Mentha aquatica, Glyceria maxima, Ranunculus* sp. Buchwald (1994) suggested that such plant species (via their similar growth form) are used by *C. mercuriale* as an indirect cue to the proximity of ground water or springs during habitat selection and in turn to the permanence of the water supply and year round high temperatures. He points out that the latter, unlike factors such as substrate, flow and exposure, could not be perceived directly by individuals. In fact all the species listed in this paragraph are associated with proximity to sources and ground water in Germany as are *Phalaris arundinacea, Ranunculus trichophyllos, Elodea* sp. *Callitriche* sp, *Groenlandia* sp. *whilst Mentha aquatica, Berula erecta* and *Callitriche* sp. are absent in areas which dry out.

On British heathland sites, *Hypericum elodes* and *Potamogeton polygonifolius* are associated with areas of water movement on mires (Sanderson 1998) whilst the association of *Rorippa nasturtium aquaticum* and *Ranunculus* sp., with year round high temperatures on chalkstreams was described in section 2.3.4. Butcher (1927) noted that the area occupied by patches of vegetation on the river Itchen did not change between summer and winter and that submerged plant species such as *Ranunculus fluitans, Ranunculus pencillatus, Apium nodiflorum, Potamogeton densus* and *Callitriche* sp. were perennial in this situation. Thus it appears that vegetation on British sites as well as on German sites could be used by *C. mercuriale* during habitat selection as a cue to the permanence of water supply and in turn to the stability of temperature and vegetation cover. Selection experiments have shown that other odonates such as *Ceriagrion tenellum, Cercion lindeni* and *Erythromma viridula* are able to distinguish between stands of different plant species (Buchwald 1992; Buchwald 1994), though whether distinctions are made on the basis of the species themselves or their growth forms is difficult to ascertain.

Brown flocculent deposits of algae, including Baccillariaophyta, Chlorophyta, Tabellaria and Chaetophora, have also been noted on a number of *C. mercuriale* sites in Pembrokeshire (Skidmore 1996). Though such brown deposits were not noted across many sites in Britain, information on algae was not widely recorded and may merit further emphasis in future monitoring exercises.

Finally, *C. mercuriale* uses bankside vegetation in several ways. Tussocky vegetation, including *Molinia caerulea*, *Juncus effusus*, ericaceous species and gorse, is used for feeding and roosting (Skidmore 1996; Hold 1997; Hopkins & Day 1997; Strange 1999; James & Wiggers 2000, pers. obs.). It is often found next to watercourses containing *C. mercuriale* populations (e.g. 10/15 sites where bankside vegetation as described in documents). Indeed, most individuals roost in tussocks within 5-10m of the stream though some are found up to 50m away on heathland sites (pers. obs) and up to 300m away on chalkstream sites (Strange 1999). Similary, in Germany, *C. mercuriale* have been observed to use reeds (but not scrub or bramble) at heights of 40-50cm for roosting on meadows brooks and ditches (Sternberg *et al.* 1999) and roost up to 10m from the breeding site and up to 100m in large populations (Roske 1995). In calcareous spring mires, the optimal bankside vegetation height was 20-40cm (Buchwald 1989) reflecting the fact that these runnels are smaller and more easily overshadowed. Most British sites occupied by *C. mercuriale* were grazed by cattle and horses, perhaps reflecting this species' structural requirements with regards to bankside vegetation. The type of grazing animal used influences the structure of bankside vegetation (Bacon 1990; Kirby 1992). Sheep grazing produces a very short even sward, grazed to the level of the root stocks. Cattle graze less evenly and pull up vegetation, producing a mosaic of tall tussocks and shorter open areas. This not only provides roosting areas but also feeding areas for *C. mercuriale* since such structural diversity favours a range of invertebrates.

Although horses are more selective and can wipe out some species of plant, they are also tolerant of quite poor grazing which may be found in the vicinity of some *C. mercuriale* sites. Specific plant species required for roosting may also be favoured by the employment of a particular stock type. For example, cattle grazing on wet lawn habitats, reduces *Molinia* dominance but maintains cover of *Juncus acutiflorus* (Sanderson 1998). It appears that poaching (trampling) of stream margins by heavier grazing animals (especially cattle) is also favoured by *C. mercuriale*, being associated with areas used by the species in 13 out of 24 sites in Table 2.11. This process opens up areas or bare silt or mud encouraging the rooting of shallow water plants (Painter 1999) and emergent herbs (such as *Apium nodiflorum*) (Strange & Burt 1994). It also provides areas of variable depth and flow, producing shallow, slow flowing areas (sometimes on the edge of streams that flow too fast in the main channel) favoured by *C. mercuriale*. Trampled, gently sloping ditches also support a diverse insect fauna in general (Kirby 1992; Painter 1999).

A degree of shelter from trees and shrubs is also found in many sites (referred to as carr/scrub in Table 2.7). Recent scrub removal and suggested removal has been targeted at areas of watercourse, wet heath and mire in order to retain shelter in surrounding areas (specified in 7 out of 22 cases of suggested removal). In addition, *C. mercuriale* has been noted to use *Myrica gale* (Stevens & Thurner 1999 – 1 site) on the watercourse and surrounding tussocks (Hold 1997) for breeding activity including mate location. Indeed, *Myrica gale* formed a main component of stream vegetation in 9 heathland sites (present in14) and of the surrounding vegetation in 11 sites (present in 10). In odonates in general, there has been some suggestion that population size depends on the presence of herbaceous areas near streams where adults can roost and forage and find microclimates suitable for basking (Corbet 1999).

2.3.7 Range of chemical parameters found in watercourses occupied by *C. mercuriale.*

2.3.7.1 pH, conductivity and temperature

A wide range of pH was found in the watercourses on *C. mercuriale* sites (Fig. 2.15), although the majority of sites had pH's of 7.0-7.5. This range of pH is similar to that found in the Upper Rhine valley (6.6 – 8.5 \ (Buchwald 1989). pH is seldom the proximate factor determining odonate distribution and numerous species show tolerance to a wide range of values (Corbet 1999) similar to that found here for *C. mercuriale*. With regards to aquatic invertebrates in general, direct detrimental effects of low pH are only shown below pH 4.5 (Allan 1995). Indeed, in a zygopteran, *Enallagma civile*, an increase in mortality, caloric content and respiration rate of larvae was only found at pH 3.5 not at pH 4.5 or 5.5 (Gorham & Vodopich 1992).

However, pH can indirectly affect invertebrates through its effect on vegetation. In *C. mercuriale* sites on heathland, the existence of often base-rich water (due to under-lying soft calcareous rocks – Section 2.3.3) flowing over acid peat produces a mosaic of acid-requiring and base-requiring plant species. This is because the sites often have high water tables and are close to springs such that the properties of the groundwater or flushes will significantly influence the vegetation. Prevalent acid-requiring species included *Hypericum elodes, Potamogeton polygonifolius* (the two commonest species in heathland streams (Table 2.9), distributed across most regions (Table 2.11)), *Drosera rotundifolia* and *Narthecium ossifragium.* More base-requiring species included *Anagallis tenellum, Apium nodiflorum, Mentha aquatica,* and *Carex* sp. Brown mosses found on some New Forest (S.Cooch, pers. comm) and Pembrokeshire (Evans 1989) sites were indicative of base-richness. Sites without an acidic substrate were dominated by base-rich vegetation with few or no acid-requiring species (e.g. Anglesey, chalkstream sites - Table. 2.11).

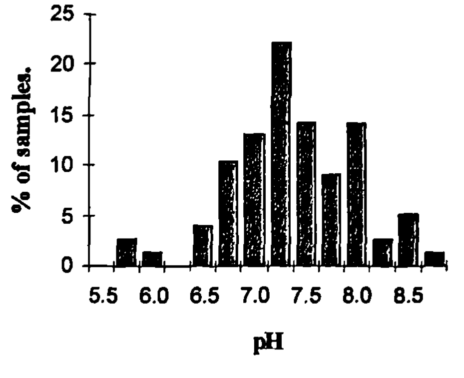


Fig. 2.15 Percentage distribution of sites across pH values (*n*=77).

Consistent with measurements of pH, the base status of NVC communties (from Rodwell, 1991) associated with *C. mercuriale* streams ranged from base poor (e.g. M29, pH 4-5.5) to base rich (e.g. M13b, pH 6.5-8.0). Some communities are found on highly calcareous waters (range in calcium concentration of waters for M13b is 60-200mg/l) but others are found on less calcareous watercourses (range in calcium concentration of waters for M14 is 5-35mg/litre).

Conductivity measures the electrical conductance of the water and is thus an approximate predictor of the total dissolved ions such as calcium, magnesium, sodium and potassium. Fig. 2.16 shows that most sites have fairly low values for conductivity (most are less than 150 µs/cm). Highest values for conductivity are found in Anglesey, Oxford and on the Itchen and Test (Butcher 1927) which may reflect the higher input of calcareous water in these sites (Table 2.12).

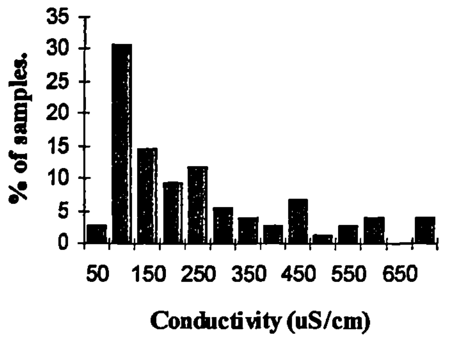


Fig. 2.16 Percentage distribution of sites across conductivity values (*n*=75).

The mean and range of pH and conductivity (and other water chemical parameters) across monthly samples is shown in Table 2.12 whilst Fig. 2.17a-c shows a frequency distribution of pH, conductivity and temperature, values obtained on a half hourly basis from a datasonde in place over winter. Although pH was one of the least variable of the chemical parameters at Glan-yr-afon Uchaf (V* in Table 2.13), the range of pH found across months (Table 2.14a) and half hourly periods (Fig. 2.17c) was as wide as that found across sites for *C. mercuriale*. Conductivity was less variable within a site than across sites. Both of these parameters and temperature showed considerable diurnal variation (Fig. 2.18). pH and temperature remained at low levels through the night from 7-8 pm to 9am and then rose rapidly to peak at 1-2pm. Conductivity showed the reverse pattern remaining at relatively high levels through the night and falling to a trough in the middle of the day. These patterns occur due to the interdependence of carbon dioxide concentration and (Allan 1995). Photosynthesis, and thus carbon dioxide fixation and oxygen production, occurs only in the day time and proceeds more quickly at higher temperatures. The decrease in carbon dioxide that results is buffered by bicarbonate ions (produced by weathering of rocks) and results in only a 1 fold (0.1 pH units) increase in hydrogen ion concentration. In highly productive lowland streams with luxuriant macrophyte growth a pH rise of as much as 0.5 units can occur at mid day (Allan 1995). The significance of these patterns for *C. mercuriale* is that oxygen concentration (due to photosynthesis) probably shows a similar diurnal rise to pH and temperature during the day increasing the oxygen availability for respiration to larvae of *C. mercuriale* during the time of peak activity. The extent of this rise will depend on the density of macrophyte growth and may provide one reason for the association of this species with abundant macrophyte cover. In addition, the small magnitude of the rise in pH and the concommitant decrease in conductivity suggests that these small streams have a high buffering capacity. It is significant that over winter, the temperature always remained above 0°C and mostly lay between 4 and 8°C (Fig. 2.17c). This lends some support to the suggestion that this species requires high minimum temperatures, though similar data from many sites would be required to confirm this.

Table 2.13 Mean (± s.e.), range and coefficient of variation (V), for chemical parameters from monthly samples from Glan-yr-afon Uchaf.

	n	μ ± s.e.	Range	V
pH	9	6.62 ± 0.13	5.94-7.07	6.2
Conductivity(μs/cm)	9	54.80 ± 5.19	31-78	29.2
Temperature (^{0}C)	9	12.11 ± 1.59	7.6-20.6	40.4
Ammonia (mg/litre)	10	0.017 ± 0.004	0.01-0.05	80.6
Oxidised nitrogen (mg/litre)	10	0.037 ± 0.008	0.013-0.074	67.1
Nitrate (mg/litre)	10	0.033 ± 0.007	0.01-0.07	70.8
Nitrite (mg/litre)	10	0.004 ± 0.001	0.002-0.009	55.1
Hardness	9	14.29 ± 2.52	4.7-25.2	54.3
Chloride Ions	9	10.51 ± 0.69	8.9-15.8	20.1
Sodium (filtered)	9	6.41 ± 0.49	4-8.2	23.4
Potassium (filtered)	9	0.278 ± 0.036	0.1-0.43	40.2
Magnesium (filtered)	9	2.08 ± 0.36	0.7-3.59	53.1
Magnesium	9	2.57 ± 0.58	1.27-3.59	69.9
Calcium (filtered)	9	2.31 ± 0.42	0.73-4.2	56.2
Calcium	9	2.32 ± 0.42	0.73-4.2	55.8
Zinc (filtered)	9	0.006 ± 0.001	0.002-0.01	40.7
Zinc	9	0.017 ± 0.007	0.004-0.07	127.9
Aluminium (filtered)	9	0.056 ± 0.010	0.024-0.118	55.1
Aluminium	9	0.086 ± 0.013	0.033-0.146	46.3
Organic carbon (filtered)	9	3.73 ± 0.525	0.75-6.43	43.4
Iron (filtered)	9	0.078 ± 0.014	0.038-0.173	55.5
Iron	9	0.109 ± 0.014	0.062-0.183	40.1
Sulphate ions	9	2.37 ± 0.26	1.3-3.8	33.5
Dissolved oxygen - percentage saturation	9	93.44 ± 1.34	91.4-100.5	4.4
Dissolved oxygen - in solution	5	9.76 ±0.60	7.58-11.03	14.4

The ionic concentration of rain is typically much more dilute than most river water. Higher concentrations of magnesium, chlorine, calcium and sulphate were found at Glan-yr-afon Uchaf (Table 2.13), compared to those in typical marine and coastal rainfall (from Berner & Berner, 1987 cited in Allan 1995). Higher levels of these ions may result from weathering of rocks that has taken place before springs emerge. However, the difference between the stream concentrations and rainwater concentrations were not as substantial as those between river water concentrations and rain water (Allan 1995) and indeed stream concentrations of potassium, nitrate and ammonia were similar to rainwater or lower. Although there is considerable monthly variation in width and depth (Chapter 4) due to evaporation and rainfall, these small, heathland streams may maintain relatively dilute and constant ionic concentrations due to the continual flow of water from springs. These conditions may provide a more stable ionic environment for stream invertebrates.

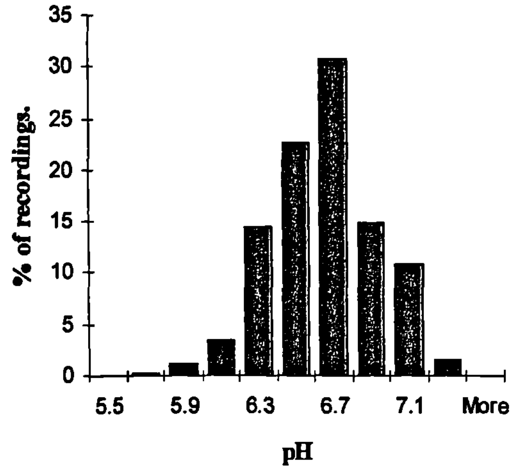


Fig. 2.17a Percentage distribution of datasonde recordings over different pHs (Dec-Feb 1999).

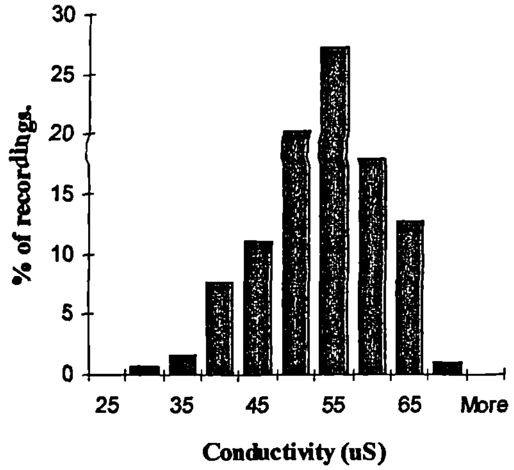


Fig. 2.17b Percentage distribution of datasonde recordings over different conductivities (Dec-Feb 1999).

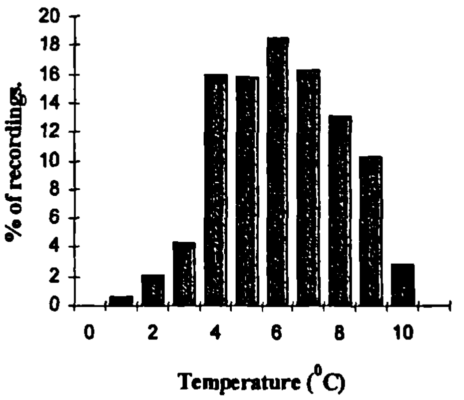


Fig. 2.17c Percentage distribution of datasonde recordings over different temperatures (Dec-Feb 1999).

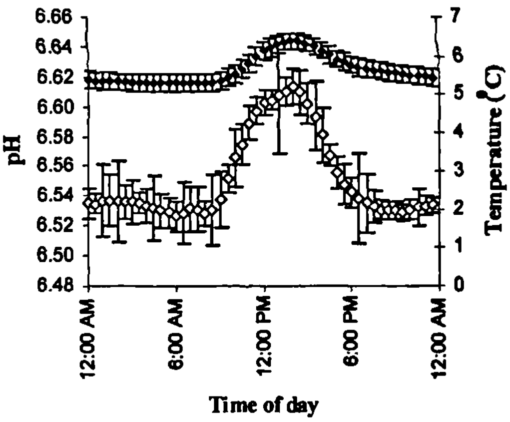


Fig. 2.18a Mean (± s.e.) pH (closed squares) and temperature (open squares) in each half hour time period in a day (n=70).

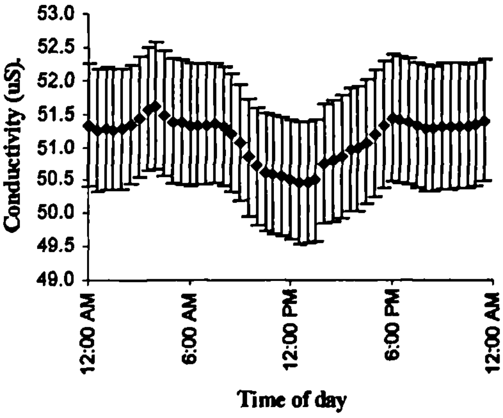


Fig. 2.18b Mean conductivity (± s.e.) in each half hour time period in a day (n=70).

2.3.7.2. Phosphates and nitrates

Levels of all types of phosphate were below 0.025 mg/l in most watercourses occupied by *C. mercuriale* (Fig. 2.19a-d). The data were not accurate enough to discuss the relative contribution of different types of phosphate. A few sites had particularly high levels of phosphate including those in the Itchen Valley Country Park (but not King's Sombourne and Mariner's Meadow), Dry Sandford Pit and one of the Waun Fawr samples. Most samples also had low levels of nitrates (less than 0.2 mg/litre, Fig. 2.20) although a substantial portion had very high values that exceeded twice the maximum value on the calibration curve for this parameter. This portion included both sites that were surrounded by improved and semi-improved grassland (e.g. Mariner's Meadow, Pont Clegyr, and King's Sombourne) as well as those surrounded by unimproved grassland or dry heath (e.g. Povingdon, Corfe Common East and Applemore). Thus it is not possible to relate nitrate or phosphate levels to surrounding land use with these data. In fact, only four sites were perceived to be threatened by nutrient run-off from agricultural land (both Dartmoor sites, Hartland Moor and Rhossili Down).

The finding of generally low levels of phosphates and nitrates on heathland sites indicates that *C. mercuriale* is found in oligotrophic or dystrophic conditions. This is consistent with the range of plant species found on sites (Tables 2.8-2.9). *Potamogeton polygonifolius, Ranunculus flammula, Menyanthes trifoliata* and *Eriophorum angustifolium* are dystrophic species (found in conditions of negligible nutrients) whilst many of the others (e.g. *Juncus articulatus, J. bulbosus, Eleocharis* sp.) are oligotrophic species (Haslam 1978). The presence of *Molinia caerulea* both on an around streams may indicate that *C. mercuriale* generally inhabits nutrient impoverished conditions on heathlands. NVC communities found on heathland streams were also associated with nutrient poor or oligotrophic conditions (Rodwell 1991). Indeed nutrient enrichment in such communtities would allow dominance of several species including *Juncus effusus* and *Juncus acutiflorus* (on M6c), *Juncus subnodulosus* (on M9) and *Phragmites* fen (on M14) and thus compromise the structural suitability of the habitat for *C. mercuriale*. Chalkstreams seem to be generally higher in phosphates and nitrates and contain plants indicative of mesotrophic or eutrophic conditions such as *Berula erecta, Ranunculus pencillatus* sp. Some fenland sites such as Cors Erddreiniog, in Anglesey, the Oxford sites and some of the Dorset heathland sites may also be more mesotrophic.

In meadow brooks and ditches in Europe, *C. mercuriale* is also found in oligotrophic and mesotrophic waters (Buchwald 1989; Grand 1996). The species avoids eutrophic conditions in Germany since, in these conditions a bacterial or algal film forms on the water surface and cover of submerged aquatic vegetation decreases (Buchwald 1989; Sternberg *et al.* 1999). There is a shift from herbs with a nasturtuid growth form (see above) to vegetation dominated by *Phalaris arundinacea* or species such as *Solidago canadensis, Filipendia ulmaria,* and *Rubus* sp. In contrast, populations in calcareous spring mires are found in dystrophic conditions where there is an extreme lack of ions especially nitrate and ammonia (Buchwald 1983).

Regional variation in vegetation associated with *C. mercuriale* (Buchwald 1994) is partly attributable to chemical parameters. As described above, *C. mercuriale* is associated with six different communities on meadow brooks and ditches on the

Upper Rhine and tolerates a high proportion of *Phalaris arundinacea* which arises in areas of adjacent intensive agriculture. On the south-west of its range, in the pre-alpine region and the Black Forest, *C. mercuriale* is associated with a narrower range of base rich communities (Pre-alpine region - *Primulo-Schoenetum ferruginei* with *Scorpido-Utricularietum, Mentha aquatica, Carex* sp. *Juncus subnodulosus*; Black Forest - *Glyceria flutians,* S*parganium neglecti*) with only occasional *Phalaris arundinacea.* This combined with the narrower range of watercourse preferences in these regions (section 2.3.4) compared to the Upper Rhine has lead Buchwald (1994) to suggest that *C. mercuriale* is more stenotopic at its range edges.

2.3.7.3 Ammonia

Levels of ammonia were usually low (less than 0.1 mg/litre – Fig. 2.21) though wide range of values up to 0.55 mg/litre were found. Sites with high levels of ammonia again were not associated with particular surrounding land use but three sites with such levels consisted of wide areas of very shallow flushes (Widden Bottom, Cors Erddreiniog, Corfe Common East, Povingdon Orchard Cottage Mire). Where such conditions prevail in shallow spring marshes in Germany, ammonia may build up (with a decrease in oxygen) in sunny conditions due to detritivore activity (Sternberg *et al.* 1999).

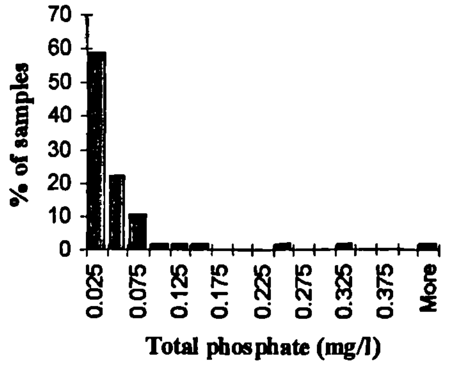


Fig. 2.19a Percentage distribution of total phosphate (n=68).

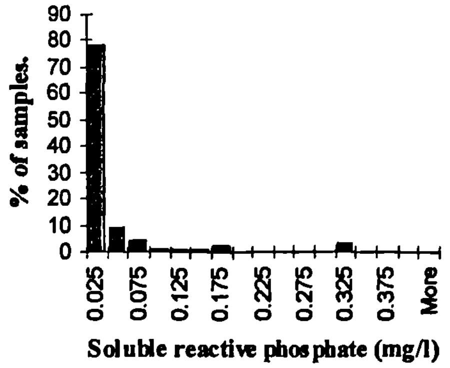


Fig. 2.19b Percentage distribution of soluble reactive phosphate (n=91).

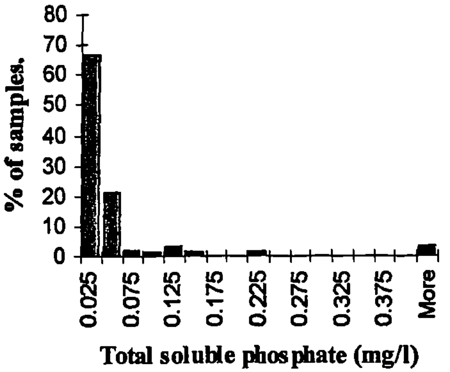


Fig. 2.19c Percentage distribution of total soluble phosphate values (*n*=91).

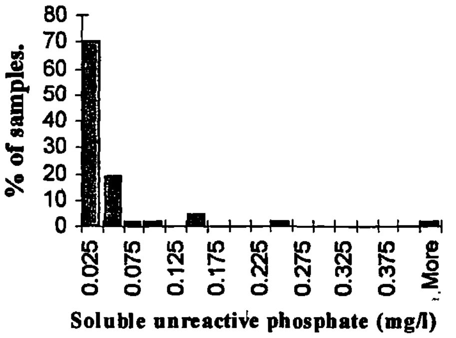


Fig. 2.19d Percentage distribution of soluble unreactive phosphate values (*n*=63).

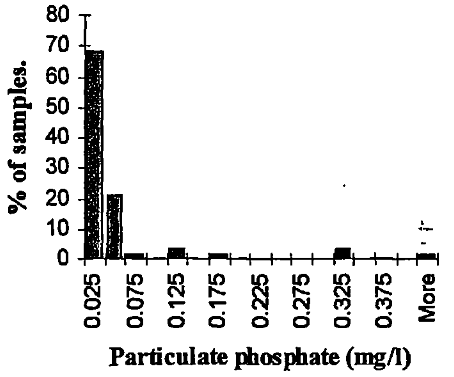


Fig. 2.19e Percentage distribution of particulate phosphate values (*n*=66).

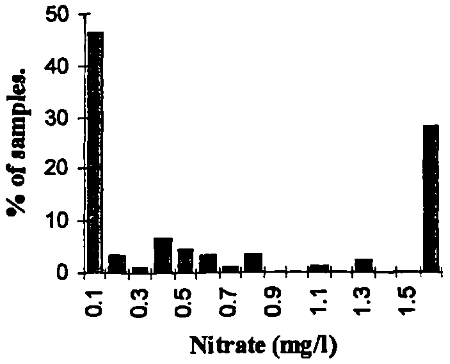


Fig. 2.20 Percentage distribution of nitrate values (*n*=91)

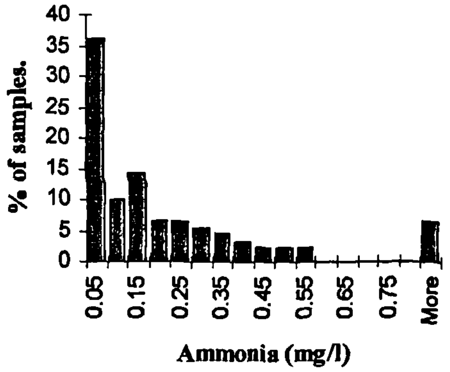


Fig. 2.21 Percentage distribution of ammonia values (*n*=91)

2.3.7.4 Oxygen concentration

Groundwater can be very low in dissolved oxygen and enriched in carbon dioxide due to microbial processing of organic matter as water passes through the soil. In small, flowing streams with limited pollution, diffusion maintains oxygen and carbon dioxide near saturation (Allan 1995) even near groundwater sources. In monthly samples from Glan-yr-afon Uchaf, oxygen concentration ranged from 91%-100% saturation (Table 2.13) and the mean amount of oxygen in solution was close to that found in pure water (9.8 mg/litre at 15°C at sea level). In Germany, on meadows in the Upper Rhine valley, *C. mercuriale* is found in well-oxygenated water with concentrations ranging from 2.5-30 mg/litre (Buchwald 1989). Sternberg (1999) suggests that *C. mercuriale* is less well adapted to low oxygen content than standing water species such as *Ceriagrion tenellum* due to its relatively small caudal lamellae. The latter provide a surface for gas exchange in odonates and their effectiveness in this respect is proportional to their area (Williams, 1936 cited in Sternberg *et al.* 1999). Thelen (1992) found that larval populations of *C. mercuriale* were associated with mean oxygen saturation of 76% on the Upper Rhine. The association of *C. mercuriale* populations with areas of flow, high vegetation cover and proximity to springs may reflect this species requirement for well-oxygenated water.

Table 2.14a Range and mean ± s.e.(in parentheses) of pH, conductivity, nitrate and ammonia in samples from extant sites in each region. * range or single values of parameters found in stream sources.

	No. of sites and samples	pH	Conductivity	Nitrate	Ammonia
Oxford	2 sites, 2 samples	7.2-7.8 - -	680 - -	0-high - -	0 - -
Dorset 1998	6 sites, 9 samples	7.1-8.5 (7.68 ± 0.15) -	160-420 (311 ± 32) -	0-2.47 (0.49 ± 0.26) -	0.12-0.48 (0.32 ± 0.04) -
Devon	2 sites, 6 samples	7.1-7.4 (7.23 ± 0.06) -	60-234 (126 ± 38) -	0 ± 3.44 (1.48 ± 0.88) *3.25	0 - *0.025 at
Dartmoor	1 site, 2 samples	7.5*-7.8 - -	110 - -	0.65-2.09* - -	*0-0.057 - -
New Forest	26 sites, 30 samples,	6.0-8.1 (7.21 ± 0.10) -	70-530 (182 ± 24) -	0-0.83 (0.90 ± 0.34) *0.58-1.08	0-1.02 (0.18 ± 0.05) *0.13-0.18
Anglesey	1 site, 4 samples	7.8-8.4 (8.18 ± 0.11) *7.8	540-700 (633 ± 38) *690	0.36-11.60 (6.70 ± 2.34) *0.36	0-1.39 (0.43 ± 0.32) *1.39
Pembrokeshire (except St David's)	11 sites, 19 samples	6.3-7.6 (6.82 ± 0.07) *6.7-7.1	40-110 (74 ± 5) *60	0-2.4 (0.39 ± 0.19) *0-1.53	0-3.4 (0.30 ± 0.20) *0.10-0.14
St David's	2 sites, 4 samples	7.3-7.8 (7.62 ± 0.12) -	450-590 (520 ± 38) -	4.66-6.07 (5.42 ± 0.29) -	0-0.51 (0.23 ± 0.13) -
Gower	2 sites, 4 samples	5.6-8.6 (6.93 ± 0.78) -	180-340 (245 ± 38) -	0-0.08 (0.02 ± 0.02) -	0.06-0.09 (0.19 ± 0.12) -
Itchen Valley Country Park	1 site, 3 samples	8.0 (Mayo & Welstead 1983)	- - -	1.25-3.25 (2.42 ± 0.61) -	0.04-0.16 (0.12 ± 0.04) -
	3 sites, 3 samples	- -	- -	4.03-5.06 (4.55 ± 0.52)	0.03-0.13 (0.08 ± 0.05)

Table 2.14b Range and mean ± s.e.(in parentheses) of different types of phosphate in samples from extant sites in each region. * range or single values of parameters found in stream sources.

	Soluble reactive phosphate	Total soluble phosphate	Soluble unreactive phosphate	Total phosphate	Particulate phosphate
Oxford	0-0.163 - -	0.024-0.124 - -	0.024 - -	0.014-0.244 - -	0.121 - -
Dorset 1998	0.006-0.017 (0.010 ± 0.001) -	0-0.041 (0.018 ± 0.005) -	0.018-0.026 (0.017 ± 0.004) -	0-0.062 (0.030 ± 0.007) -	0.005-0.050 (0.018 ± 0.005) -
Devon	0-0.007 (0.003 ± 0.002) *0.010	- - -	- - -	- - -	- - -
Dartmoor	0.004-0.011* - -	0.000 - -	- - -	0-0.006* - -	0-0.006* - -
New Forest	0-0.138 (0.047 ± 0.017) *0.012	0-0.111 (0.080 ± 0.034) *0-0.048	0-0.055 (0.064 ± 0.032) *0.035	0-0.478 (0.054 ± 0.023) -	0-0.401 (0.019 ± 0.037) -
Anglesey	0-0.021 (0.010 ± 0.005) *0.015	0-0.028 (0.010 ± 0.007) *0.000	0.007-0.015 (0.005 ± 0.007) *0.000	- - -	- - -
Pembroke-shire (except St David's)	0-0.2 (0.019 ± 0.010) *0.003-0.015	0-0.2 (0.025 ± 0.012) *0-0.026	- - -	0-0.308 (0.037 ± 0.017) *0.019-0.021	0-0.019 (0.012 ± 0.021) -
St David's	0-0.067 (0.035 ± 0.015) -	0.014-0.031 (0.025 ± 0.004) -	- - -	0.022-0.074 (0.041 ± 0.012) -	0-0.046 (0.016 ± 0.010) -
Gower	0.008-0.122 (0.058 ± 0.024) -	0.009-0.053 (0.024 ± 0.010) -	- - -	0.019-0.117 (0.056 ± 0.022) -	0.010-0.107 (0.043 ± 0.028) -
Itchen Valley Country Park	0.306-0.320 (0.314 ± 0.004) -	0.437-0.816 (0.607 ± 0.111) -	0.132-0.499 (0.293 ± 0.108) -	- - -	- - -
Test Valley	0.049-0.072 (0.060 ± 0.012) -	0.113-0.127 (0.120 ± 0.007) -	0.041-0.078 (0.060 ± 0.018) -	- - -	- - -

2.3.7.5 Pollution

Data were not available on levels of chemical pollutants across sites. However, most heathland sites receive clean supplies of water from springs that are fairly remote from agricultural land or are protected (Jenkins *et al.* 1996). The loss of a colony on Mynydd preseli has been attributed to the dumping of sheep dip (Evans 1989). Chalkstream sites are more likely to be effected by eutrophication as described above. Defaecation by grazing animals may significantly effect streams but only on small sites or when large numbers of ponies are employed since these animals defaecate repeatedly in the same patches (Kirby 1992). In addition, some cattle wormers such as Ivomectin are thought to be detrimental to invertebrates (Strange 1999). The species is associated with high water quality on European sites (Grand 1996b). Given the low tolerance of other odonates to pollutants, it is safest to assume that *C. mercuriale* requires unpolluted water. In addition, most sites are characterised by clarity of the water (pers. obs.). An increase in suspended solids from the clay pit outflow on Povingdon may have contributed to a decline in population numbers on the Outflow mire (James & Wiggers 2000) exacerbated by siltation due to excessive poaching (section 2.3.4).

2.3.8. Odonates associated with *C. mercuriale.*

Information on which species of odonate co-occur on sites with *C. mercuriale* was obtained for 57 sites (Kerry 1994; Winsland 1994b; Smallshire 1995; Smallshire 1998; Stevens & Thurner 1999; Woodman 1999). *Coenagrion mercuriale* co-exists with a wide range of species, most commonly *Ceriagrion tenellum, Coenagrion puella, Ischnura elegans* and *Pyrrhosoma nymphula* among the Zygoptera, and *Orthetrum coerulescens, Sympetrum striolatum* and *Cordulegaster boltonii* among the Anisoptera (Table 2.15). The fact that *Coenagrion mercuriale* is found on the same sites as these species does not mean that it is as eurytopic as some of these species. Winsland (1993) pointed out that, despite overlapping in range with many species, *C. mercuriale* adults seldom utilises the same stretches of stream. Evans (1989) noted that very few other odonates larvae were found in areas with the densest concentrations of *C. mercuriale. Pyrrhosoma nymphula* (found on 7 sites), *Orthetrum coerulescens* (7 sites), *Cordulegaster boltonii* (4 sites), and *Sympetrum striolatum* (2 sites) are the only species that have been found in the same stretches of stream as *C. mercuriale* in the larval stage on more than one site (Evans 1989; Kerry 1994; Winsland 1994a; Skidmore 1996; James & Wiggers 2000, pers. obs.).

Table 2.15 Total and regional frequency of occurrence of species of Odonata on British sites occupied by *C. mercuriale*, for species that occurred on 5 or more sites.

	Region							
	Dor	Dev	Dar	NF	Pemb	Gow	I & T	Total
No. of sites with information on Odonata	6	2	2	29	3	1	14	57
Zygoptera								
Calopteryx virgo	0	0	1	10	1	0	0	12
Ceriagrion tenellum	1	1	1	25	0	0	0	28
Coenagrion puella	2	2	0	18	1	1	6	30
Enallagma cyathigerum	1	2	0	2	1	1	3	10
Ischnura elegans	2	1	0	15	0	1	8	27
Pyrrhosoma nymphula	4	2	2	22	1	0	1	32
Anisoptera								
Anax imperator	1	2	0	6	0	0	2	11
Cordulegaster boltinii	4	2	2	15	1	0	3	27
Libellula depressa	0	2	0	8	0	0	3	13
Orthetrum coerulescens	5	2	2	28	2	0	0	39
Sympetrum striolatum	2	2	0	21	0	0	5	30

Key to regions: Dor=Dorset, Dev=Devon, Dar=Dartmoor, NF=New Forest, Pemb=Pembrokeshire, Gow=Gower, I & T=Itchen & Itchen.

2.4 Discussion

This review reveals that *C. mercuriale* is rare in Britain with regards to several of the attributes used to assess rarity (Schoener, 1987; Rabinowitz *et al.* 1986). Firstly, it has a restricted and declining distribution both nationally and globally and has undergone a 38% decline since 1985. At a coarse scale it occupies 28 of the 10km squares in Britain (0.84%), which is many fewer than virutally all other British odonates (Merritt *et al.* 1996). Those 15 species that occupy fewer 10km squares are mostly occasional migrants. Secondly, it has small population sizes in many sites in Britain though many may be larger than those found in core populations in Germany (Roske 1995). This is worthy of further investigation given that that edge-of-range populations are usually less dense and more variable in space and time than those in range centres (Brown *et al.* 1995; Brooks 2000; Channell & Lomolino 2000).

Thirdly, this species is restricted to two fragmented biotopes in Britain and it has very specific habitat requirements within these. This was indicated by the discontinuity of its distribution compared to the distribution of its biotopes on a national scale as well as the extremely localised nature of population distribution within sites (Corbet 1957; Knights 1983; Evans 1989). Examination of habitat features common to locations of *C. mercuriale* populations and features that had positive or negative impacts on population size revealed a range of features used by this species. Proximately, habitat use is a behavioural consequence of an individual selecting where to live (or passively remaining in a habitat). Ultimately, habitat use is determined by selection on survival and reproduction, arising from differential fitness between habitats (Boyce 1999). Table 2.16 summarises the proximate cues or habitat features used by *C. mercuriale* in Britain elucidated in this review. Possible ultimate factors selecting for the use of these features are suggested.

To assess the stenotopy of *C. mercuriale*, it is important to distinguish between those habitat features required by all odonates from those required particularly by *C. mercuriale*. Percentage cover of vegetation, water temperature and shade are important predictors of zygopteran and anisopteran distributions, with species of the former usually tolerating a wider range of these factors (Samways 1993; Samways & Steytler 1996). Steytler (1995) defines stenotopic species as those with multidimensional requirements for factors such as sunlight, shade, vegetation structure and water flow. The range of factors elucidated in this review suggests that *C. mercuriale* falls into this category. Buchwald (1994) points out that all central European lotic odonates require some water current (e.g. Wingfield Gibbons & Pain 1992) and exposure to sunlight. However, *C. mercuriale* is the only one of these species (apart from *Orthetrum coerulescens*, a species it is often associated with) that requires proximity to springs or groundwater in addition to these two factors.

Table 2.16 Summary of the proximate cues/features used by *C. mercuriale* in Britain (with associated or indicated features) and the possible ultimate factors governing selection of these features.

Proximate cues	Associated/Indicated features	Possible ultimate factors
Physical features		
1. Low altitude, mostly < 90m a.s.l.	Relatively high temperatures	features 1, 4, 5, 7, 9, 11 – ensure minimum stream temperature thresholds/regimes for larval development, oviposition and emergence.
2. Gently sloping ground, < 10% slope.	Slow to moderate flow	
3. Water sources arising from soft deposits of sandstone, limestone and clay.	Increased buffering capacity of water?	
4. Inorganic substrate overlaid with shallow organic peat or silt	Dark substrates absorb radiant heat	features 1, and 9, ensure minimum air temperatures for adult activity whilst factor 12 ensures the availability of areas for roosting, maturation, feeding, displaying and basking.
5. Shallow narrow waterbodies on heathlands, small ditches on chalkstreams	Relatively large rates of temperature increase when exposed	
6. Slow to moderate but permanent water flow	Ensure minimum oxygen concentrations	
7. Proximity to springs or groundwater	Ensure permanence of flow, high oxygen concentrations, stable thermal regimes with high minimum winter temperatures and ice free conditions	features 9, 10, 11, 13, 8, ensure the provision of open stream areas with substrates for oviposition and egg development.
Vegetation features		
8. Remoteness from improved agriculture?	Prevent eutrophication, encroachment of invasive tall emergents and algae	features 2, 6, 7, 8, 10, 11,and 14, ensure sufficient oxygen for larval and egg development. Factor 11 provides cover for the larval stage for feeding and refuge from predators.
9. Open and exposed watercourses (maintained by grazing, cutting, scrub removal and some channel clearance)	Relatively high temperatures	
10. Medium to high cover of submergent and emergent stream vegetation (low to medium height)		
11. Herbaceous, perennial stream vegetation	Permanence of water supply and high minimum winter temperatures	
12. Shelter on bankside and sometimes within the stream (e.g. *Myrica gale*).		
Chemical features		
13. Dystrophic to oligotrophic conditions	Prevent encroachment of tall emergents and algae	
14. Unpolluted water		
15. High oxygen concentrations		

Coenagrion mercuriale is similar to other odonates in that its distribution is influenced by vegetation physiognomy not by the presence of particular plant species (Samways 1993; Samways & Steytler 1996) but stenotopic in that the plant communities it is associated with indicate proximity to springs or groundwater. Thermal requirements of *C. mercuriale* were reflected both in its European and British distributions and in its microhabitat selection within sites (features 1, 4, 5, 7, 9, 11 on Table 2.16). Many species occupy narrower niches within biotopes towards the northern edges of their ranges since they require coincidence of basic resources with substantially warmer microclimates for that latitude or altitiude (Thomas 1983; Cherrill & Brown 1990a; Cherrill & Brown 1990b; Hill *et al.* 1999; Thomas *et al.* 1999). For example, *Myrmica sabuleti* (red ant) requires frequent day temperatures of 20-25 °C at the soil surface (between April and October) due to its long period of subterranean larval growth. On its range edge, in Britain, it obtains this exposure by the use of South facing slopes with short swards (<5 cm). Further south, in France, such exposed areas are too hot such that the species occupies tall swards (>20cm) on all slopes except for south facing ones (Thomas *et al.* 1999 and references therein).

Buchwald (1994) suggests that *C. mercuriale* has a more restricted niche at its range edges within Germany. In the meadow brooks and ditches in the core of its range (south and middle of Upper Rhine plateau), it inhabits a range of stream dimensions, flow types and substrates and is associated with six different vegetation communities at a variety of distances from stream sources (Buchwald 1989). In the two biotopes on the south western range edges, in the pre-alpine region and the Black Forest, it is restricted to very small base rich water bodies, with one particular plant community in each biotope near to spring outlets (Buchwald 1994). These edge-of-range populations occur at higher altitudes that the core populations and their location near to springs may compensate for exposure to relatively cooler temperatures. In Britain, *C. mercuriale* occupies lower altitudes than those populations on the German range edge and thus are less stenotopic with regards to their use of waterbodies (except on heathlands) plant species and communities. It would be interesting to compare the use of slopes of differing aspects across this species' range to look more closely at the interaction between microhabitat use and latitude or altitude.

The selection of thermally advantageous microclimates has limited *C. mercuriale* to an early seral stage of succession. This is true of many other species on their northern range edges. For example, *Plebejus argus* is restricted to sheltered south-facing slopes in Britain and requires early seral stages due to its habit of ovipositing on food plants at the margin between vegetation and bare-ground (Lewis *et al.* 1997). On chalk grassland, females of *Decticus verrucivorus*, found in only four sites in southern England, lays its eggs on exposed short turf or bare ground that will reach high temperatures for embryonic development. Males require taller tussocks 20cm in height for basking and transmission of stridulation (Cherrill & Brown 1990a). Such early seral stages provide particularly unstable habitats (Usher & Jefferson 1991) requiring very active management regimes (such as grazing, burning, cutting, scrub and channel clearance) to prevent extinction of associated species (Warren *et al.* 1984; Samways 1994). The perception of overgrowth of runnels or bankside vegetation as the main threat to British *C. mercuriale* sites illustrates the dynamic nature of *C. mercuriale* habitat and the need for active management to prevent extinction of this species.

Other insects that rely on early seral stages maintained by disturbance are often characterised by relative mobility (Samways 1996), selected for by the relatively rapid decline in habitat suitability in any given habitat patch. For example, *Ischnura pumilio*, a species also restricted to early successional habitats in Britain, is highly mobile and capable of completing its development in one year before succession has proceeded too far (Fox 1994). However, where the rate of fragmentation is high (or extensive) or succession of habitat is rapid, selection of more mobile phenotypes may not occur quickly enough to prevent local population extinction. Mobility of *C. mercuriale* is investigated in Chapter 7 and related to the level of fragmentation and rate of succession of its biotopes. For many invertebrates rotational management on different areas of a site has been adopted since this produces a mosaic of different seral stages (Usher & Jefferson 1991). The timing of the rotation must be appropriate to the life cycle of the species (e.g. Greatorex-Davies *et al.* 1992; Greatorex-Davies *et al.* 1993) and the spatial separation of different areas must allow dispersal between them. The alternative is arresting succession at a particular stage (Usher & Jefferson 1991). Appropriate *measures to achieve this in C. mercuriale sites are discussed in* Chapter 8.

In other thermophilic species that have their northern range margins in Britain, models of the effect of global warming on distribution suggest that small increases in mean temperature may lead to a large increase in microhabitat availability within and across sites (Hill *et al.* 1999; Thomas *et al.* 1999). For *Plebejus argus*, such models predicted an increase in habitat area and connectivity and an increase in the length of time that a seral stage could be occupied with a 2-3°C rise in temperature. Although northward expansions have been described in a range of other odonates including *Ceriagrion tenellum* and *Gomphus pulchellus* (Sternberg *et al.* 1999) such expansion is constrained by fragmentation (Hill *et al.* 1999). In addition, *C. mercuriale* is not only limited by temperature but also by oxygen concentration and water availability. Since the second most significant threat to *C. mercuriale* habitat was found to be reduction in water availability, and rises in temperature would lower water tables, northward expansion may be less likely in this species.

When a species' resource distribution can be mapped explicitly within its biotope, it is possible to model population persistence in relation to patch quantity, patch quality and isolation. The latter is possible, for specialist herbivores such as butterflies (Thomas & Hanski, 1997) or for eurytopic species of odonates where resource distribution can be approximated by the distribution of water bodies within an area. The multidimensionality and complexity of the requirements of *C. mercuriale* precludes this approach given the current state of knowledge. Direct assessment of habitat use by field experiments which allow the construction of resource selection functions (*cf.* Boyce 1999) are required. For odonates, separate such functions may be required for adults and larvae since adult distribution does not always reflect larval habitat use (e.g. Painter 1998).

Chapters 4 and 5 investigate larval growth and development and habitat use at emergence and oviposition to investigate which of the possible ultimate factors (Table 2.16) determine large scale habitat use in this species. Management and monitoring recommendations (including indicators of condition for *C. mercuriale* habitat) arising from this review are described in Chapter 8.

Finally, it is necessary to consider whether the small population sizes seen in *C. mercuriale* in Britain, are low enough to influence long term population persistence and adaptation of this species (*cf* Soule 1987). Small populations not only have a higher probability of complete extinction through random environmental events but are also particularly susceptable to some processes that result in loss of genetic variation. Continuous genetic variation (of the sort influenced by genes at many loci) is central to smooth adaptive responses to environmental change (Brakefield 1991). Random genetic drift, where alleles are lost randomnly from the population over time occurs rapidly in small populations. Inbreeding i.e. frequent mating between related individuals, is also more likely in small populations. Genetic variation can also be reduced by founder events, where a population is founded from a small subset of the parent population (e.g. the *C. mercuriale* population on Aylesbeare Common was founded from less than ten individuals - Kerry 1994)) and by population bottlenecks where, during an environmental change, natural selection focuses on a small subset of characters. Although minimum viable population sizes have not been investigated for *C. mercuriale*, some generalisations can be made on the basis of work on other species. Brakefield (1991) states that a management programme that maintains population sizes in the order of a few hundred individuals is unlikely to be unsuccessful due to a loss of genetic varitaion. Most populations of *C. mercuriale* in Britain probably have population sizes within this order of magnitude. Even if population sizes are lower than this and suffer intermittent short bottlenecks of a few 10s of individuals, genetic variation is likely to influence population persistence less than variation in ecological conditions (Brakefield 1991). Since management directed at minimising ecological extinction already aims to maximise population size, management strategies aimed specifically at the maintenance of genetic diversity are unecessary in most cases.

Chapter 3 Emergence in an edge of range population of *Coenagrion mercuriale* and *Ceriagrion tenellum.*

3.1 Introduction

Since odonates are almost exclusively aquatic in their larval stages, metamorphosis to the adult stage includes a niche shift from the aquatic to the terrestrial habitat (Corbet 1980). When an animal can be sampled as it passes from one part of its habitat to another part at a specific stage in its life history, it is possible to derive useful information about the population entering the next stage (Southwood 1978). In particular, examination of odonates at emergence allows sex ratio, mean body size, numbers and seasonal patterns to be investigated before any bias by dispersal or differential mortality appears (Michiels & Dhondt 1989).

Seasonal regulation is the array of responses by which development is restricted to a particular season (Corbet 1999). In odonates, it is the emergence period, which is restricted to a particular season (Corbet 1954), despite differences in development rate accumulated between individuals in the larval stage. These differences may be due to differential hatch dates (Johnson 1991) or differences in the nutritional condition of the individuals (e.g. Harvey & Corbet 1985). Ultimately, the selective advantages of restriction of emergence probably include; ensuring frequent encounters (and thus matings) with conspecifics; and ensuring maturity is achieved at a time when environmental conditions permit the full range of adult activities (Corbet 1964). Seasonal regulation is achieved in odonates by different diapause characteristics in the larvae, distinct responses to critical day length and temperature thresholds in different instars (Corbet 1957b; Sternberg 1994).

The potential form of the emergence curve and the degree to which emergence is synchronised within the emergence period reflect the mode of seasonal regulation. Here, the actual form of the emergence curve is examined for the first time (in an edge-of-range population) in *C. mercuriale* and related to baseline information on diapause and larval development provided in Chapter 4. In the Eastern united States, Crowley (1982a) found that some odonate species had shorter flight periods at the edge of their ranges than in the centre. Previous studies indicate that there is considerable geographical variation in flight period of *C. mercuriale* described (Table 3.1) and that flight periods in small, edge of range populations seem to be shorter. Given that populations of thermophilic species at northern ranges edges are expected to be strongly restricted by climatic factors (section 1.4), the influence of these factors on the actual form of the emergence curve is investigated.

Table 3.1 Geographical variation in flight period of *C. mercuriale.*

Region	Site name	Core or edge population	Dates of flight season	*Length in days	Year	Source
Britain						
New Forest	Crockford	edge	15th May - 10th August	88	1992	(Jenkins 1995)
Anglesey	Cors Eddreiniog	edge	8th June - 24th July	47	1998	(Colley & Howe 1999)
Devon	Aylesbeare	edge	7th June – 2nd August	53	1998	B.Purse
Europe						
Bavaria		core	early June - mid-August	max 76		(Kuhn 1998)
Alpine and pre-alpine marshes		edge	mid-June - mid August	max 62		(Kuhn 1998)
Mediterranean		core	early April - early November	max 153		(A. Compte-start pers. comm. to Grand, 1996)
Central Europe		core	mid-May – late August	max 109		Robert 1958

*To calculate length of flight period for Europe, 'early' was taken as 1st, 'mid' as 15th, 'late' as 31st.

Certain temperature thresholds for development and the extent of thermic plasticity seem to be species-specific (Sternberg 1994) and may provide a mechanism by which ecologically related species can achieve temporal niche separation. On the Norfolk Broads, Johannsson (1978) found that, where *Ischnura elegans* and *Erythromma najas* co-occurred in the larval stage, differences in development time prevented size overlap between the species at all times but mid-winter and thus achieved temporal niche separation. Restriction of emergence may also permit avoidance of interspecific competition in the adult stage. For example, the flight period of *Aeshna juncea* is up to 16 weeks longer in the Black Forest, since other Aeshnids are rare in such bog habitat. In other parts of it range, where the flight period is shorter, this species often co-exists with a range of Anisopterans (Sternberg 1994 and refs. therein). The form of the emergence curve of *Ceriagrion tenellum* (hereafter referred to as *C. tenellum*), a species that co-exists on site with *C. mercuriale* is examined. *C. tenellum* is listed as scarce on the UK red list and has a southwestern distribution in Europe where it is widespread (Winsland 1997).

The significance of developmental polymorphism in conservation biology has been discussed (section 1.6). The survival of a species depends on the maximal or optimal survival of all developmental stages (Samways 1994). For rare odonates, survival through emergence is particularly worthy of investigation since it has been suggested that this may be a period of substantial mortality (Crowley *et al.* 1987). This is expected of a life-history stage that is concentrated in space and time (Corbet 1962) and in which individuals are immobile and defenceless. Possible mortality factors at emergence include competition for perches, predation (e.g. *Pyrrhosoma nymphula* - Bennett 1993) and desiccation or deformation. In *Onychogomphus uncatus*, this is caused by heavy wind during hardening of the new cuticle (Jakob & Suhling 1999). Within a few hours tenerals (newly emerged individuals) leave the water area and some days (the pre-reproductive period) are required to attain sexual maturity (Corbet 1980). It is useful to estimate the duration of the latter to interpret the dynamics of adult populations (Corbet 1999). The time required for maturation will depend on food availability and external weather conditions (Corbet 1999) and is often longer in females than males if the former require relatively more food for provisioning of eggs (Anholt *et al.* 1991).

Operational sex ratios can determine which sex will compete for mates and the intensity of sexual competition (Kvarnemo & Ahnesjo 1996). Biases often exist in these ratios in diploid insect populations and there is controversy over whether these are real or an artefact of sex biases in behaviour or recapture probability (Stoks 2001a). The sex-determination mechanism in odonates predicts a sex ratio of unity in the zygote (Kiauta 1969) so sex ratio imbalances in the mature adult stage can be attributed to differential mortality in a preceding developmental stage. Suggested mechanisms include size-selective predation on larger female larvae, sex differences in maturation time (producing temporarily biased sex ratios), mortality during and after maturation (Lawton 1972; Corbet & Hoess 1998; Stoks 2001b). This study examines sex ratio at emergence in *C. mercuriale* whilst subsequent chapters report sex ratios in the larval and mature adult stage and investigate sex biases in survival. This should facilitate determination of the life stage at which a sex bias in operational sex ratio could arise and permit speculation on the mechanisms that produce such a bias.

In this study, daily collections of a standard proportion of the emerging adult population of *C. mercuriale* and *C. tenellum* were made, using emergence cages, at a site on which the two species co-occur in high densities. This is the first study in which cages have been used to provide quantitative information on emergence. Both the seasonal pattern of emergence (the emergence curve) and the daily variation in emergence were quantified and interpreted in light of information on diapause in both species and in comparison with the patterns found in core European populations.

For *C. mercuriale*, the rarer species, mortality at emergence was quantified and mark-recapture techniques were used to investigate the length of the immature period and to infer survival through the pre- and post-reproductive period. These are discussed in accordance with information available from studies of other, less threatened odonates and also from core European populations of *C. mercuriale*.

3.2 Materials and Methods

3.2.1 Study site

Populations of *C. mercuriale* and *C. tenellum* were sampled daily from 26th May 1999 to 2nd August 1999 at Upper Crockford, Beaulieu Heath, New Forest, Hampshire (SU350990 - Fig. 3.1a). Fig. 3.1b shows that this stretch is almost entirely valley mire with some areas of wet heath at the top and the bottom of the site. The habitat surrounding the mire is a mainly humid heath but with dry heath, humic acid grassland, gorse and bracken further from the stream. The mire itself is as a subtle transition between national vegetation communities of M29, M1, M21 and M16. For the purposes of this study, the following subhabitats were recognised as shown on Fig. 3.1c; humid heath (tall tussocks), humid heath (low tussocks), low mire/sphagnum runnels and stream. An area of burnt heath, areas of scrub and well-vegetated stream areas (suitable for emergence) are also marked on Fig. 3.1c. The stream section ranged from 5 to 20m in width and 0.05 to 1m in depth. The extent of the stream reduced considerably during the flying season by up to 5m from each bank in places.

3.2.2 Design and use of emergence cages - seasonal pattern and daily variation in emergence

Three main methods have been used previously to study emergence in odonates; collection of exuviae from emergent vegetation (e.g. Lawton 1970b; Banks & Thompson 1985a; Gribbin & Thompson 1990b; Gribbin & Thompson 1991); provision of artificial substrates as supports for emerging adults (Ingram & Jenner 1976; Bennett & Mill 1993); collection of emerging adults from emergence cages placed over emergent vegetation (Macan 1949; Gower & Kormondy 1963). Due to the habitat occupied by *C. mercuriale*, only emergence cages could have provided quantitative information on emergence in this species.

The streams occupied by *C. mercuriale*, are shallow and narrow and have short, dense tussocky vegetation interspersed with more open areas. This made exuviae difficult to find (e.g. *Pyrrhosoma nymphula* Bennett & Mill 1993). Artificial substrates in the form of screens were unsuccessful in a pilot study since they did not resemble natural emergence supports (species such as *Juncus articulatus*, *Myrica gale* and *Eleocharis palustris*) to a sufficient degree. The screens (made of plastic greenhouse shading (50cm deep with a mesh size of 0.75cm) attached to bamboo supports) were positioned on site and checked daily for the first two weeks of the study. In this time only one individual was observed to use them as an emergence perch.

Since both *C. mercuriale* and *C. tenellum* make extensive use of short emergent vegetation and because the streams were small, cages could be used to enclose a standard area of emergence habitat. Thus, in contrast to previous studies (Macan 1949; Macan 1964; Bennett & Mill 1993), a standard proportion of the emerging population could be collected daily, and the sex and fate (e.g. cause of mortality) weight and size of each individual could be recorded.

4

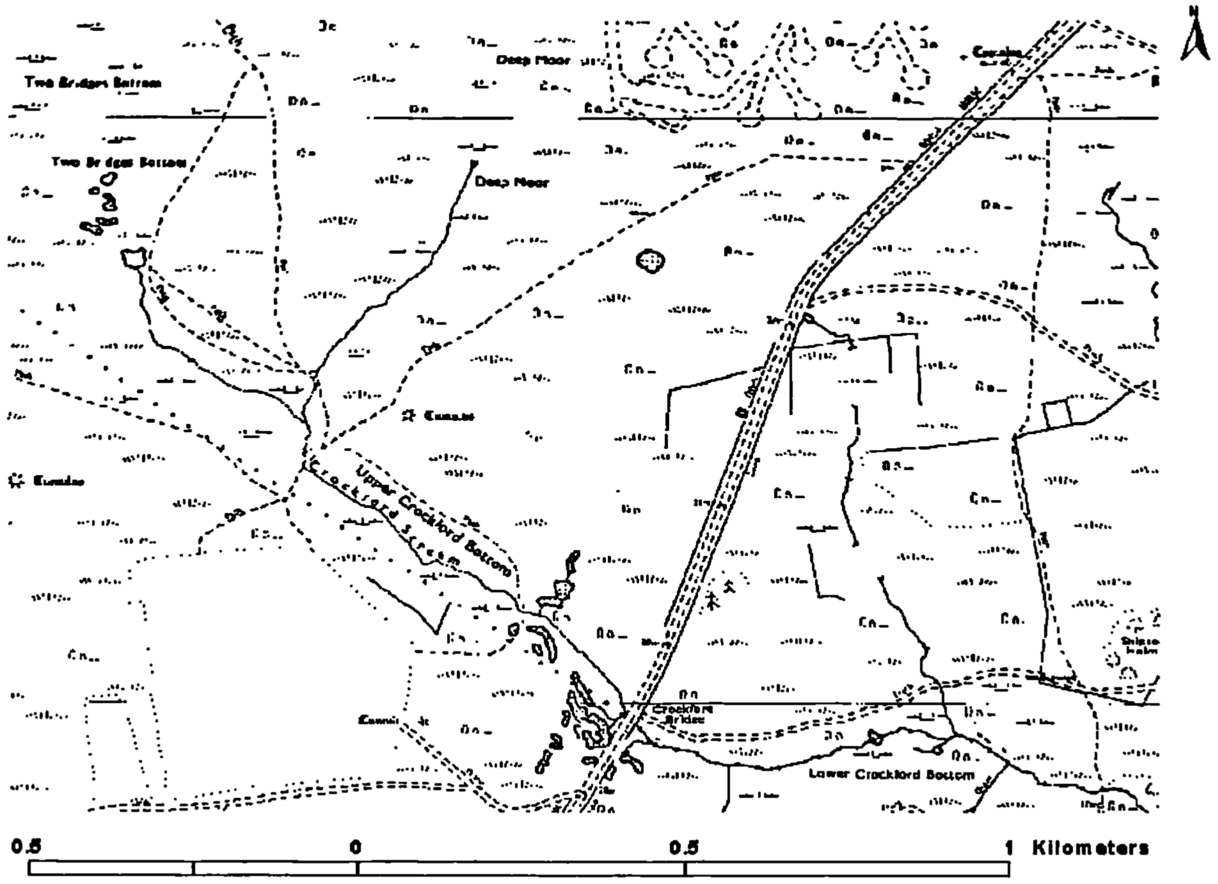


Fig. 3.1a Location of 250m study stream section at Upper Crockford (limits marked by lines perpendicular to stream)

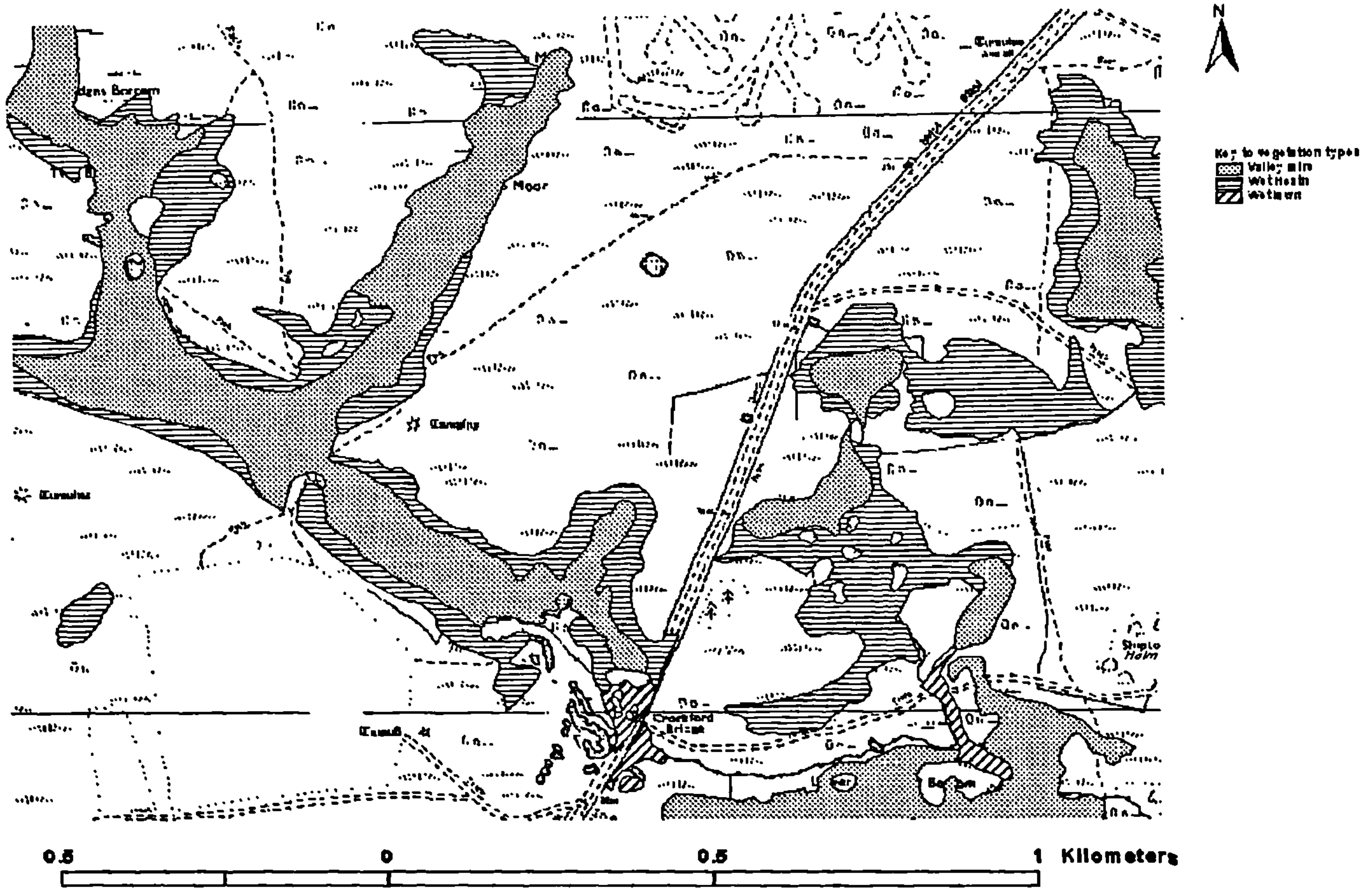


Fig. 3.1b Habitat types surrounding the stream at Upper Crockford (Clarke & Westerhoff 1988 – New Forest Vegetation Map)

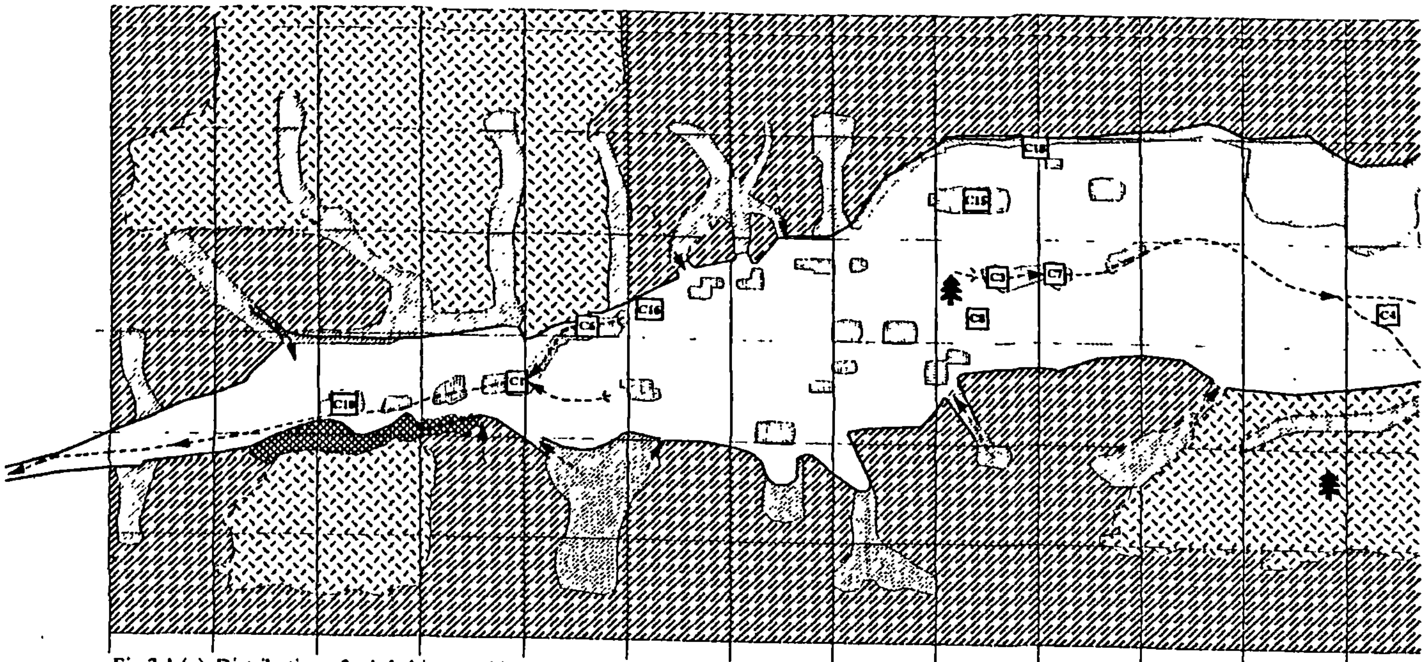


Fig 3.1 (c) Distribution of sub-habitats and location of emergence cages at Upper Crockford. Grid shown is 10m x 10m, arrows indicate direction of stream flow.

[ ] stream
▨ scrub
▨ tall wet heath tussocks
▨ isolated trees
▨ emergence habitat
▨ mire / sphagnum runnel
▨ low wet heath tussocks

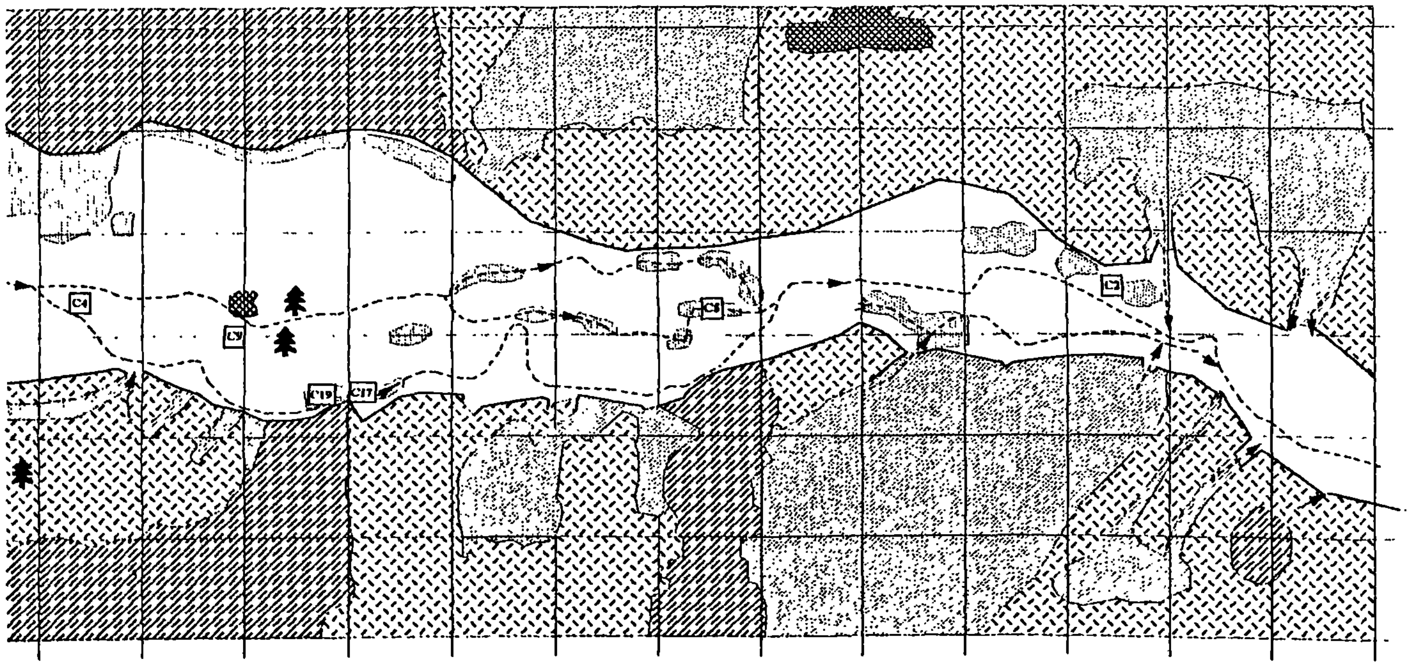


Fig 3.1 (c) continued.

The distribution of cages is shown in Fig. 3.1c. In order to elucidate the actual from of the emergence curve accurately, it was necessary to obtain a large number of emerging individuals each day. In light of this, all cages were placed in similar habitat, habitat that was presumed to be suitable for emergence (i.e. areas which were open, shallow, unshaded, with at least 50% cover of submerged aquatic vegetation and upright emergent vegetation for emergence perches). Thus no attempt was made to quantify the suitability of different habitat types for emergence.

Ten cages (1-10) were put in place on 26th May and another 5 (11-15) were put in place on 9th June when screens had proved ineffective in a pilot study. Each cage covered an area of 0.72m^2 (Fig.3.2) stream and consisted of a light, A-frame clotheshorse covered by transparent, fine mesh netting. It was permanently anchored to the stream substrate. Access was gained to the interior of the cage (while it was fixed in position) via a netting sleeve on one seam. The cages were checked daily for newly emerged individuals in the afternoon since most emergence occurred in the morning. Daily checks minimised loss of individuals due to predatory invertebrates that also emerged in the cages. Cages were checked until 9th August.

'Teneral' refers to the condition of an adult for a short period, fewer than 24 hours after emergence, when the body is soft and the wings are shiny. These will subsequently be referred to as teneral adults whilst sexually mature adults will be referred to as mature adults. For *C. mercuriale*, tenerals were removed, transferred to gauze-covered, plastic pots and retained overnight to allow them to harden. To measure body size, left forewing length was measured (cf. Fincke 1982; Banks & Thompson 1985a) ± 0.01mm using dial callipers and body weight was measured ± 0.1mg using a 50mg torsion balance. Each teneral was given a unique mark consisting of a combination of a dot of Tippex on the thorax and a felt tip pen number on the left forewing. They were released the next morning outside the cage in which they had been caught to avoid artificially increasing the density of individuals at one position on site. Due to time constraints, tenerals of *C. tenellum* were not retained, marked or measured but were sexed and then released onto surrounding vegetation. Exuviae of both species were removed and retained in 70% alcohol. Measurements of daily weather conditions were obtained for Everton Meteorological Station (SZ302937) from the British Atmospheric Data Centre. The station is 7km away from Upper Crockford.

The synchrony of emergence was measured by calculating EM$_{50}$ i.e. the time (expressed as days elapsed since emergence began) by which 50% of the annual population has emerged (Taketo 1960). In order to investigate the daily variation in numbers emerging it is necessary to test if individuals were randomly dispersed between days. Calculating a dispersion index as follows tests this:

$$I^D = \frac{s^2(n-1)}{\textit{sample mean}}$$

where n is the number of samples, I^D is approximately distributed as χ^2 with n-1 degrees of freedom (Southwood 1978) . If the distribution is in fact Poisson, the value of I^D will not lie outside the limits (taken as 0.95 and 0.05) of χ^2 for n-1 d.f. as given in standard tables. The same index of dispersion was used to examine whether individuals were randomly distributed between cages.

3.2.3 Mark-release-recapture protocol - estimates of pre- and post- reproductive survival and the length of the immature period

A 10m by 10m grid was marked onto the study site (Fig. 3.1c). A mark-recapture exercise was carried out every day by searching the grid squares within 20m of the baseline for adults. This area includes roosting areas of humid heath vegetation thus reducing the potential bias resulting from sex or age differences in habitat use (Fincke 1986)). The identity and state of maturity of adults (marked as teneral adults or mature adults) were noted to provide information on the length of the pre-reproductive adult period, and to allow survival during this period to be compared to post-reproductive adult survival. Lifespan was estimated as the interval between the first and last recapture of an individual. Since this quantity was influenced by capture intensity and made no distinction between mortality and emigration, lifespan represents the number of days present in the field rather than number of days alive (Michiels & Dhondt 1989). Comparison of lifespans between groups was performed using exact two-sample Komolgorov-Smirnov tests due to either small or unbalanced samples (Sokal & Rohlf 1995). Throughout this thesis, sample means are indicated by the symbol μ and are given ± the standard error (s.e.).

3.3 Results

3.3.1 Seasonal pattern, sex ratio and body size at emergence

Since sampling effort was not uniform across cages, the cages and days from which data were derived are specified. Figs. 3.3-3.8 show data for cages 1-10 (abbreviated to C1-10 hereafter) from 26th May-2nd August 1999.

The total number of *C. mercuriale* and *C. tenellum* emerging on each day throughout the season (C1-10) are shown in Figs. 3.2 and 3.3 respectively. The duration of emergence was 60 days for male *C. mercuriale* (day 1-60) and 63 days for female *C. mercuriale* (day 1-64). EM_{50} for *C. mercuriale* was day 22. The day of peak emergence was day 23 i.e. 15th June.The duration of emergence in *C. tenellum* was shorter than that of *C. mercuriale* at around 50 days. It started to emerge on day 20 (12th June) and finished on day 67 (29th July) although it is possible that a few individuals may have emerged after the end of the observation period. EM_{50} for *C. tenellum* was 30 (day 50). Day 50 and 56 (12th and 18th July) were days of peak emergence. The shape of their emergence curves (two-sample K-S, z=7.908, p<0.001 see Fig. 3.4) and the median day of emergence differs significantly between the two species (Wilcoxon two-sample test, W=143998.5, p<0.001). Males and females were combined for each species in this analysis.

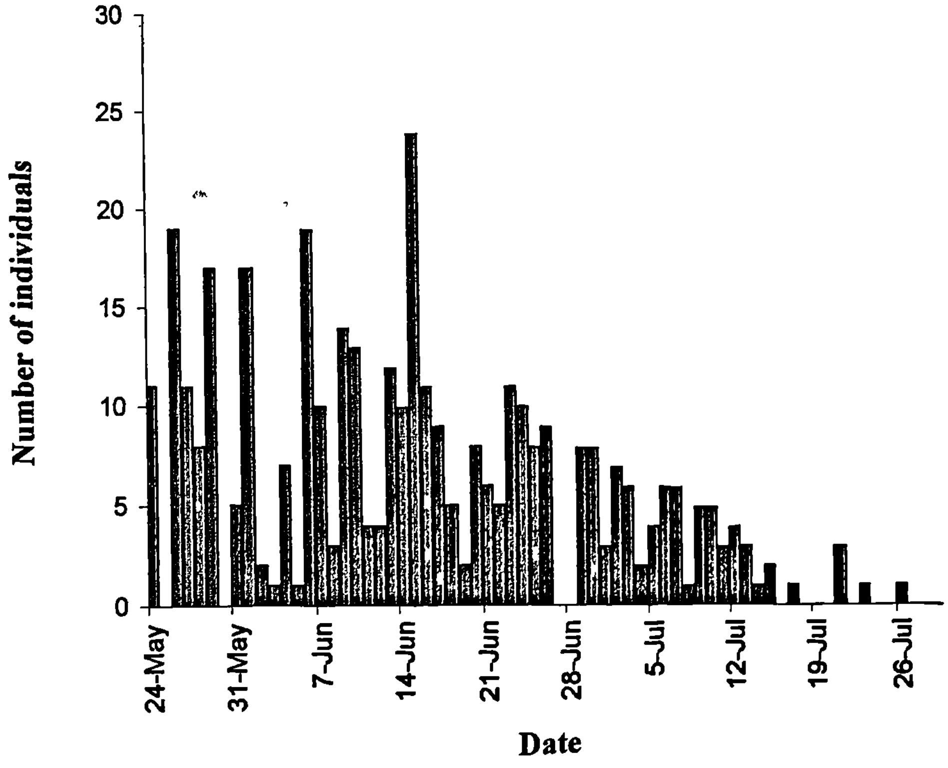


Fig. 3.2 Daily emergence of *C. mercuriale*.

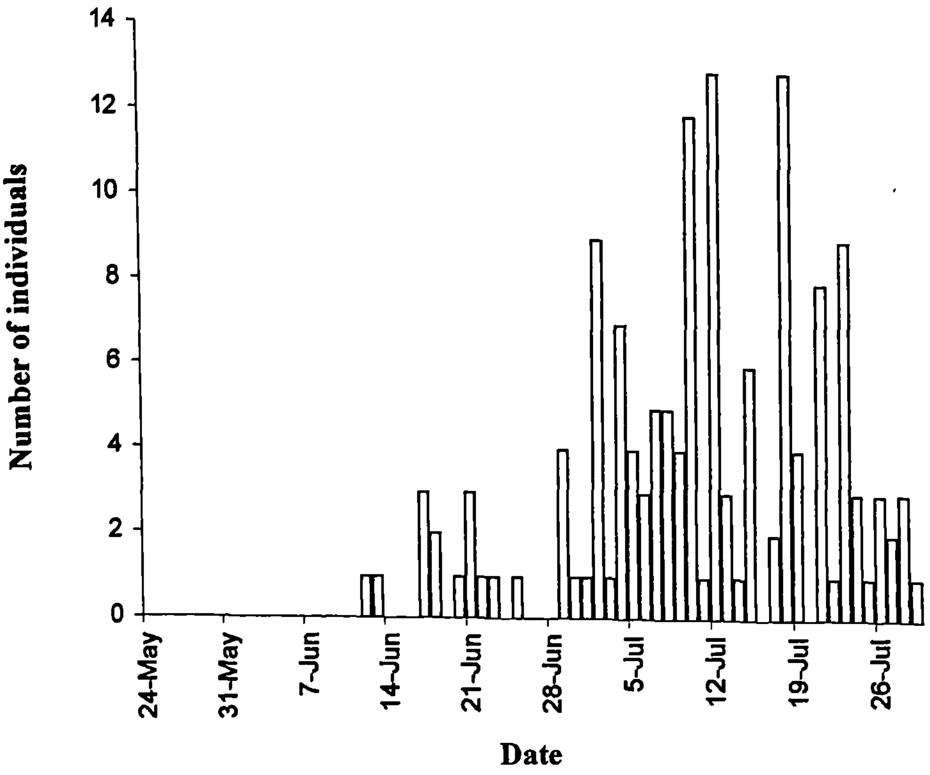


Fig. 3.3 Daily emergence of *C. tenellum*.

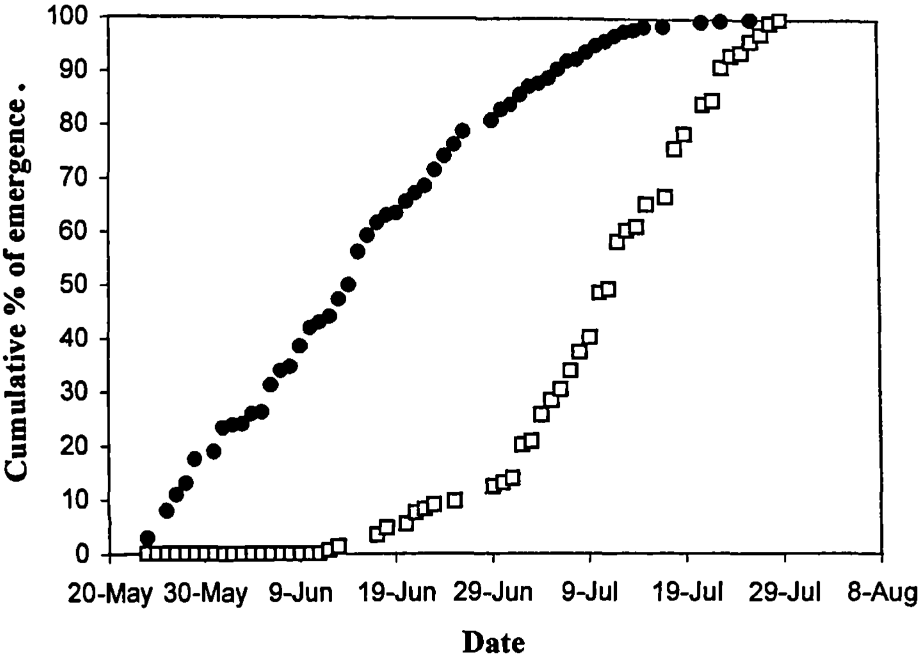


Fig. 3.4 Cumulative percentage of *C. mercuriale* (closed circles) and *C. tenellum* (open squares) emerging each day (C1-10).

The degree of slope of the cumulative percentage emergence curves reflects the rate at which individuals emerge into the population. For *C. mercuriale*, individuals emerged into the population at a high rate from the beginning of its emergence such that 79% of the population emerges in 34 days (by 26th June). The rate of emergence then slowed down. In contrast, for *C. tenellum*, individuals emerged slowly for the first 10 days (with only 10% of the population emerging by 25th June). The rate of emergence then increased to a similar level (indicated by the similarity in slopes of cumulative emergence curves) to the initial rate in the *C. mercuriale* population.

The total sex-ratio of males:females of *C. mercuriale* emerging throughout the season (C1-15), at 1.35 (293:217), was significantly different from 1:1 (χ^2=11.33, 1 *d.f.*, p<0.005). The total sex ratio of males:females of *C. tenellum* emerging throughout the season, at 1.04 (119:115), was not significantly different from 1:1 (χ^2=0.02, 1 *d.f.*, p=0.90). Appendix 3 shows the sex ratio in each emergence cage.

Figs. 3.5 and 3.6 show cumulative percentage emergence curves for males and females of *C. mercuriale* and *C. tenellum* respectively. Median day of emergence (Table 3.2) does not differ between the two sexes for *C. mercuriale* (Wilcoxon two-sample test, W=74443.0, p=0.8) or *C. tenellum* (Wilcoxon two-sample test, W=14214.5, p=0.653). The shape of the emergence curve does not differ between males and females for *C. mercuriale* (two-sample K-S, Z=1.034, p=0.235, n_1=293, n_2=217) or *C. tenellum* (two-sample K-S, Z=0.544, p=0.928, n_1=119, n_2=115). There was no correlation between sex ratio and emergence date (Fig. 3.7-3.8) for either species (Spearman's rank correlations; *C. mercuriale:* n=41, r_s=-0.124, p=0.440; *C. tenellum*; n=32, r_s=0.287, p=0.112). This is in accordance with the absence of any difference in emergence pattern between males and females.

Table 3.2 Median day of emergence for each sex for *C. mercuriale* and *C. tenellum*

	Male		Female		Total	
Species	*n*	Median	*n*	Median	*n*	Median
C. mercuriale	293	Day 23	217	Day 24	510	Day 23
C. tenellum	119	Day 47	115	Day 48	234	Day 47.5

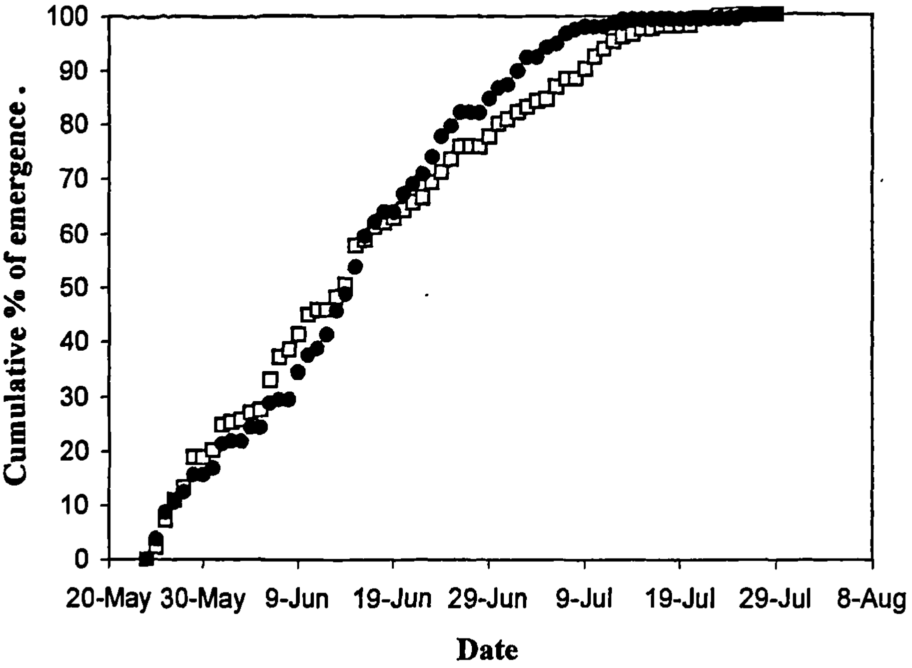


Fig. 3.5 Cumulative percentage of males (open squares) and females (closed circles) of *C. mercuriale* emerging each day (cages 1-10).

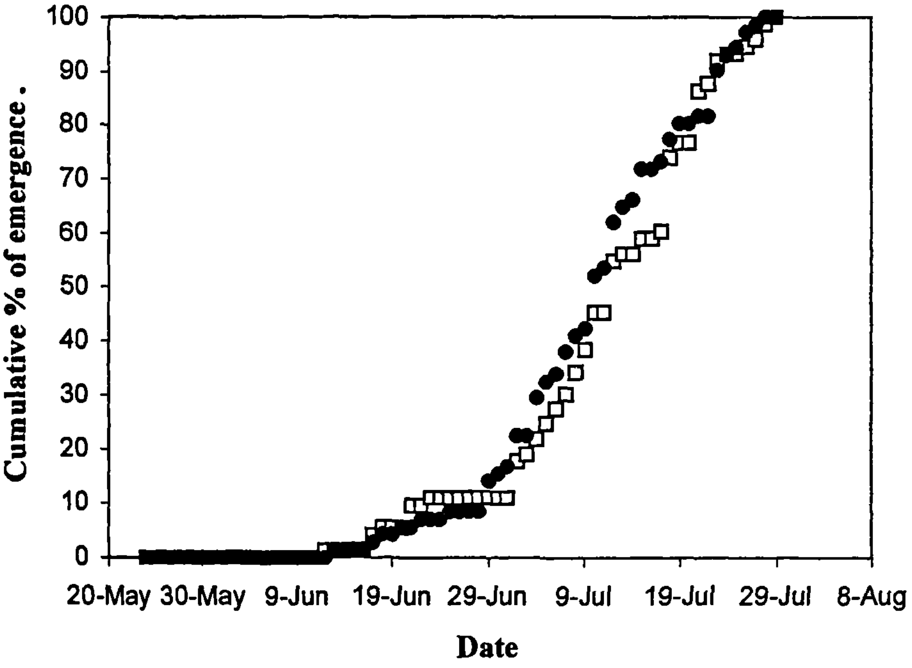


Fig. 3.6 Cumulative percentage of males (open squares) and females (closed circles) of *C. tenellum* emerging each day (cages 1-10).

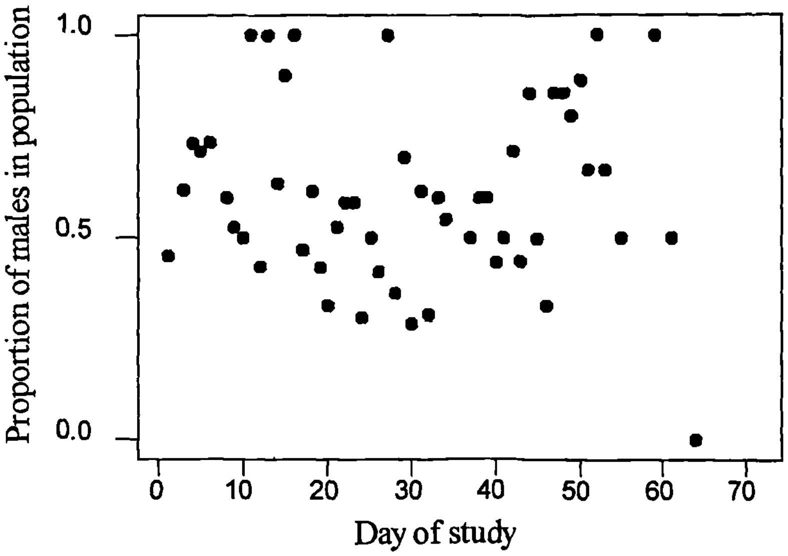


Fig. 3.7 Proportion of males in the emerging population of *C. mercuriale* on each day of study (day1=24th May).

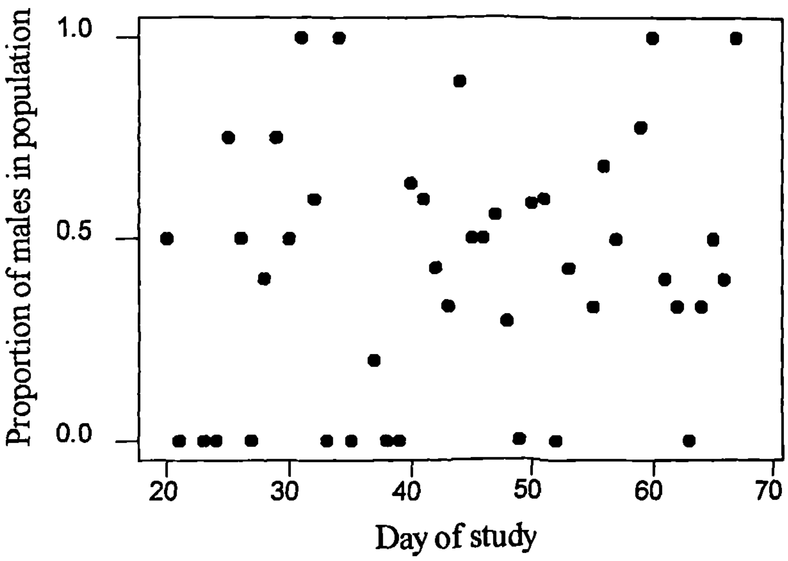


Fig. 3.8 Proportion of males in the emerging population of *C. tenellum* on each day of study (day1=24th May).

3.3.2 Body size at emergence in *C. mercuriale*

Left forewing length and body weight were log transformed to normalise the distribution of their variances. There was a highly significant correlation between body size (length of left forewing) and fresh body weight at emergence in males (Pearson's correlations on log-transformed data; r_p=0.640 p<0.001, n=161,) and females (r_p=0.654, p<0.001, n= 132) (Table 3.3 and Figs. 3.9-3.10).

Table 3.3 Mean left forewing length and fresh body weight for teneral adults of *C. mercuriale.*

Variable		Teneral		Mature	
		n	$\mu \pm s.e.$	*n*	$\mu \pm s.e.$
Left forewing length (mm)	Male	262	16.51±0.04	2135	16.50±0.02
	Female	200	18.16±0.05	345	18.15±0.04
Fresh body weight (mg)	Male	167	21.59±0.24	-	-
	Female	137	26.41±0.38	-	-

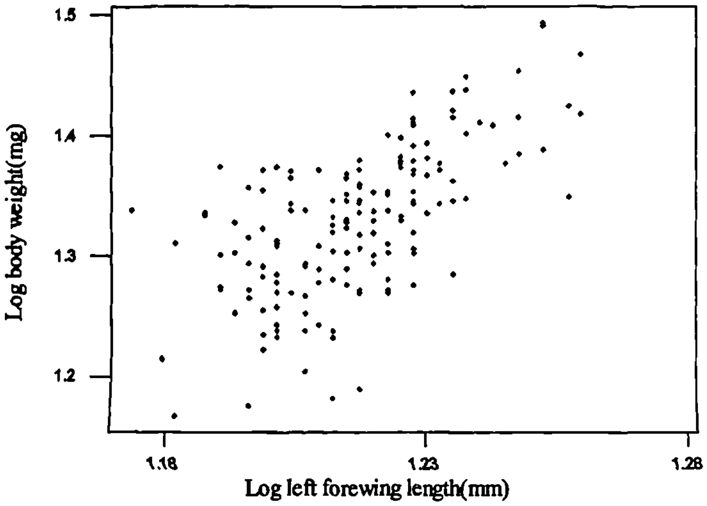


Fig. 3.9 Relationship between body weight and body size for males (log-transformed data).

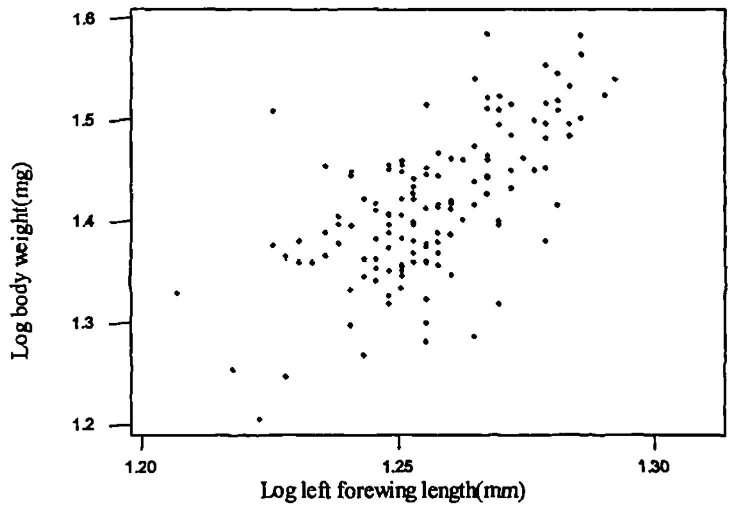


Fig. 3.10 Relationship between body weight and body size for females (log-transformed data).

Given this relationship, left forewing length was chosen to investigate the difference in body size between males and females and whether there is a significant decrease in body size through the season (Fig. 3.11 - tenerals; Fig. 3.12 – adults). Mean body size (log-transformed) was compared between male and female tenerals (sex) using an analysis of covariance (ancova) with day of emergence (day) as a covariate. Table 3.4a shows that there was a significant interaction between sex and day of emergence in their effect on body size at emergence. Therefore mean body size differed between males and females (females being larger) and decreased with time (date of emergence). The degree to which body size decreased with time depends on sex. However, the negative relationship between body size and time is weak for both males (Spearman's rank correlation r_s=-0.143, p=0.021, n=262) and females (Spearman's rank correlation r_s=-0.303, p<0.001, n=200).

For adults, mean body size differed between males and females (females being larger) and body size decreased with time (date of 1st capture – Fig. 3.12) (Table 3.4b). There was no significant interaction between sex and day of emergence in their effect on body size.

Table 3.4a Ancova table comparing body size of male and female tenerals.

Source	d.f.	*F*-ratio	*p*	
Model	3	261.08	< 0.001	R^2=0.631
Intercept	1	904232.86	< 0.001	
Sex*Day	1	10.11	0.002	
Sex	1	299.68	< 0.001	
Day	1	25.52	< 0.001	

Table 3.4b Ancova comparing body size of male and female mature adults.

Source	d.f.	*F*-ratio	*p*
Model	2	793.95	< 0.001
Intercept	1	2375733.8	< 0.001
Sex	1	1519.25	< 0.001
Day	1	156.31	< 0.001

R^2=0.391

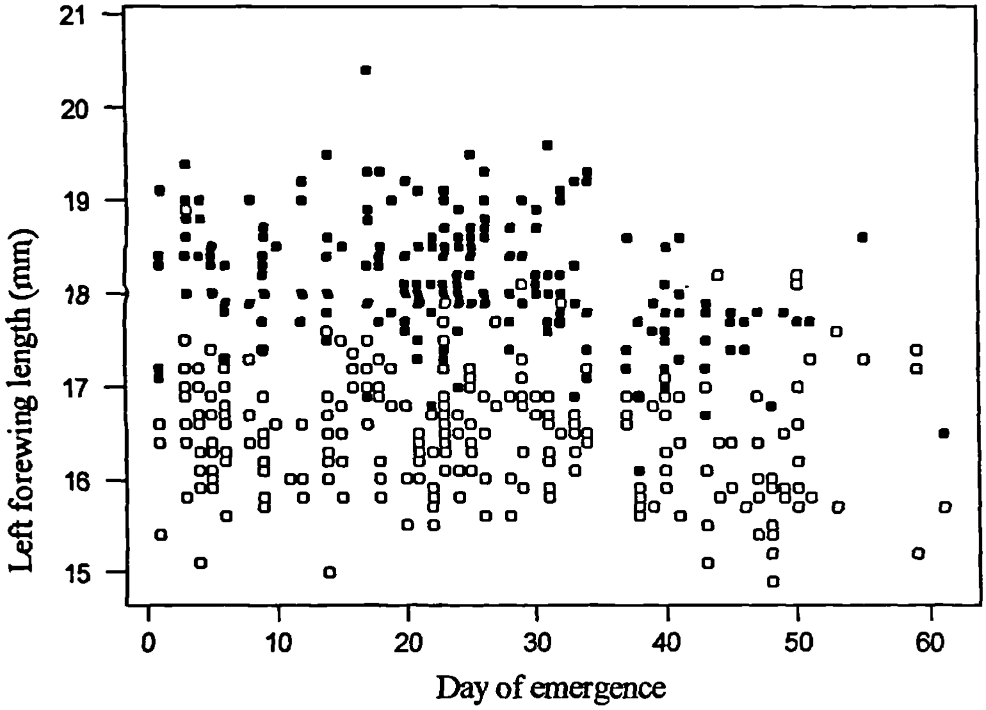


Fig. 3.11 Relationship between body size and day of emergence for male (open circles) and female tenerals (closed circles).

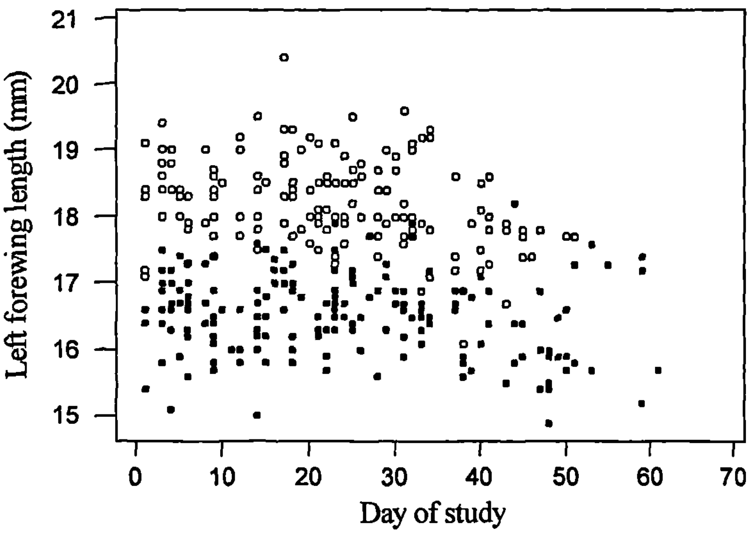


Fig. 3.12 Relationship between body size and day of emergence for male (closed circles) and female adults (open circles) from cages 1-10.

3.3.3 Daily variation in numbers emerging

To investigate whether emerging individuals are distributed at random through time, the index of dispersion was calculated using the total number of individuals emerging each day (cages 1-15 between 9th June and 2nd August). For both species, I^D was well above the critical value of $\chi^2_{0.05}$ and the variance:mean ratios were larger than one (Table 3.5). Therefore, the emerging individuals of *C. mercuriale* and *C. tenellum* were not distributed at random between days and it is necessary to investigate factors affecting daily emergence (using cages 1-15 between 9th June and 2nd August). Weather data from Everton climate station was used to generate the following normal weather variables for each day (Table 3.6).

Table 3.5 Index of dispersion for total number of *C. mercuriale* and *C. tenellum* on each day.

	C. mercuriale	*C. tenellum*
Mean no. emerged each day	6.42	4.98
Variance	44.21	24.52
Variance:mean ratio	6.88	4.93
n-1	54	46
I^D	371.95	226.55
Critical value of $\chi^2_{0.05,n-1}$	84.50	75.70

Table 3.6 Definition of weather variables

Weather variable	Definition

Sun	Sunshine duration in 24 hours units: 0.1 hours
Log rain	Log$_{10}$(Precipitation amount over 24 hours units: 0.1mm)
Temperature at 9am	Temperature at 9am over 24 hours units: 0.1 °C
Minimum Temperature	Minimum temperature over 24 hours units: 0.1 °C
Maximum Temperature	Maximum temperature over 24 hours units: 0.1 °C
Sun Prev	Sunshine duration in previous 24 hours units: 0.1 hours
Log rain Prev	Log$_{10}$(Precipitation amount over previous 24 hours units: 0.1mm)
Temperature at 9am Prev	Temperature at 9am in previous 24 hours units: 0.1 °C
Minimum Temperature Prev	Minimum temperature in previous 24 hours units: 0.1 °C
Maximum Temperature Prev	Minimum temperature in previous 24 hours units: 0.1 °C

To look at the effect of weather variables on daily emergence whilst controlling for season, residual numbers of *C. mercuriale* emerging each day were obtained from a regression of numbers emerging on day of season (Fig. 3.13). Since, weather variables were likely to show multicolinearity, the residuals were regressed against the eight weather variables using a forward stepwise regression procedure. The criterion for addition of a variable to the model was that the probability of the F-statistic was less than 0.05, whilst the criterion for removal of a variable was that the probability of the F-statistic was more than 0.10. Sun Prev i.e. the duration of sunlight in the previous 24 hours, showed a significant positive relationship with residual daily emergence of *C. mercuriale* (Table 3.7). The number of emerging *C. mercuriale* was then regressed against Day of emergence and Sun Prev (using an 'enter' multiple regression where all variables are forced into the model rather than a stepwise model) (Table 3.8). The regression model accounts for 64.3% of the variation in daily emergence suggesting that both amount of sunlight and day of season were important in determining emergence in *C. mercuriale*. The same analysis was not performed on *C. tenellum* since numbers emerging could not be normalised by any transformation.

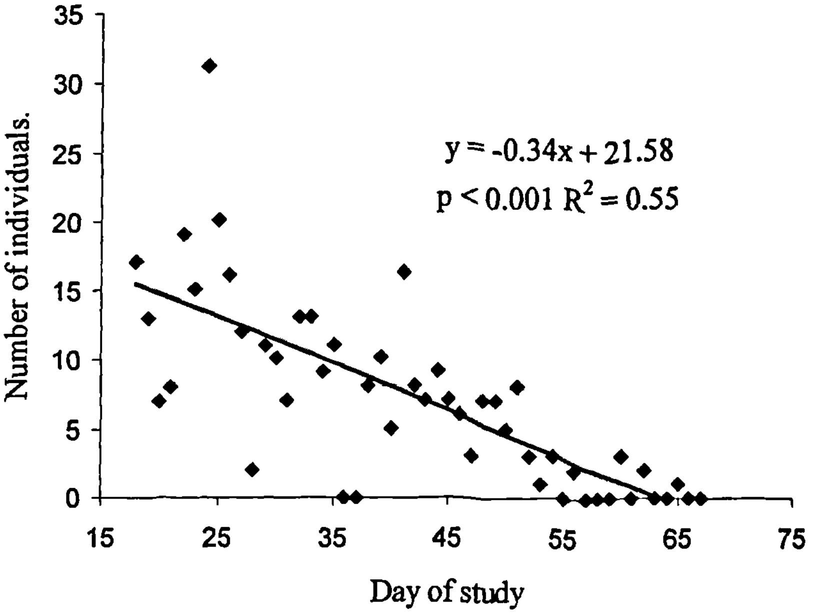


Fig. 3.13 Regression of number of individuals emerging on day of study for *C. mercuriale.*

Table 3.7 Stepwise regression model for variation in residual daily emergence in *C. mercuriale.*

Model	d.f.	Mean square	F	p
Regression	1	240.113	11.837	0.002
Residual	34	20.285		
Total	35			
$R^2 = 0.258$				
Coefficients	β	se	T	p
Constant	-4.917	1.632	-3.012	0.005
SunPrev	0.0651	0.019	3.440	0.002

Table 3.8 'Enter' multiple regression model for variation in daily emergence in *C. mercuriale.*

Model	d.f.	Mean square	F	p
Regression	2	696.80	42.263	< 0.001
Residual	47	16.49		
Total	49			
$R^2 = 0.643$				
Coefficients	β	se	T	p
Constant	18.755	1.975	9.495	< 0.001
Day	-0.358	0.040	-8.921	< 0.001
SunPrev	0.0451	0.013	3.350	0.002

3.3.4 Mortality and deformity at emergence in *C. mercuriale*

The numbers of emerging *C. mercuriale* affected by different causes of mortality are shown in Table 3.9. Individuals dying in the pot whilst hardening were omitted since this does not strictly constitute a death at emergence. There was no difference between the proportion of males and females affected by deformity (χ^2=0.08, 1 *d.f.*, *p*=0.78 (Yates correction)) or death at emergence (χ^2=0.005, 1 *d.f.*, *p*=0.943(Yates correction)).

Table 3.9 Mortality at emergence in *C. mercuriale.*

Cause of death	Number of individuals affected (% given in brackets)		
	Males *n*=293	Females *n*=217	Total *n*=510
Abdomen curved/crumpled	1	0	1
Wings crumpled	2	0	2
Unspecified deformity	0	1	1
Predation on perch by spider	1	2	3
Fallen into water	1	0	1
Total	5 (1.7)	3 (1.4)	8 (1.6)

Table 3.10 Deformity at emergence in *C. mercuriale*

Type of deformity	Number of individuals affected (% given in brackets)		
	Males *n*=293	Females *n*=217	Total *n*=510
Abdomen curved/bent	5*	2	7 (1.37)
Wings crumpled	6	5**	11(2.16)
Exuviae still attached i.e. Incomplete ecdysis	0	2	2 (0.39)
Unknown/unrecorded	1	1 *	1(0.20)
Total	12 (4.09)	10 (4.61)	22 (4.31)

'*'indicates at death at emergence from a particular type of deformity.

The number of emerging *C. mercuriale* affected by different types of deformity are shown in Table 3.9. The most common forms of deformity were bent abdomens and crumpled wings. Out of 2694 adults marked on the site only 2 individuals were recorded as having crumpled abdomens and only 5 were recorded as having incompletely expanded wings. The proportion of deformed individuals in the teneral adult population was significantly larger than the proportion of individuals in the mature adult population (χ^2=74.032, 1 d.f, $p < 0.001$ (Yates correction)). This may indicate that deformed individuals are unlikely to survive to sexual maturity although it is difficult to tell when the proportions being compared are low. If so, the 18 individuals that were deformed but did not die at emergence probably died soon afterwards, increasing the percentage mortality at emergence to 5.1% (26/510). Thus mortality probably has a negligible effect on population density or dynamics.

3.3.5 Probability of recapture, longevity and maturation period in *C mercuriale*

Mature males had a significantly higher recapture proportion (Table 3.11) than mature females (χ^2=40.21, *d.f.*=1, *p* <0.001 (Yates correction)) whilst teneral males and females did not differ in recapture proportion (χ^2=2.38, *d.f.*=1, *p*= 0.123 (Yates correction)). Mature adults were more likely to be recaptured than teneral adults for both males (χ^2=72.71, *d.f.*=1, *p*<0.001) and females (χ^2=20.09, *d.f.*=1, *p*<0.001). Left forewing length did not differ between recaptured (R) and non-recaptured (NR) individuals for mature males, mature females or teneral females (Table 3.11). For teneral males, individuals that were recaptured were larger than those that were not recaptured (Table 3.11). Appendix 4 shows the frequency of individuals recaptured on 0-6 occasions.

Table 3.11 Mann Whitney U-tests to compare left forewing length of recaptured($_{\mathrm{R}}$) and non-recaptured ($_{\mathrm{NR}}$) individuals of *C. mercuriale.*

Age/sex category	n_R	n_{NR}	Recapture proportion	Median$_{\mathrm{R}}$ forewing length	Median$_{\mathrm{NR}}$ forewing length	U	*p*
Mature males	670	1463	0.31	16.5	16.5	483147.50	0.598
Mature females	53	292	0.15	18.1	18.2	1554063.5	0.803
Teneral Males	16	246	0.06	16.9	16.5	1192.0	0.008*
Teneral Females	6	194	0.03	17.8	18.1	408.0	0.212

Lifespan did not differ between sexes (tenerals - exact Komolgorov-Smirnov; Z=0.908, *p*=0.202; mature adults - exact Komolgorov-Smirnov; *Z*=0.635, p=0.558 – Table 3.12). Lifespan of mature adults versus tenerals differed for females (exact Komolgorov-Smirnov; *Z*=1.261, *p*=0.026 – Table 3.12) but not for males (exact Komolgorov-Smirnov; *Z*=0.841, *p*=0.281). However, this difference arose probably because only very long-lived teneral females were likely to be recaptured as adults.

Table 3.12 Mean and median lifespan for *C. mercuriale.*

Age Category	Tenerals			Adults		
	$\mu \pm s.e.$.	*n*	Median	$\mu \pm s.e.$.	*n*	Median
Males	8.18 ± 2.28	18	4	6.15 ± 0.26	1316	4
Females	14.83 ± 5.04	6	12.50	6.77 ± 1.16	56	3.50

Since a low proportion of tenerals was recaptured and they were not always recaptured on the first day of maturity, it is impossible to estimate maturation time precisely from these data. However it is possible to state the minimum time in which maturation could occur. Appendix 5 shows the state of maturity of each individual on each recapture. Individuals re-caught on the 1st - 3rd day after their first recapture were all immature. One individual caught on its 4th day was mature, one was immature and for one the state of maturity could not be determined. All individuals caught on their 5th or 8th day (or afterwards) were mature. From these data, it is possible to infer that the minimum time required for maturation after emergence in this species is between 5 and 8 days.

3.4 Discussion

The results presented here form a detailed description of emergence in *C. mercuriale* at Upper Crockford, an edge-of-range population. The subsequent discussion compares these emergence characteristics with those of core European populations of *C. mercuriale* and those of other odonates. Seasonal regulation in *C. mercuriale* is discussed in light of information on growth and diapause in the larval stage (Chapter 4).

3.4.1 Seasonal pattern, sex ratio and body size at emergence

Patterns of voltinism and diapause often correlate with other life history traits in insects with complex life cycles (Tauber *et al.* 1986). This phenomenon has been noted for odonates. Corbet(1954) distinguished between populations that overwinter (and diapause) in the final instar and have a closely synchronised and often early emergence ('spring' species) and those that overwinter in one or more earlier stadia, have less synchronised emergence and emerge later ('summer species'). Both *C. mercuriale* and *C. tenellum* show a non-synchronous emergence pattern, typical of 'summer' species (sensu Corbet 1954). EM_{50} is similar to values for other 'summer' species such as *Aeshna cyanea* (EM_{50} =25 \ Corbet, 1962 #279). In contrast, in a 'spring' species, *Lestes rectangularis* EM_{50} is 7 days (Gower & Kormondy 1963). These asynchronous emergence patterns arise because the senior age group of both species overwinters in a range of instars (between the antepenultimate and final instars) in Britain (Chapter 4; Corbet, 1957). For example, in *C. mercuriale*, by the time emergence began at Glan-yr-afon Uchaf 67% of the 2^{nd} year larvae were still in the antepenultimate and penultimate instars(Chapter 4).

A few days of emergence may not have been sampled at the beginning of the flight period of *C. mercuriale* and the end of that of *C. tenellum.* Given the long duration of the sampling period, the number of animals missed in these periods would have a negligible impact on estimates of EM_{50}. Emergence of *C. mercuriale* was slightly more synchronised than in *C. tenellum*, since, in Britain, a higher proportion of *C. mercuriale* than *C. tenellum* overwinter in the penultimate instar (Corbet 1957b) and only had to pass through two stadia before emergence. In addition, the initial rate of emergence in *C. tenellum* was slower than that of *C. mercuriale*, and seemed to increase at the same point at which the rate of emergence decreased in *C. mercuriale.* Since both species used the same habitat for emergence and oviposition at Upper Crockford (Chapter 5), it is plausible that there is selection for temporal separation of emergence between these two species to avoid interspecific competition between adults. Temporal separation has been observed in other odonates where species co-exist, in both the larval and adult stages (Benke & Benke 1975; Johannsson 1978; Crowley & Johnson 1982b; Sternberg 1994). Such separation may be pronounced in larger odonate communities where congeneric species overlap extensively across habitats (Crowley & Johnson 1982b) but in most other communities, spatial separation may be more important than temporal separation (Johannsson 1978; Crowley & Johnson 1982b).

There was no difference between the sexes in the pattern of emergence for either species conforming to the pattern shown in most odonate species (Corbet 1999). Consistent with this, there was no correlation between sex ratio and emergence date for either species.

Peak emergence of *C. mercuriale* occurred in mid-June and the flight period extended from mid May (pers. obs.) to late July. *C. mercuriale* shows variation in flight period between years at Crockford (*cf.* Benke, 1975) and wide variation between edge-of range and core populations (section 3.1). The shorter flight period in edge populations (Britain and alpine or pre-alpine Germany) compared to core populations can be attributed to the Atlantic climate with lower absolute values of temperature. The shallow streams and ditches occupied by central European and Mediterranean populations will be subject to higher air temperatures so that the water temperature will rise more quickly and become suitable for metamorphosis and emergence earlier in the year and adults will be able to fly for longer. Such widening of temporal niches in favourable climates is common (Sternberg 1994) but, in core high-density populations, may also arise as a mechanism of intra- or interspecific competition avoidance. Since *C. mercuriale* rarely occupies the same habitat as other odonates (even where it occurs on the same sites) and occurs in high density populations in Britain as well as in Europe (Chapter 1), the width of its temporal niche is likely to be largely governed by climatic factors. Regional variation in larval development is discussed in Chapter 4 and the effect of temperature on activity and survival in mature adults is discussed in Chapter 6.

For *C. tenellum,* there is a paucity of data on the core populations. In Britain, the flight period is said to begin in early June and continue until late August. The flight period observed in this study was shorter, perhaps indicating that the final days of emergence were missed.

The absence of a bimodal emergence pattern for *C. mercuriale* indicates that cohort splitting did not occur in this British population. Cohort splitting is where, in a semi-voltine population, some of the junior age group can complete their development within one year and emerge late in the season forming a second smaller peak in the emergence curve. This is a phenomena observed in some other zygopterans (e.g. *Pyrrhosoma nymphula* (Corbet & Harvey 1989) *Anax imperator* (Corbet 1957c) and may occur in core European populations of *C. mercuriale* (see Chapter 4). It often occurs when individuals are limited by food availability, time left in season or predators and chose to delay development until the following year. For example, In *Lestes sponsa,* larvae kept at low food levels under a perceived time-constraint had a very slow development rate and a large mass at emergence (Johansson *et al.* 2001). Voltinism is discussed further in Chapter 4. The frequency with which cohort splitting occurs may be particularly significant in *C. mercuriale* since it provides a mechanism for genetic admixture between age groups. Such admixture is important in small isolated populations where genetic variation is too low to allow adaptation to rapid habitat change. Kiauta & Kiauta (1988) found an extremely small recombination index (a measure of the frequency of recombinant genes produced during meiosis) in an isolated, edge-of range population of *C. mercuriale*, and the limited dispersal ability of this species (Chapter 7), cohort-splitting may be the only mechanism of genetic admixture in some populations and may thus reduce inbreeding.

In common with other zygopterans (Corbet & Hoess 1998), the sex ratio of *C. mercuriale* at emergence differed significantly from 1:1, with males making up 57.4% of the study population. No such difference was found for *C. tenellum*. The sex-determination mechanism in odonates predicts a sex ratio of unity in the zygote (Kiauta 1969) so sex ratio imbalances at emergence can be attributed to differential mortality of eggs or larvae. One postulated source of differential mortality is size-selective predation on larger female larvae. Although females are significantly larger than males in adult (controlling for emergence date), and larval *C. mercuriale*, male biased sex ratios were not observed in larval instars (Chapter 4). Data from a range of populations of *C. mercuriale* are required to determine whether male-biased sex ratios at emergence occur consistently in this species. Sex ratios in in the mature adult stage are discussed in Chapter 6. However, further investigation of mortality during the maturation period is required since it has been postulated that relatively higher maturation probabilities (due to reduced predation owing to their lower activity and mass increase) in males is the most plausible mechanism producing male-biased sex ratios in Zygopteran populations (Stoks 2001b).

In male and female *C. mercuriale*, body length (left forewing length) is related to body weight at emergence. Large individuals emerge early in the season and small individuals emerge late in *C. mercuriale.* This negative relationship has been described in many temperate odonate species (Banks & Thompson 1985a; Michiels & Dhondt 1989; Corbet 1999) and in other insects with complex life cycles (Rowe & Ludwig 1991). Rowe & Ludwig (1991) suggest that there is a trade-off between gaining mass and delaying reproduction. Since the benefits of gaining mass decrease with size large larvae emerge early. In contrast, early in the season, it is beneficial for small larvae to attain more mass and to pay the costs of delayed reproduction. Later in the season these costs (such as exclusion from preferred refuges/oviposition sites by larger conspecifics, increased likelihood of predation in the larval stage) outweigh the benefits of mass gain. Benefits of large adult size in other odonates include, a greater capacity for dispersal (Anholt 1990) (but see Thompson 1991), increased longevity (Banks & Thompson 1985b; McVey 1988; Michiels & Dhondt 1991), fecundity (Richardson & Baker 1997) or increases in other components of mating success (Sokolovska *et al.* 1998). Large size has not been found to be advantageous in dispersal (Chapter 7), survival (Chapter 6) or lifetime mating success for *C. mercuriale* (Chapter 5).

3.4.2 Daily emergence

Whilst the potential form of the emergence curve is determined by an odonate's mode of seasonal regulation, its actual form may depend on proximate factors such as temperature before and after emergence (Corbet 1957c; Lutz 1968; Gribbin & Thompson 1990b), barometric pressure (Gribbin & Thompson 1990b) and wind (Jakob & Suhling 1999). Emerging individuals of both *C. mercuriale* and *C. tenellum* were not distributed randomly amongst the days of the season. The duration of sunlight on the previous day was significantly ($p < 0.001$) related to the daily number of *C. mercuriale* emerging (controlling for date). This variable is likely to be related to other weather variables, making it difficult to confirm which weather variable is most important in influencing daily variation, but some relationship with temperature has been shown. *C. mercuriale* may have the ability to postpone emergence (for considerable periods) following metamorphosis, as indicated by the presence of the adult labium lying retracted in the larval prementum of some individuals for three weeks before emergence, a condition which lasts 2 to 3 days in most odonates (Corbet 1955). It may be adaptive for individuals to postpone emergence until temperatures are high since emergence in odonates proceeds more quickly at higher temperatures (e.g. Ubukata 1973), reducing the risk of predation during hardening. Such an adaptation would produce a daily emergence pattern that was related to temperature as well as season.

A close relationship may be found between daily emergence pattern and temperature due to the shallowness and low rate of flow in the waterbodies inhabited by larval *C. mercuriale*. Such a relationship was found in populations of *Lestes eurinus* inhabiting small shallow ponds and was attributed to the lack of thermal lag between ambient and water temperatures in such waterbodies (Lutz 1968). Such rapid warming may decrease the time taken for emergence and hardening. The existence of such waterbodies is cited as one of the four factors of importance in determining the presence of *C. mercuriale* in Germany (Buchwald 1994). Although sometimes cited as possible causes of mortality at emergence, wind (speed) and rainfall were not important factors in determining the daily numbers emerging.

3.4.3 Mortality (deformity) at emergence in *C. mercuriale*

Percentage mortality of *C. mercuriale* at emergence was low (5.1% including deformed individuals) compared to other odonates where estimates for *Pyrrhosoma nymphula* range from between 3.3% (Bennett & Mill 1993) and 28% (Gribbin & Thompson 1991). In this study, mortality due to avian predation would have been reduced due to the presence of cages. However, although a wide variety of birds have been seen to take odonates during emergence, few have been responsible for high mortaliy (Corbet 1999). Causes of mortality in *C. mercuriale* included incomplete ecdysis or failure to expand wings, predation by spiders and falling from the emergence perch into the water. Thus mortality at emergence is unlikely to have a significant effect on population density or dynamics of *C. mercuriale* compared to that occurring in other life stages (*cf* Ubukata 1981).

3.4.4 Probability of recapture, lifespan and maturation period of *C. mercuriale*

Relatively few tenerals were recaptured, as often found in odonates (Corbet 1980) especially in stream-dwelling species where suitable breeding habitat may be more diffuse and difficult to monitor than in pond habitats (Bennett & Mill 1995; Stettmer 1996). Mark-recapture effort was concentrated on the breeding stream. Teneral recapture rates were lower then those of mature adults of *C. mercuriale* since tenerals utilise tussocks for roosting and maturation (Roske 1995; Skidmore 1996; Hopkins & Day 1997). In addition, it has been suggested that dispersal occurs during the 'maiden flight' of the teneral stage, although there is little empiracal evidence to support this. Higher mortality in the pre-reproductive period than the post-reproductive period may also contribute to the difference in these proportions. Lifespan did not differ between mature adults and tenerals in *C. mercuriale*, as for *C. puella* (Banks & Thompson 1985a). Such a difference may only be detected with a larger data set.

Male adults were more likely to be recaptured than female adults in *C. mercuriale*. This common odonate phenomenon is often attributed to higher mortality in females (e.g. Anholt 1992; Bennett & Mill 1995). Lifespans of males and females did not differ in *C. mercuriale* (for adults or tenerals), such that differences can be explained here by the cryptic colouration of females and the fact that females of most odonate species come to the water only to breed (Corbet 1980). Sex and size differences in survival in mature adults is examined in detail in Chapter 6, using methods that account for differences in recapture probability, and are discussed further there.

The minimum time required for maturation in *C. mercuriale* of between 5 and 8 days, falls within the range documented for other zygopterans i.e. 2 days to one month (Corbet 1980). For example, in another coenagrionid, it lasts 13-14 days (*Pyrrhosoma nymphula* - Bennett(1995)). It is also consistent with the 4-5 day maturation period described in populations of *C. mercuriale* in Baden-Wurttemburg (Sternberg *et al.* 1999). The data for *C. mercuriale* obtained in this study do not represent the full range of maturation periods for the population and the length of this period in other odonates varies within an emergence period due to weather conditions (e.g. Ubukata 1973) and between years at the same site. However, given that the mean lifespan of mature adults is 6 or 7 days, the pre-reproductive period occupies approximately half of the adult lifespan in this species.

Temporal and spatial patterns of emergence have been examined in edge-of-range populations of two rare damselfly species. Both *C. mercuriale* and *C. tenellum* exhibit non-synchronous emergence through the season with no indication of bimodality or, in turn, cohort splitting. Other chapters in the thesis examine survival at other stages of the life cycle and look further at the effect of climatic variables on survival and habitat use in these stages. The next chapter (Chapter 4) relates the form of the emergence curve to the binomics of the larval stage (Corbet *et al.* 1960).

Chapter 4 Voltinism and larval growth pattern in *C. mercuriale*

4.1 Introduction

The significance of developmental polymorphism for conservation biology has been discussed (Sections 1.6, 3.1). There is considerable developmental polymorphism in odonates because, whilst the adult stage is terrestrial, the aquatic stage is almost exclusively aquatic (Corbet 1980). Each stage is subject to differing intensities of factors that affect survivorship, growth and reproduction (Crowley *et al.* 1987). This study is a baseline investigation of voltinism (number of generations per year) and larval growth pattern in the aquatic stage of *C. mercuriale.* The only previous such study was carried out by Corbet (1957b). In the intervening period, it is likely that the environment has changed considerably. For example, there has been accelerated global warming of up to 0.8°C per decade (Lyman 1990). An expansion of the initial investigation in this endangered species is therefore pertinent.

The division of the life cycle into active and diapause stages has been crucial to the success of many temperate-zone insects (Tauber *et al.* 1986). Often patterns of voltinism and diapause are correlated with other life-history characters such as fecundity and disperal (Tauber *et al.* 1986). In *C. mercuriale*, the location of diapause is examined and related to the form of the emergence curve and the mode of seasonal regulation as described in Chapter 3. In particular, Corbet (1957b) proposed a diapause mechanism that would produce the asynchronous and late emergence observed in 'summer' species. He suggested that a rising series of lower temperature thresholds for entry into successive larval instars would mean that early instars would resume growth first in spring as the temperatures rise. This hypothesis is contrasted against one of a facultative diapause in the penultimate instar in Autumn. The resulting size structure of the population is examined since it has implications for the type and intensity of population interactions that may occur between different stages (Butler 1984).

Since dragonflies are thermophilic insects (section 1.4), their development and seasonality as well as their distribution and habitat use are likely to be restricted by temperature (May 1978). In this chapter, the pattern of development of *C. mercuriale* in Britain is compared to the pattern found in other European populations of the species and to patterns found in other odonates. This permits prediction on the extent to which development and, in turn, the distribution of *C. mercuriale* may be influenced by climatic factors.

Since only 18% of odonate families are restricted to lotic waters (Ward 1982), few studies of larval development have been carried out on stream-dwelling odonates and still fewer on species that inhabit such small, exposed stream habitats. Chapter 2describes the extent of variation in physical and chemical habitat factors in the streams occupied by *C. mercuriale* in comparison to variation found in other types of freshwaters. Again, I speculate on the influence of such factors on development and highlight areas for further investigation.

Whilst many authors have considered sex ratio at emergence in odonates (see review in Corbet & Hoess 1998), few have studied sex ratios in the larval stage (but see

Lawton 1972; Garrison & Hafernik 1981; Pickup *et al.* 1984; Baker *et al.* 1992; Duffy 1994).

The aims of this field experiment on the larval stages of *C. mercuriale* were to investigate the following;

(1) voltinism and the length of the growth period in edge of range population of this species

(2) the location of diapause in relation to seasonal regulation and the placement of the emergence curve (Chapter 3).

(3) the size distribution of larval cohorts and (qualitatively) habitat use by different cohorts (for prediction of the consequences for intraspecific interference competiton and predation)

(4) sex ratio in the larval stage

(5) variation in larval abundance and physical parameters of the small stream environment.

4.2 Materials and Methods

4.2.1 Study site

The study stream is on the Glan-yr-afon Uchaf catchment (SN118345-SN118346) on Mynydd Preseli in Pembrokeshire. Fig. 4.1a shows the location of Mynydd Preseli in Wales whilst Fig. 4.1b shows the location of Glan-yr–afon uchaf among the populations of *C. mercuriale* that have been recorded on Mynydd Preseli since 1980. Mynydd Preseli is an extensive area of unenclosed common that undergoes extensive grazing (up to stream margins) producing a sedge/*Molinia*/herb rich sward. The habitat at Glan-yr-afon consists of wet heath/soligenous valley mire with short stands of heavily grazed gorse (*Ulex gallii*). The streams are small shallow, narrow, spring-fed, runnels that run all year in which the substrate consists of peat (less than 30cm in depth) over clay deposits. Mature adult populations of over 2000 individuals were marked along this stream in 1997 (Chapter 7). There are a number of populations of *C. mercuriale* in a north-west orientation on the north face of the common up to an altitude of 170m a.s.l. (Skidmore 1996). The section chosen for study (see map) was located 150m below the stream source (Fig. 4.1c). These sections correspond to D to G (Hopkins & Day 1997) used in the 1997 study of dispersal.

The vegetation was broadly similar between the three sampling positions and can be described thus:

- Bankside vegetation included *Myrica gale, Molinia caerulea, Calluna vulgaris, Erica tetralix and Carex* sp. *(C. dioica, C. spicata) Agrostis* sp.

- Emergent/ edge vegetation consisted mainly of *Juncus* sp. (mainly *J. articulatus*, with some *J. effusus, J. bulbosus, J. subnodulosus*) and *Eleocharis palustris* with some *Drosera rotundifolia, , Eriophorum angustifolium, Rhynchospora alba.*

- Submerged vegetation consisted mainly of *Hypericum elodes, Potamogeton polygonifolius, Eleogiton fluitans,* and *Sphagnum* sp. (including *S. auriculum*), with some *Anagallis tenella, Scirpus* sp. *Ranunculus fluitans.* Aquatic algae are present including filamentous diatoms (*Diatoma, Tabellaria*), single diatoms (*Synedra, Navicula*), some desmids (*Closterium* sp. *Selenastrum* sp.), *Ullothrix* and *Bulbochaete.*

Three sampling sites were chosen in the study stream, hereafter referred to as the Top (T), Middle (M) and Bottom (B) sites. The Top site and Bottom site both usually contained around 50% cover of aquatic vegetation within the stream channel and *Potamogeton polygonifolius* and *Juncus articulatus* predominated. The Middle site was very well vegetated, containing 100% cover of aquatic vegetation within the channel. Here, *Eleogiton fluitans* usually predominated with some *Potamogeton polygonifolius* and *Juncus articulatus.*

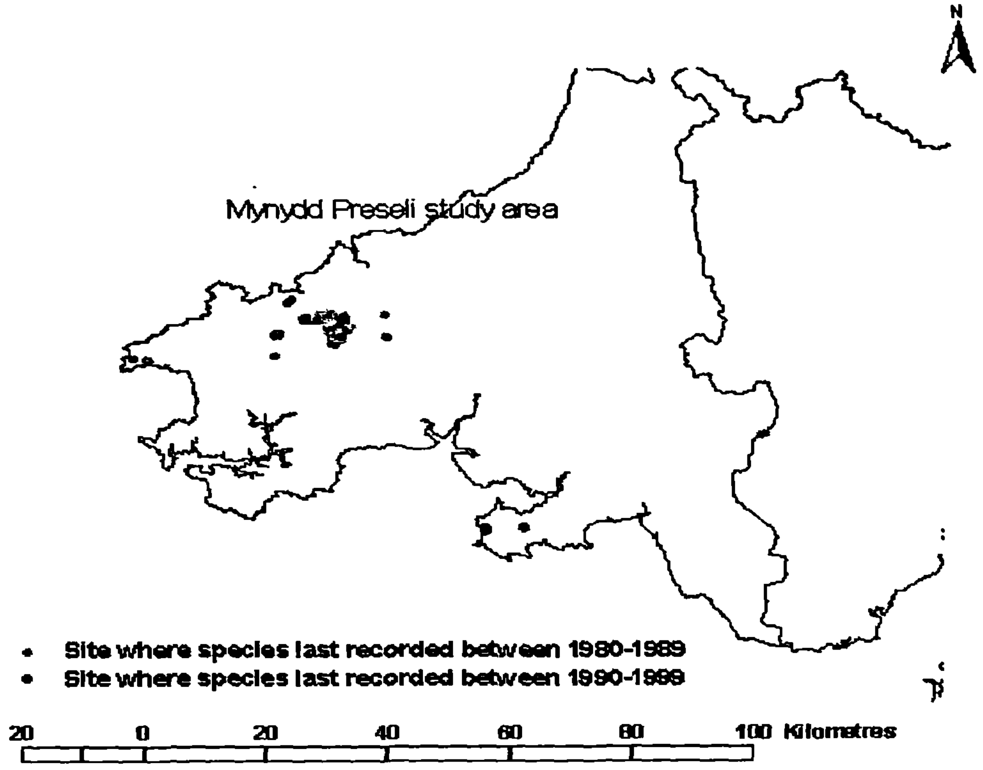


Fig. 4.1a Location of Mynydd Preseli in Wales.

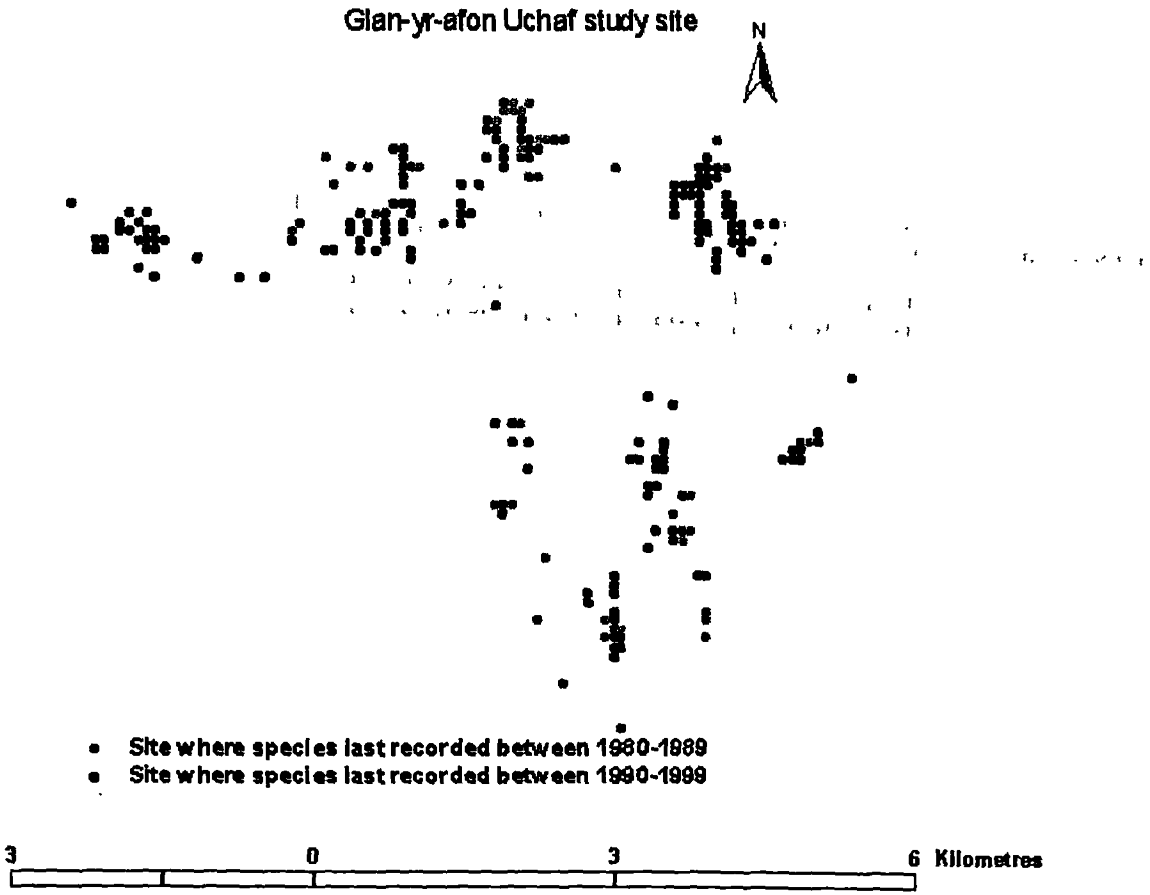


Fig. 4.1b Location of Glan-yr-afon Uchaf among the *C. mercuriale* populations recorded on Mynydd Preseli since 1980.

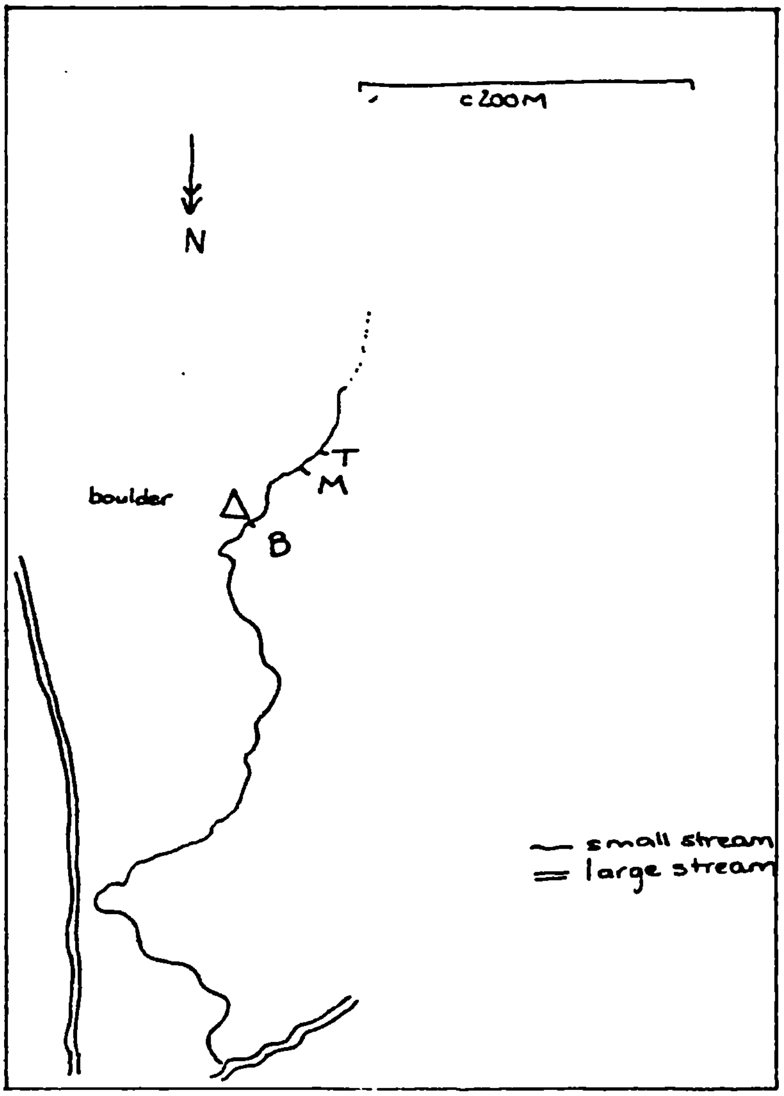


Fig. 4.1c Diagram of study stream showing the three larval sampling positions.

4.2.2 Larval sampling method

For odonates, several methods have been used to sample a known unit of habitat to estimate larval population density. These include the use of mechanical devices, which confine a fixed amount of plant material and cut this off from the surrounding habitat e.g. Gerking samplers (e.g. Duffy 1994); drop boxes(e.g. Benke 1970; Benke & Benke 1975; Wissinger 1988a); and the use of bin samplers, which enclose a given volume of water and vegetation temporarily whilst animals are removed (e.g. Lawton 1970b; Banks 1985). Since *C. mercuriale* inhabits shallow, narrow streams on the Glan-yr-afon catchment, the operation of such devices would have been unfeasible and destructive to the habitat. As an alternative method, artificial substrates have been used as colonisation samplers to provide a standardised unit of habitat that allows direct comparison of data from different areas (Jackson 1997). These have been successful where the vegetation structure in the natural habitat is fairly homogeneous and easy to represent artificially. Johannsson (1978) was able to use artificial macrophytes structurally similar to *Phragmites communis* reed beds to sample zygopteran larvae. Given the small dimensions of the habitat and heterogeneous nature of macrophyte fauna in the Glan-yr-afron stream, pilot sampling with artificial substrates was unsuccessful, yielding only a few individuals of *C. mercuriale*. In contrast, hand nets are versatile for semi-qualitative sampling (Waringer & Humpesch 1984; Hellawell 1986; Jackson 1997), and pilot sampling yielded large numbers of individuals and caused the minimum of damage to the habitat. Thus, hand-netting was chosen as the sampling method but no attempt was made to estimate population densities from the samples (Downing 1984).

The use of stratified sampling, where sampling is carried out in different sub-habitats, has allowed previous authors to look at how habitat use varies through seasons, across instars and between species (Lawton 1970b; Benke & Benke 1975; Duffy 1994). Such an approach was inappropriate for *C. mercuriale* since the habitat could not be divided into subhabitats and because the full range of instars was present in the submergent vegetation. Furthermore, pilot sampling in the peat substrate of the stream yielded no larvae.

A standard net sweep was defined as the sweeping of a fine mesh pond net (25cm by 25cm) at a depth of 12.5cm (half depth of net) up stream for a distance of 1m. This was performed three times in total over the same 1m stretch. The contents of the net were tipped into a shallow white enamel tray containing a 2cm depth of water. Material remaining on the net surface was washed into the tray. The weed was stirred several times to dislodge larvae from perches. The material was sorted in the field until all damselfly larvae had been removed (approximately 30 minutes), taking care to search for all the small, early instar larvae once the large individuals had been removed. Each larva was placed in a 30ml tube with stream water and a perch (cocktail stick) and transported in a cool box to the laboratory.

Ten samples were taken as above at three different positions along a 50m stretch of the stream at Glan-y-afron. Four samples were taken at positions M and T whilst 2 samples were taken at position B. From 18th October 1999 to 28th September 2000 samples were taken at intervals ranging from 28 days to 53 days (mean interval 39.7 ± 2.3 days). A shorter interval between samples was used during summer because larval growth was expected to take place more quickly at higher water temperatures (see Banks 1985).

In the laboratory, head width, hind tibia length and wing bud length were measured under a binocular dissecting microscope using an eye piece graticule calibrated with a slide micrometer (magnification was 15 – 30 X, depending on the size of the larvae) . Head width is the maximum width of the head capsule measured across the eyes. Hind tibia length was measured from the proximate point of the tarsus to the end of the joint with the femur. This was measured by placing the animal on its back on a slide with the tibia trapped across the abdomen by a second slide. Wing bud length was measured from where the anterior of the mesothoracic wing bud meets the prothorax to the distal point of this wing bud. Larvae were kept in cool boxes in the lab and returned to the stream positions within 5 days of collection.

4.2.3 Monthly variation in stream characteristics

Since a stratified sampling method was inappropriate for this species, the same stream positions were sampled for larvae each month to minimise the effect of habitat heterogeneity between months. Despite this it was necessary to quantify monthly variation in those stream characteristics, such as stream dimensions, temperature, vegetation structure and water flow rate, which may influence the ease of sampling or survival of larvae. These were measured for each stream position. In addition water chemical parameters were measured on a monthly basis (Chapter 2). Stream width and stream depth were measured with a steel tape measure at each position. Plant species present at each site were recorded. Flow rate was measured in March, June, July and September using an electromagnetic flow meter. Dissolved oxygen was measured using a Clark-type polarographic electrode, calibrated against percentage local saturation. A datasonde (Hydrolab Datasonde 3 Water Quality Logger) was placed in the stream to record temperature, pH and conductivity at half hourly intervals between 3rd December-12th February (Chapter 2).

4.2.4 Separation of larvae into species, sexes and instars

4.2.4.1 Larval identification

C. mercuriale and *Pyrrhosoma nymphula* were the only zygopteran larvae found in the samples and the abundance of *P. nymphula* was much lower than that of *C. mercuriale*. Separation of these two species was based mainly on the keys of Gardner (1950), Carchini (1983) and Corbet (1955), though these are designed for use with final instar larvae. From instar 4 onwards (*ca.* 1.6mm in body length, ca. 0.7mm in head width), *P. nymphula* larvae have black pigmentation on the apical portion of the caudal lamellae (Gardner & MacNeill 1950). Since only 1.7 % (22 out of 1333) of the total larvae sampled in this study had a head width of less than 0.7 mm, this character was sufficient to separate the majority of larvae. Larvae without caudal lamellae could be separated using the different shapes of the head and prothorax of the two species and, to some extent, the differences in the slope of the relationship between head width (HW) and tibia length (TL) shown in Fig. 4.2. For *C. mercuriale*; HW = -2.13 + 1.47 TL, F= 40717.25, n=1195, p<0.001, R^2=0.972. For *P. nymphula*; HW= -0.008 + 0.95 TL, F=8705.74, n=116, $p < 0.001$, R^2=0.987).

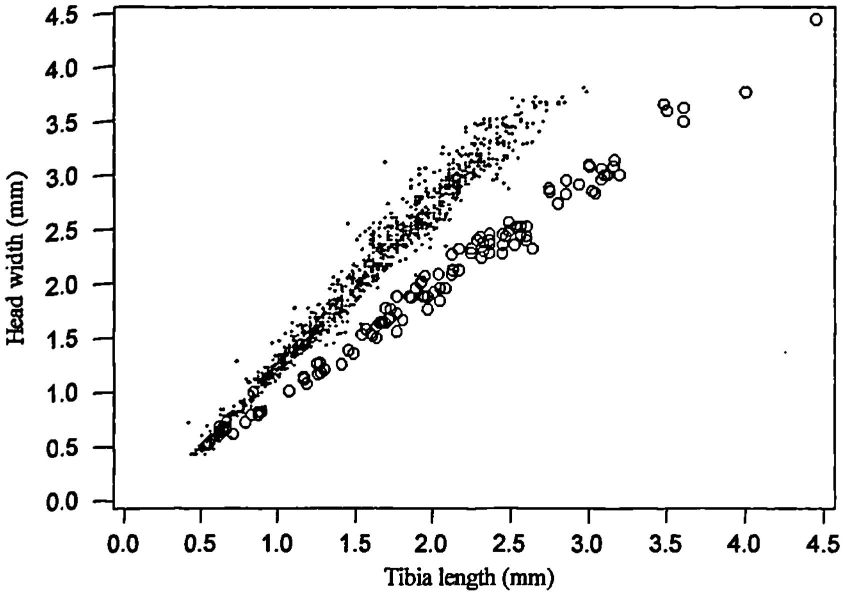


Fig. 4.2 Relationship between head width and tibia length for all *C. mercuriale* (*n*=1195, black crosses) and *P. nymphula* (*n*=129, open circles) larvae.

4.2.4.2 Assigning individuals to instar groups

In order to interpret life history and age structure of populations, it is necessary to assign individuals to instars or age categories. Insects have a discontinuous growth pattern due to their rigid exoskeleton. Increases in body size (and indeed any changes in form) occur at the moults (when a new cuticle with a greater surface area is formed) between stadia and remains fixed between moults. Thus, an individual goes through a stepwise pattern of size increase (or change in form) as development proceeds, and can potentially be assigned to a developmental stages by size or form characteristics. Growth can then be inferred from changes in the distribution of individuals between developmental stages through time.

With regards to odonates, some authors rear larvae from eggs in the laboratory to determine the number, size and form of different larval instars (see Gardner & MacNeill 1950; Ubukata 1980; Waringer & Humpesch 1984; Wissinger 1989). This is useful only if a field population is available to calibrate the laboratory determined instars (Pickup 1985; Duffy 1994). However, field sampling was preferable for *C. mercuriale* since laboratory conditions were unlikely to approximate the field conditions of a species with such specific habitat requirements (Chapter 2), and because such laboratory sampling often results in high mortality (see Corbet 1955).

To determine the number and size of developmental stages within field populations, Baker (1986) used a count of the number of abdominal segments covered by wing buds as a discriminatory characteristic. He suggests that this method avoids bias due to size overlap between instars. Fig. 4.3 shows that for *C. mercuriale* this method does not produce adequate division into developmental stages. For example, the group of individuals with 3.5 abdominal segments covered by their wingbuds have head widths ranging from 1.6 to 3.4 mm and probably range from instar 4 to instar 7 (Corbet 1955). Therefore, this method produces groupings of low resolution and may be inaccurate because the size of abdominal segments changes between instars and the abdomen is extensible. It is, however, useful in separating the last three larval instars.

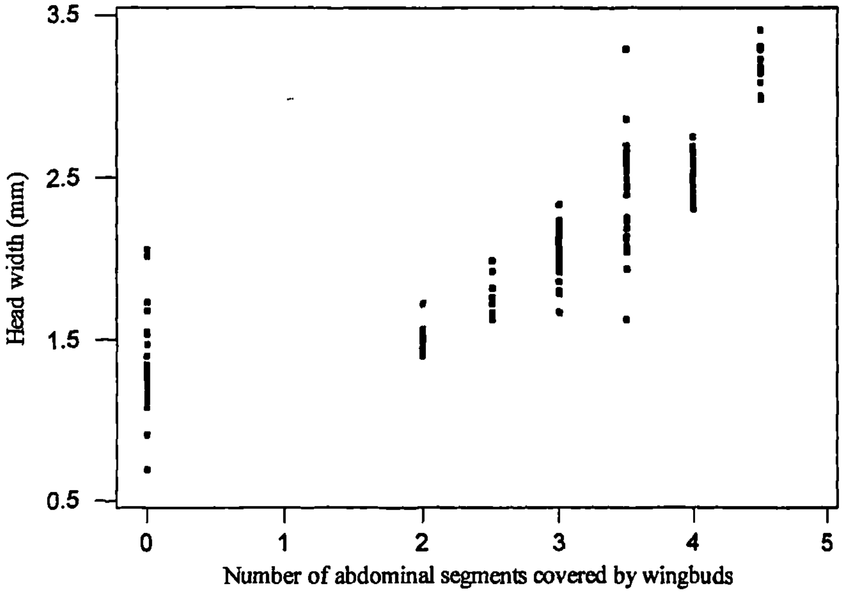


Fig. 4.3 Relationship between head with and number of abdominal segments covered by wing buds for *C. mercuriale* larvae (September 2000, *n*=162).

In the absence of measurable changes in form between different larval instars, several authors have used size-frequency distributions of one body dimension to look for periodic peaks to infer the modal size of each instar. Body dimensions used include head width (e.g. Benke 1970; Benke & Benke 1975; Baker & Clifford 1981; Wissinger 1988b; Wissinger 1989; Bennett & Mill 1993; Duffy 1994); total body length (e.g. Corbet 1956; Corbet 1957c; Corbet 1957a; Corbet 1957b; Ubukata 1980; Krishnaraj & Pritchard 1995) and wing bud length (e.g. Benke 1970; Sawchyn & Gillott 1974). The reliance on size of larvae to interpret life histories can be misleading as differences in size of aquatic insects may not reflect differences in developmental stage (Butler 1984) but may reflect differences in food intake (Baker 1982, Lawton 1980; Pickup 1984, 1990; Pickup *et al.* 1990), competitive ability (Gribbin & Thompson 1990a), parasitisation (Rohlff 1999) or temperature regimes (Pickup 1984, 1990; Pickup *et al.* 1990). However, the use of size groups that are well separated increases the likelihood that groupings reflect actual developmental stages.

Accurate separation of groups can be enhanced in several ways. Firstly, by the use of linear body measurements that show negligible change within an instar and marked changes between instars. For example, body length increases over the duration of an instar (Benke 1970; Pickup 1985) whereas head width changes very little and

correlates closely with body volume (Robinson & Wellborn 1987). Ideally, the measurement should be available for all instars. Wing buds are only measurable in the last 5 instars but, since they increase in size at a disproportionately higher rate than other linear measurements, they are useful for separation of larger instars.
Secondly, the use of X-Y plots of two body measurements (rather than size-frequency histograms of one body dimension) produces clouds of points corresponding to instars, and has allowed their separation in several studies (Edmonson & Windberg 1971; Thompson 1978b; Pickup & Thompson 1984; Banks 1985).

Thirdly, if groupings represent developmental stages they should be consistent, across body dimensions, between sexes and across samples taken at different time points. Thus, for *C. mercuriale,* 3-dimensional X-Y-Z plots (e.g. see below) and all combinations of X-Y plots were used to check clusters were consistent between head width, tibia length and wing bud length measurements. This process was carried out separately for males and females and for each month. Six instar groups (A-F) could be separated that were consistent between sexes, across months and across body dimensions. Table 4.1 shows the mean head width, tibia length and wingbud length for males and females from each instar for all 1331 larvae. Plots of head width versus tibia length marked by instar group are shown in Appendix 6. A corresponds to instars 2-6, B corresponds to instars 7-8, C corresponds to instars 9-10 whilst D, E and F corresponded to the antepenultimate, penultimate, and final instars (see Corbet 1955). For *P. nymphula,* such plots allowed separation of all 12 instar groups after the pro larva (see Table 4.2 and results). Whilst hierachical cluster analysis could be employed to statistically separate instars in insects where the size distributions of consecutive instars do not overlap to any great extent, these were not appropriate for *C. mercuriale,* due to the low sample sizes available for each month and because it was biologically meaningful to look for groups that were consistent across months. Larvae and exuviae could only be sexed at head widths greater than or equal to 1.7mm (i.e. instar groups D to F). Female larvae have an appendicular ovipositor formed from the appendages (downward pointing prongs) of abdominal segments 8 and 9. Males lack this ovipositor but have a smaller pair of spines that are the precursors to their anal claspers.

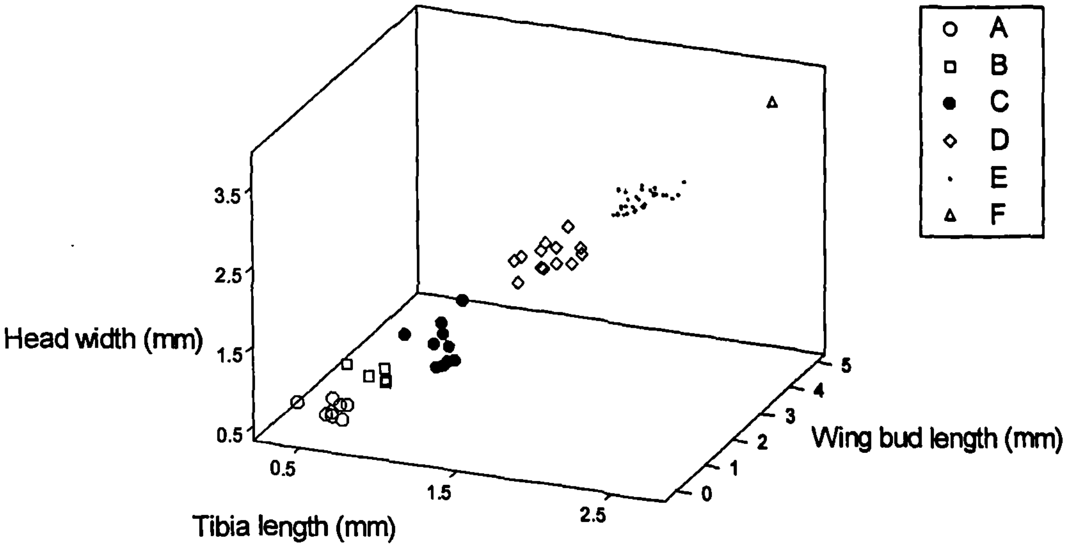


Fig. 4.4 3D plot of body size variables for females and small larave from 30/11/99 (*n*=70).

Table 4.1 Mean, range and median of head width, tibia length and wingbud length for instar groups for *C. mercuriale.*

	Instar Group	*n*	$\mu \pm s.e.$.	Minimum	Maximum	Median
Head width (mm)	A	71	0.65 ± 0.01	0.43	0.84	0.66
	B	199	1.18 ± 0.01	0.78	1.60	1.18
	C	351	1.78 ± 0.01	1.34	2.43	1.74
	D	273	2.47 ±0.01	1.94	2.86	2.48
	E	214	2.99 ± 0.01	2.28	3.30	3.00
	F	83	3.47 ± 0.02	3.20	3.82	3.46
Tibia length (mm)	A	71	0.60 ± 0.01	0.41	0.77	0.62
	B	199	0.96 ± 0.01	0.64	1.30	0.96
	C	351	1.37 ± 0.01	1.00	1.92	1.35
	D	273	1.81 ± 0.01	1.44	2.16	1.82
	E	214	2.16 ± 0.01	1.65	2.60	2.15
	F	83	2.48 ± 0.02	2.16	2.98	2.46
Wing bud length (mm)	A	2	-	-	-	-
	B	31	0.13 ± 0.03	0.00	0.89	0.00
	C	293	0.56 ± 0.02	0.00	1.72	0.53
	D	273	1.25 ± 0.01	0.65	1.84	1.26
	E	210	2.09 ± 0.02	1.56	3.56	2.08
	F	83	3.93 ± 0.05	2.45	4.80	3.96

Table 4.2 Mean, range and median of head width, tibia length and wingbud length for instars for *P. nymphula*.

	Instar	*n*	$\mu \pm s.e.$.	Minimum	Maximum	Median
Head width (mm)	2	3	0.53 ± 0.00	0.52	0.53	0.53
	4	2	0.86 ± 0.13	0.73	0.99	0.86
	5	6	1.19 ± 0.03	1.08	1.26	1.19
	6	3	1.33 ± 0.04	1.26	1.38	1.35
	7	15	1.61 ± 0.02	1.50	1.76	1.63
	8	16	1.91 ± 0.02	1.76	2.06	1.88
	9	5	2.14 ± 0.03	2.09	2.27	2.12
	10	27	2.40 ± 0.02	2.25	2.56	2.40
	11	17	2.96 ± 0.03	2.74	3.14	2.96
	12	4	3.60 ± 0.03	3.50	3.66	3.61
	13	2	4.11 ± 0.34	3.78	4.45	4.11
Tibia length (mm)	2	3	0.54 ± 0.00	0.53	0.55	0.55
	4	2	0.81 ± 0.02	0.78	0.84	0.81
	5	6	1.25 ± 0.02	1.18	1.29	1.26
	6	3	1.44 ± 0.02	1.40	1.48	1.44
	7	15	1.66 ±0.02	1.53	1.80	1.66
	8	16	1.92 ± 0.03	1.69	2.08	1.93
	9	5	2.11 ± 0.02	2.03	2.16	2.11
	10	27	2.43 ± 0.03	2.16	2.64	2.44
	11	17	2.99 ± 0.04	2.74	3.20	3.02
	12	4	3.55 ± 0.03	3.48	3.60	3.55
	13	2	4.23 ± 0.23	4.00	4.45	4.23
Wing bud length (mm)	2	3	-	-	-	-
	4	0	-	-	-	-
	5	3	0.26 ± 0.15	0.00	0.52	0.27
	6	3	0.28 ± 0.05	0.23	0.38	0.24
	7	15	0.38 ± 0.02	0.28	0.48	0.40
	8	16	0.68 ± 0.03	0.47	0.84	0.66
	9	5	0.81 ± 0.10	0.66	1.20	0.69
	10	27	1.26 ± 0.04	0.69	2.02	1.24
	11	17	2.24 ± 0.03	1.96	2.54	2.25
	12	4	4.16 ± 0.46	2.84	4.80	4.50
	13	2	5.07	-	-	-

4.3 Results

In reference to the aims of this investigation, variation in larval abundance and physical stream parameters are reported first to set out the dataset on which the subsequent results are based. Throughout this section, where figures depict variables over time, the month name is plotted on the x-axis rather than date. This is sufficiently accurate because the intervals between samples were approximately equal and because the results will not be interpreted in terms of the number of days required for developmental stages.

4.3.1 Variation in larval abundance and physical stream parameters

Coenagrion mercuriale made up a large proportion (approximately 90%) of the total number of larvae sampled in each month whilst the proportion of *Pyrrhosoma nymphula* ranged from 4% to 18% of the month's sample of individuals (Fig. 4.5) There was no correlation across months between the number of *C. mercuriale* and the number of *P. nymphula* individuals obtained in a month's sample (Spearman's rank correlation r_s=0.480, p=0.160, n=10). This may be because individuals of *P. nymphula* respond differently to monthly variation in habitat factors or because mortality factors show a different pattern of monthly variation in the two species. It is difficult to draw conclusions based on such a low sample of *P. nymphula*.

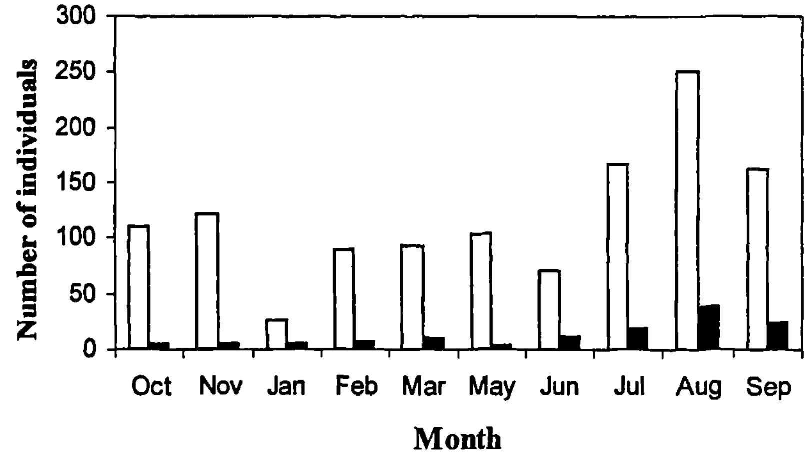


Fig. 4.5 Number of individuals of *C. mercuriale* (open bars) and *P. nymphula* (closed bars) in each month's sample across all three sampling positions.

There was considerable monthly variation in the width, depth volume and flow of these small streams (Figs. 4.6a–c, Fig. 4.7). This variation may produce monthly variation in the efficacy of the sampling method. The highest flow rate was found in September when stream volume was high (following a period of heavy rainfall) and the lowest flow rate was found in July when the stream volume was low (Fig. 4.7). Flow rate and stream dimensions seemed to follow the same pattern of seasonal variation between positions though there are insufficient data to confirm this statistically. Fig. 4.8 shows that there was no correlation between total number of larvae obtained in a month and stream volume (Spearman's r =-0.527, n=10, p=0.117). However, in January when stream volume (at 3.70 m^3) was more than twice the mean stream volume ($\mu = 0.136 \pm 0.031$ m^3), a low number of individuals was obtained. This suggests that dilution of the population occurred at high stream volumes making individuals less likely to be netted.

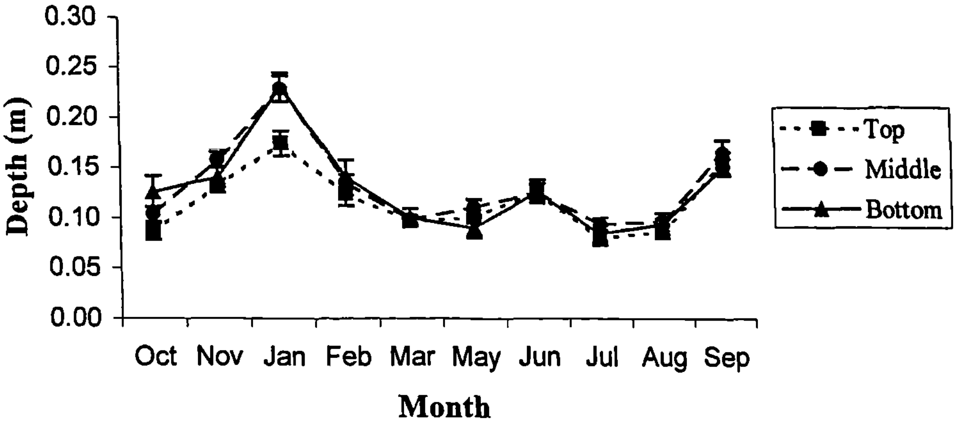


Fig. 4.6a Monthly variation in stream depth at Glan-yr-afon Uchaf.

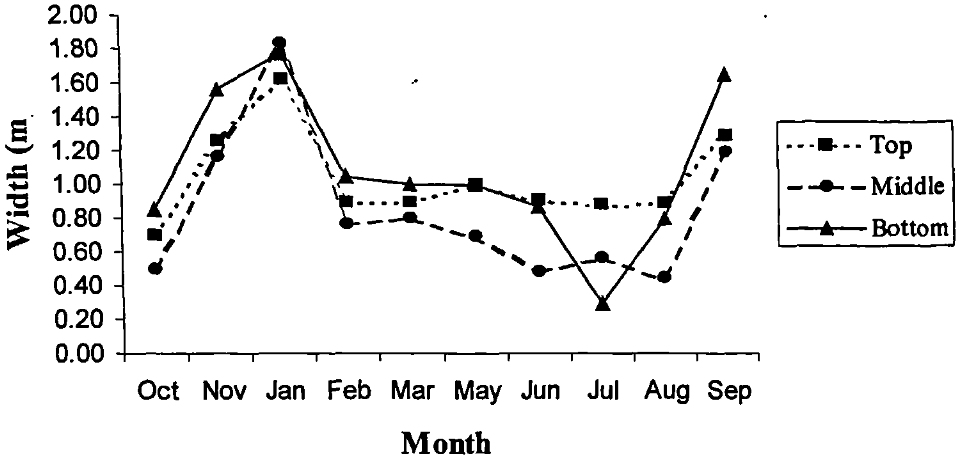


Fig. 4.6b Monthly variation in stream width at Glan-yr-afon Uchaf.

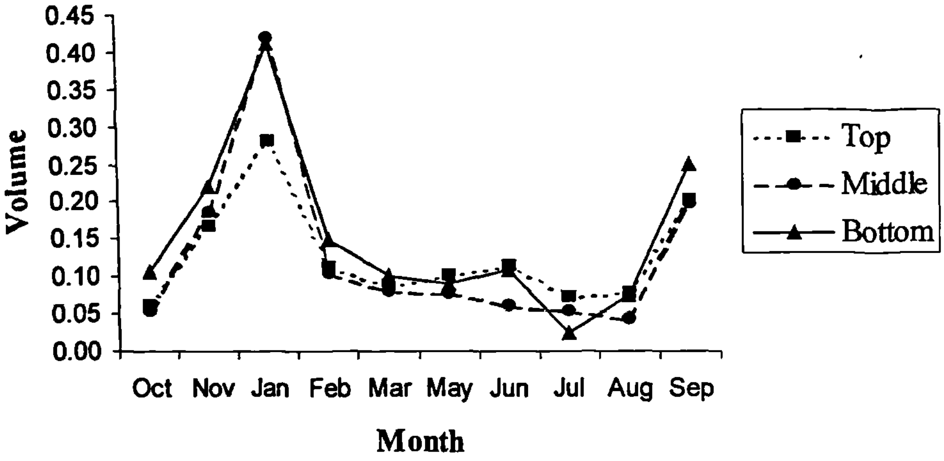


Fig. 4.6c Monthly variation in stream volume (in m^3) at Glan-yr-afon Uchaf (volume calculated as the product of width depth and 1m sweep length)

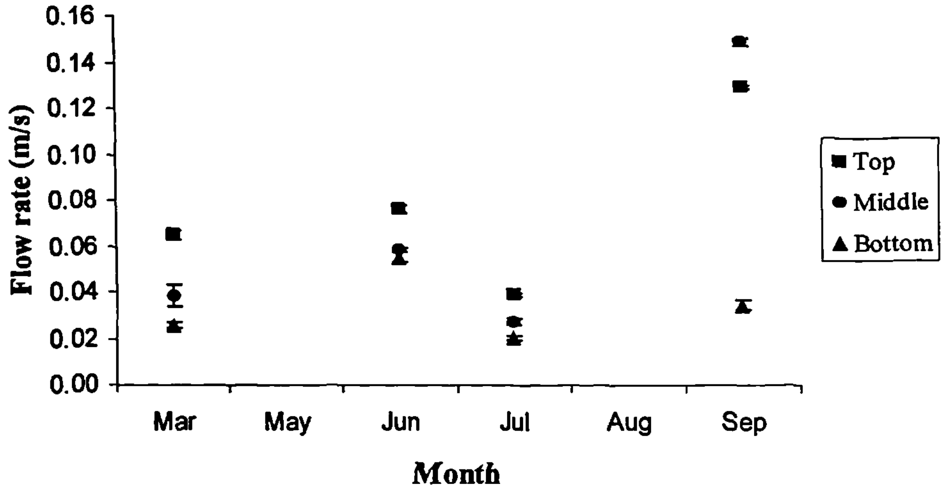


Fig. 4.7 Monthly variation in stream flow rate at Glan-yr-afon Uchaf.

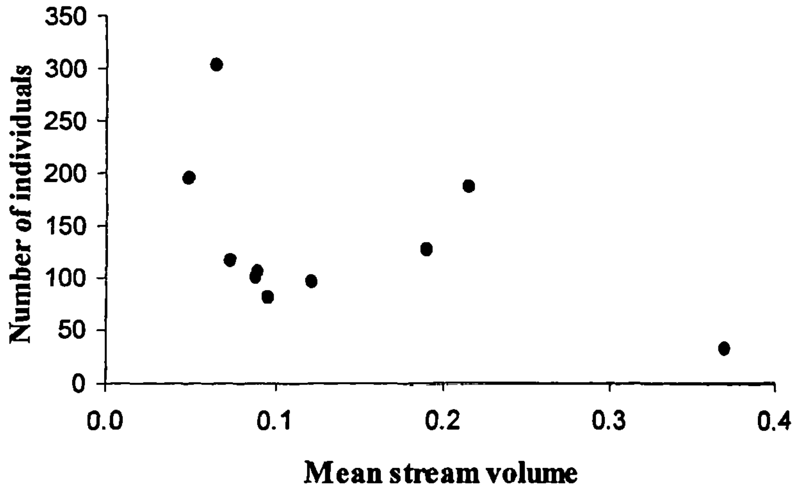


Fig. 4.8 Relationship between number of individuals obtained in each month's sample and the mean stream volume (in m^3).

4.3.2 Voltinism and length of the growth period in *C. mercuriale*.

4.3.2.1 Voltinism

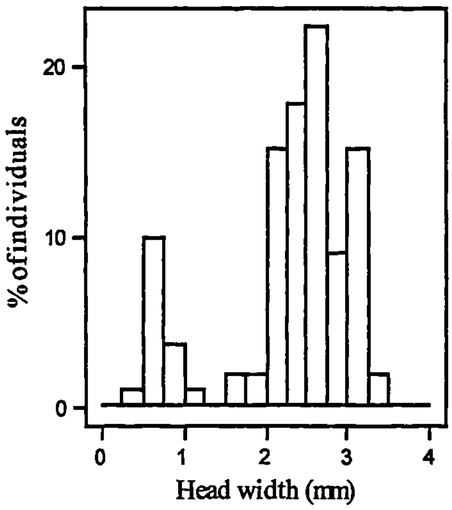
The percentage of individuals in each head width class in each month are shown in Figs. 4.9a-j. Eggs of *C. mercuriale* hatch without diapause (Corbet 1955). Therefore, the presence of two peaks on these width-percentage histograms, particularly evident in October (Fig. 4.9a), March (Fig. 4.9e) and May (Fig. 4.9f), indicates that two years were required for larval development because each peak corresponded to a year group. If *C. mercuriale* was univoltine with no egg diapause then a single peak that increased in modal width between successive months from Autumn to the following summer would be observed on such histograms.

4.3.2.2 Length of larval growth period inferred from changes in instar group composition of samples between months

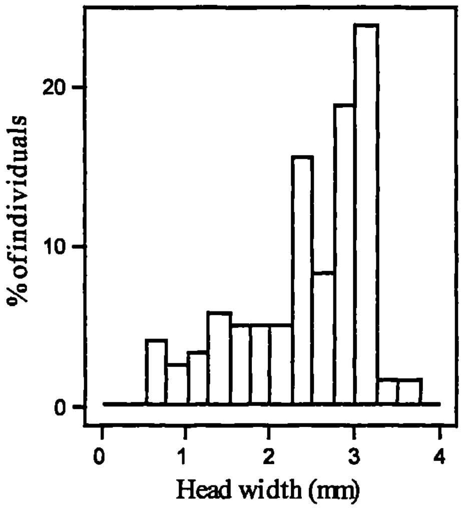
The percentage of individuals in each instar group in each month are shown in Figs. 4.10a-j. The pattern of the bars indicates the cohort to which individuals are most likely to belong in each month. Three larval cohorts were present in the sampling period. Cohort 1 (hatched in 1998) was in instars D to F in October 1999 and emerged in summer 2000. Cohort 2 (hatched in 1999) was in instars A to C in October 1999 and will emerge in summer 2001. Cohort 3 hatched in summer 2000 (appeared first in June 2000) and will emerge in 2002.

If growth is occurring within the larval population and individuals are changing instars, this change would be reflected as differences in the proportion of individuals in each instar group between consecutive months. These proportions are compared between pairs of consecutive months using chi-squared tests. Instars A and B were not detected consistently in samples, probably due to their small size.

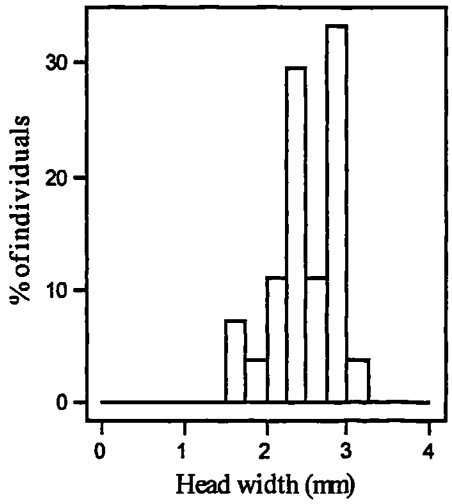
(a) 18/10/99 n=109



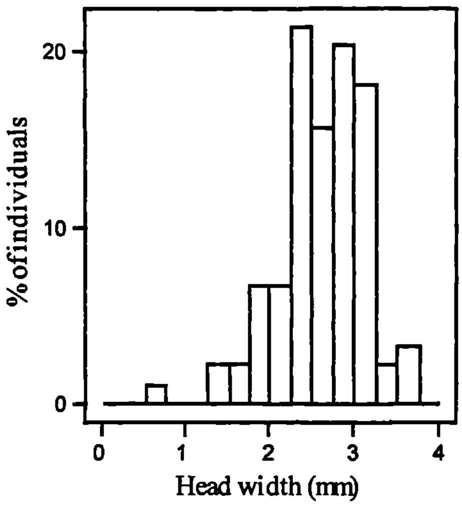
(b) 30/11/99 n=120



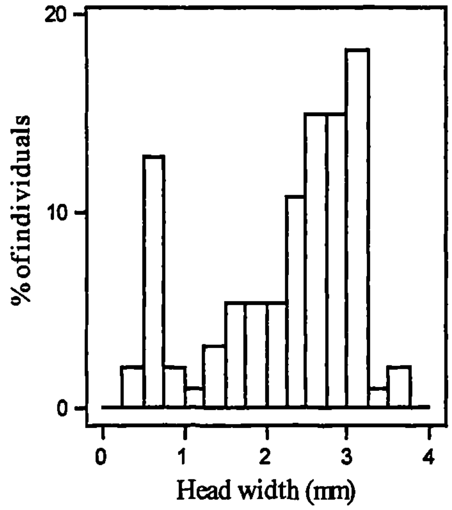
(c) 12/01/00 n=27



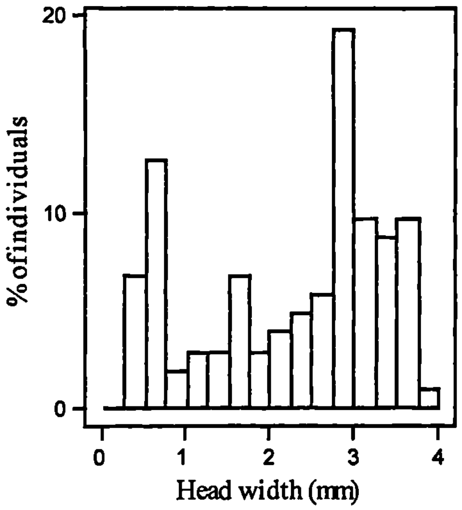
(d) 23/02/00 n=89



(e) 29/03/00 n=90



(f) 01/05/00 n=103



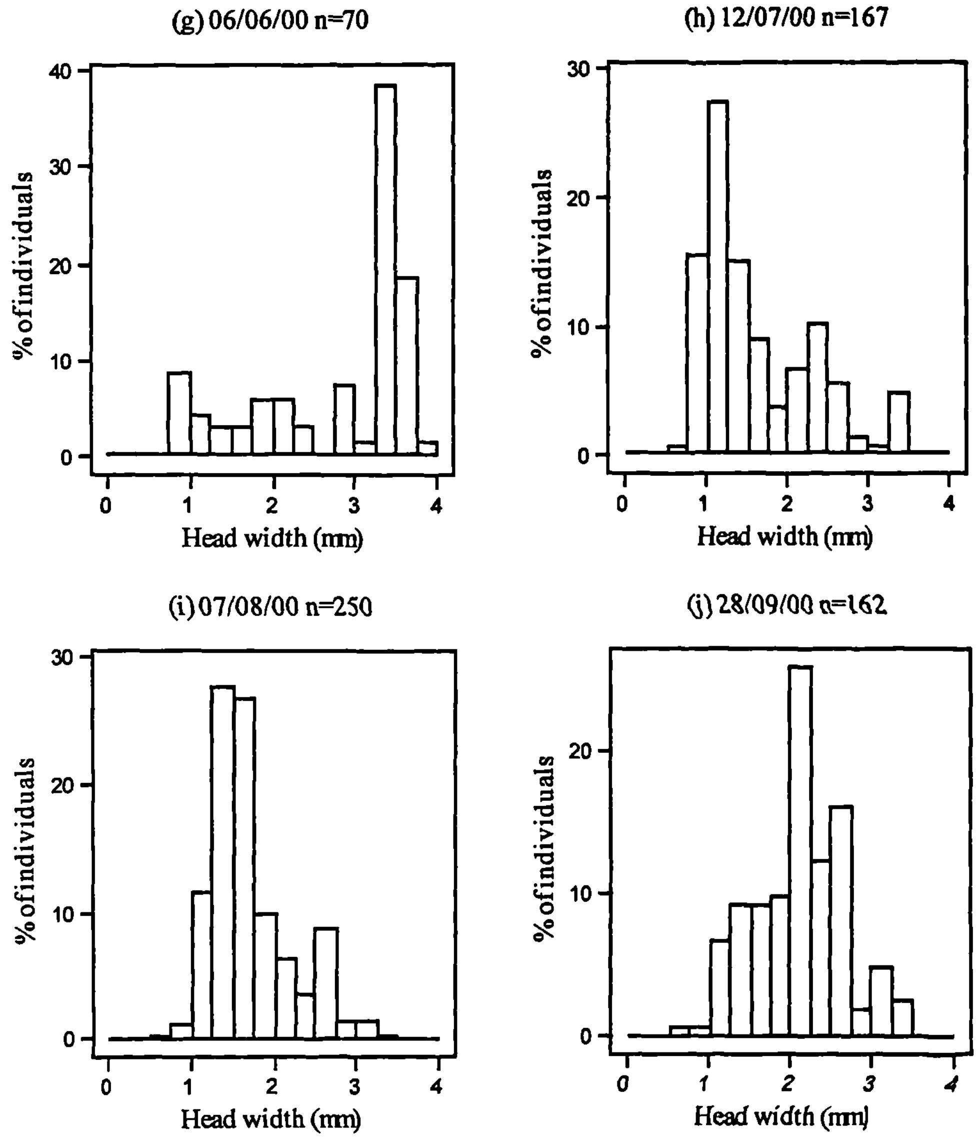
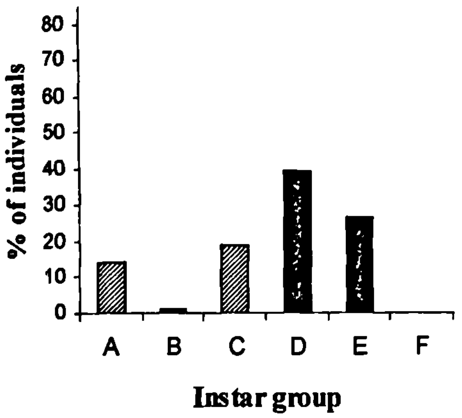
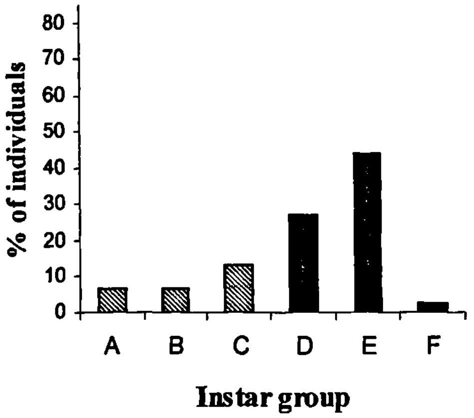


Fig 4.9 (a)-(j) Percentage of individuals in each head width class in each month's sample

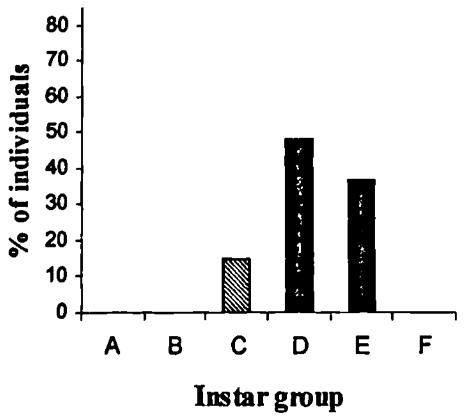
(a) 18/10/99 n=112



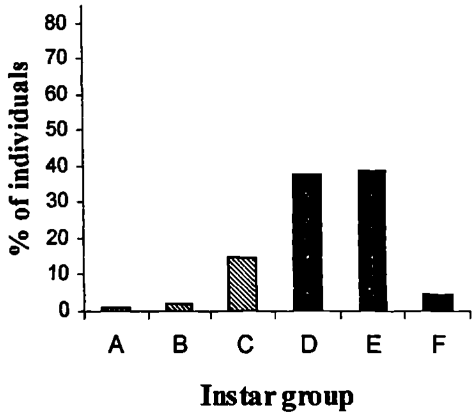
(b) 30/11/99 n=112



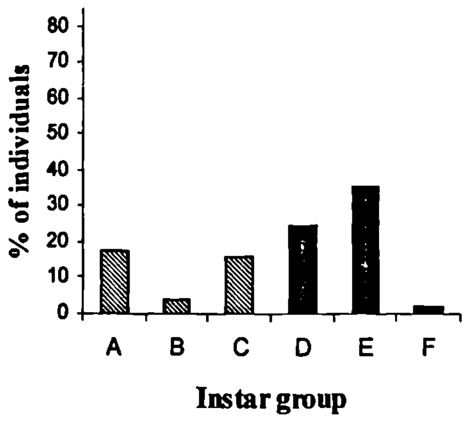
(c) 12/01/00 n=27



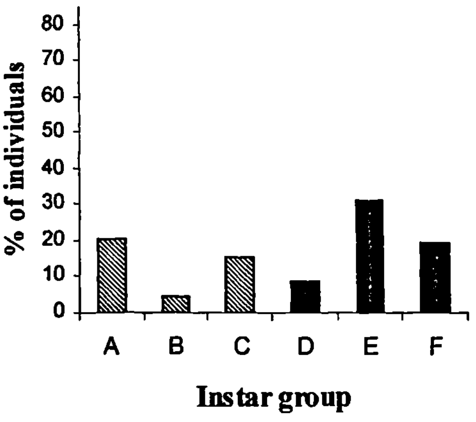
(d) 23/02/00 n=87



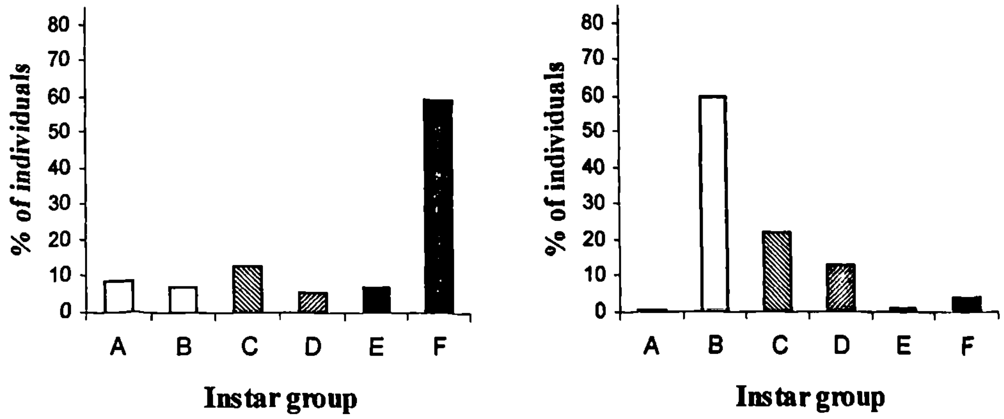
(e) 29/03/00 n=93



(f) 01/05/00 n=103



(g) 06/06/00 n=71 (h) 12/07/00 n=167



(i) 07/08/00 n=247 (j) 28/09/00 n=162

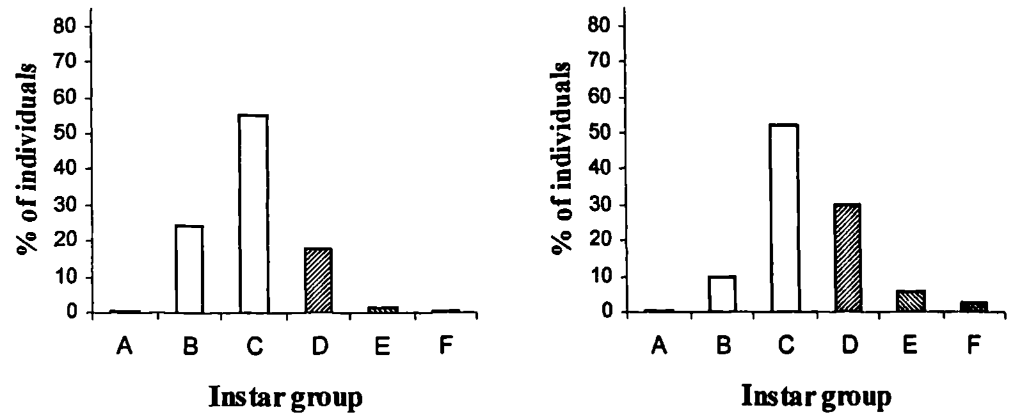


Fig. 4.10 The percentage of individuals in each instar group in each month, divided into the three cohorts present in the samples. Cohort 1 (1998-2000) is represented by closed bars, cohort 2 (1999-2001) by diagonally-striped and cohort 3 (2000-2002) by open bars.

For example in January and February they made up 0% and 4% of the population and then reappeared in March when they made up 22% of the population.. Thus instars A and B were omitted from the following chi-squared analysis. Instars E and F were amalgamated to avoid low expected values.

Table 4.3 shows that there is no significant difference in instar proportions between consecutive months between November and March. The size of the chi-square value indicates the degree of difference between instar proportions between months and reflects the amount of growth that has occurred. These indicate that a large amount of growth occurs between March and August but that some growth also occurs in October and November.

Table 4.3 Chi-square tests to compare proportion of individuals in each instar between consecutive pairs of months (* indicates differences significant at the 5% level or below).

Months compared:	χ^2	d.f.	p
October versus November	9.63	1	0.002*
November versus January	2.87	1	0.09
January versus February	0.77	1	0.38
February versus March	1.29	1	0.257
March versus May	20.81	1	< 0.001*
May versus June	29.74	1	< 0.001*
June versus July	54.67	1	< 0.001*
July versus August	18.72	1	< 0.001*
August versus September	11.03	1	< 0.001*

This is a crude analysis since amalgamation of categories reduces the degrees of freedom. Also, it does not indicate which instar groups are changing between months. To locate diapause within each year group it is necessary to consider the growth of each cohort separately.

4.3.3 Location of diapause

The mean head width for each cohort in each month is displayed in Fig. 4.11. Increases in mean head width for all cohorts occurred between May and September indicating that growth was concentrated between these months in all cohorts (consistent with the above analysis). Fluctuations in mean head width for cohort 2 during winter were probably produced by differences in availability of instars A and B rather than cohort growth.

In order to investigate in which instar groups each cohort overwinters and locate diapause, if any, the modal instar group for each cohort in each month (Table 4.4) and the percentage of individuals found in each of the instar groups in each month are examined (Fig. 4.10 –all groups, Fig. 4.12 – last three instars only). To investigate the location of diapause, if any, it is necessary to examine in which instar groups growth occurred when growth resumed in the population in spring.

Cohort 1 larvae overwintered in their second year in a range of instars, from D to F (Fig. 4.12). Between October and March, the percentage of individuals in F, the final instar ranged from 0 to 4% of the cohort with the rest of the individuals being divided equally between instars D (μ%= 47.8 ± 4.4) and E (μ%= 49.7± 3.7). Between the March and May sample, individuals moved from instars D to E (53% in May) and from E to F (33% in May). (Fig. 4.12), This left only 15% of the cohort in D by May. Between May and June, 86% of the population had moved to the final instar and emergence had begun. By July most individuals had emerged and cohort 1 made up only 7% of the total larval population. Emergence began in May at Glan-yr-afon Uchaf. Fig. 4.12 shows that, when emergence began 67% of the population were still in the penultimate and antepenultimate larval instars.

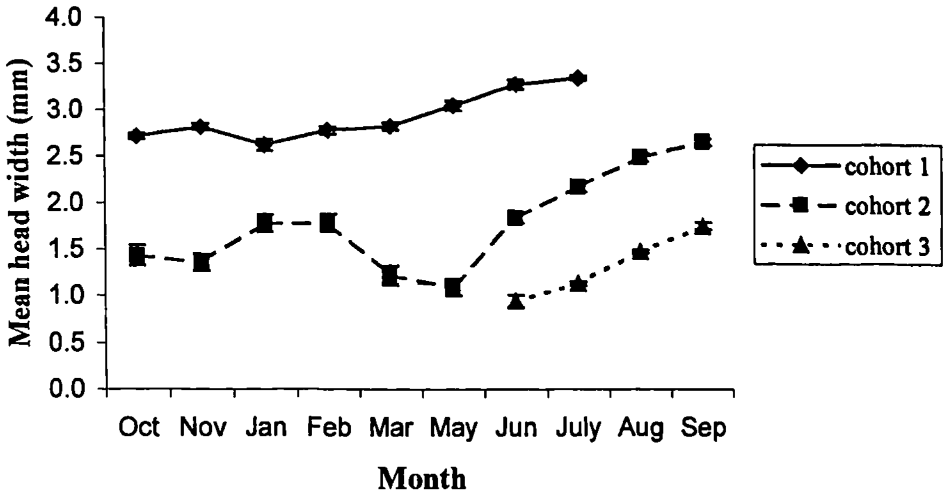


Fig 4.11 Mean head width (± s.e.) for each cohort in each month for *C. mercuriale.*

Table 4.4 Modal instar group for each cohort in each month for *C. mercuriale.*

	cohort 1	cohort 2	cohort 3
October	D	C	-
November	E	C	-
January	D	C	-
February	E	C	-
March	E	A	-
May	E	A	-
June	F	C	A
July	F	C	B
August	-	D	C
September	-	D	C

Cohort 2 larvae overwintered in a range of instars, between groups A to C (from instars 2 to 10) in their first year (Fig. 4.10, Table 4.4). Due to the disappearance of instars A and B in January and February it is difficult to estimate the proportion of the cohort that overwinter in each of these instar groups. Growth resumed in May and by June most individuals had entered instar group C. Individuals did not seem to move from C to D until July. By September all the cohort had entered instars D (79%), E(15%) and F(7%) – Fig. 4.12, 4.10. Since growth occurs between September and October, more individuals will probably pass from D to E before the second overwintering.

Cohort 3 appeared in early June (Fig. 4.10, Table 4.4). Given that the hatch period in captivity is around three weeks and hatch periods in the field are usually longer, this suggests that oviposition must have started in early May. Having hatched, between June and September cohort 3 passed rapidly through instars A, B (99% of cohort in July) and C (83% of cohort in September) – Fig. 4.10. This is further evidence that there is no diapause in the egg in *C. mercuriale.*

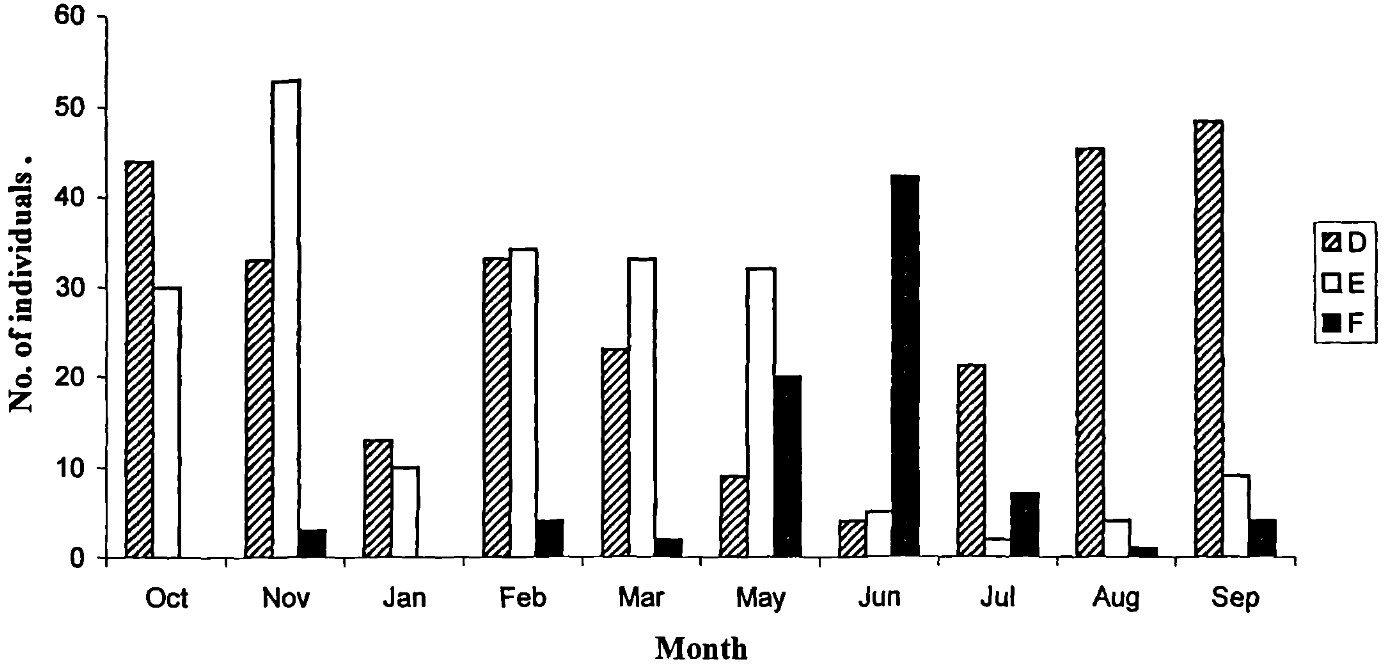


Fig. 4.12 The number of individuals found in each of the last three instars in each month (cohort 2 appears in D and E in July and August and in D, E and F in September. All other bars refer to cohort 1).

4.3.4 Size distribution of cohorts of larval *C. mercuriale*

4.3.4.1 Ratio of body size between cohorts

The degree of separation of body size between cohorts determines the potential for intraspecific predation and similarly the degree of overlap determines the potential for intraspecific competition. The former can be expressed as a ratio between the largest and smallest co-occurring instar groups (Wissinger 1988a). Here, the ratio of mean head width of instar groups A and F was used. The value of this ratio ranged from 1.65 (Jan) to 6.16 (May) with a mean of 4.89. The overwintering ratio (i.e. February) was 5.17.

4.3.4.2 Comparison of variation in larval size dimensions between *C. mercuriale* (a summer species) and *P. nymphula* (a spring species).

Figs. 4.13 - 4.14 show the relationship between head width and tibia length for *C. mercuriale* and *P. nymphula* respectively with individuals marked according to their instar (or instar group). *C. mercuriale* larva could not be divided into instars (of which Corbet(1955) suggested there were 13) but only into six groups some of which corresponded to two or more instars. *P. nymphula* larva could be divided among all 12 instars, which follow the pro-larva. Instar groups for *C. mercuriale* are less discrete than those for *P. nymphula*. The residuals from a regression of head width on tibia length for *C. mercuriale* showed significantly more variation than those derived from the same regression for *P. nymphula* (Levene's test statistic=6.707, p=0.010, σ_{cm} = 0.1351, n=1195, σ_{pn}=0.0945, n=116). Since the Levene's test accounts for differences in sample size, the additional variation between *C. mercuriale* larva was not produced by the larger sample size for this species. Variation in head width also seemed to decrease as development proceeded through the last three larval instars of *C. mercuriale*.

Table 4.5 Coefficients of variation in size dimensions (head width for larvae and left forewing length for adults) for developmental stages of *C. mercuriale and P. nymphula.*

		C. mercuriale		*P. nymphula*	
Instar group	No of instars in group	*n*	V(%)	*n*	V(%)
A	5	71	17.6	14	31.1
B	2	199	14.2	31	9.7
C	2	351	15.1	32	5.5
D	1	273	6.5	17	3.9
E	1	214	4.8	4	2.0
F	1	83	4.1	-	-
Adults 1997	1	122	6.3	-	-

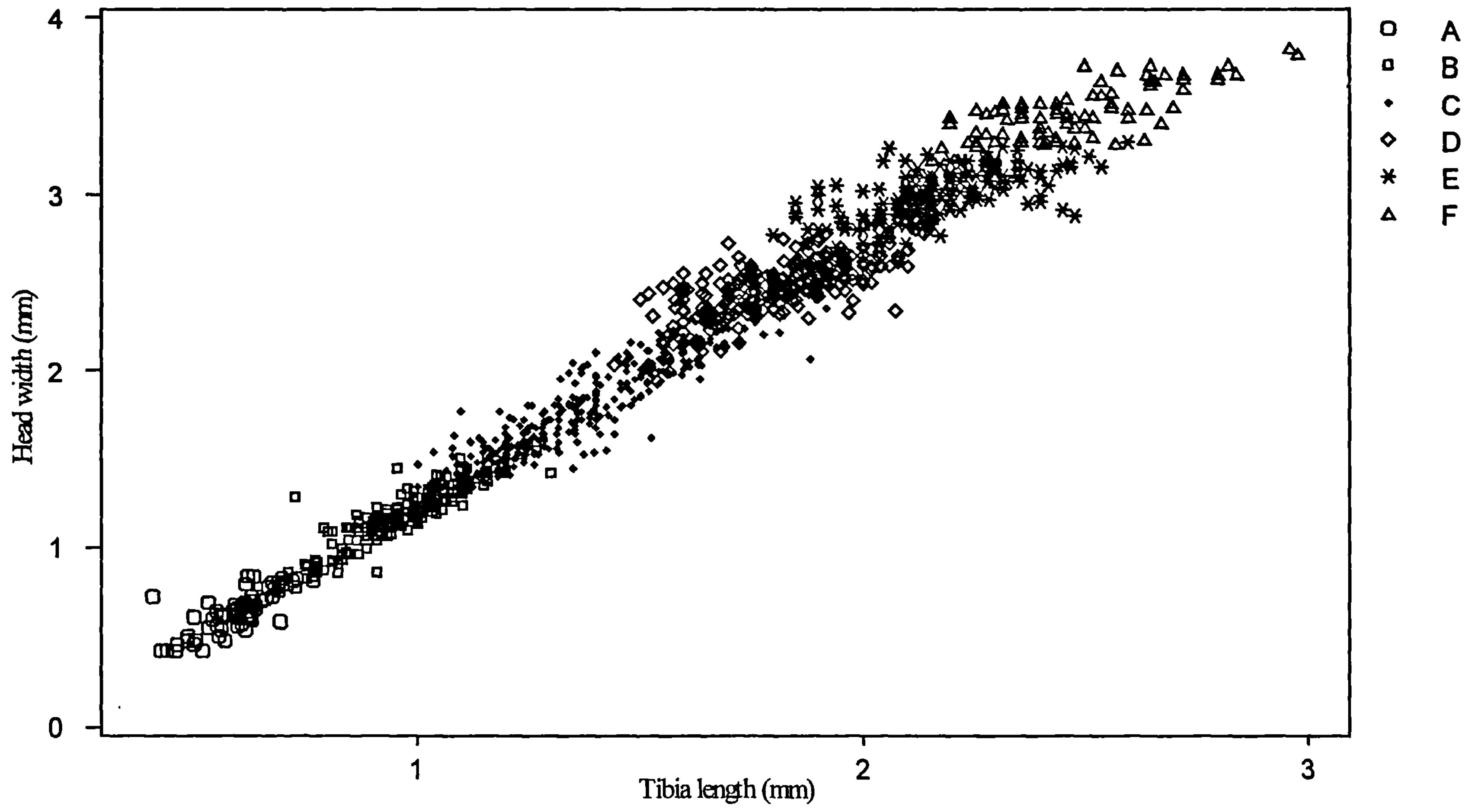


Fig. 4.13 Relationship between head width and tibia length for *C. mercuriale* larvae (n=1191) of different instar groups (see key).

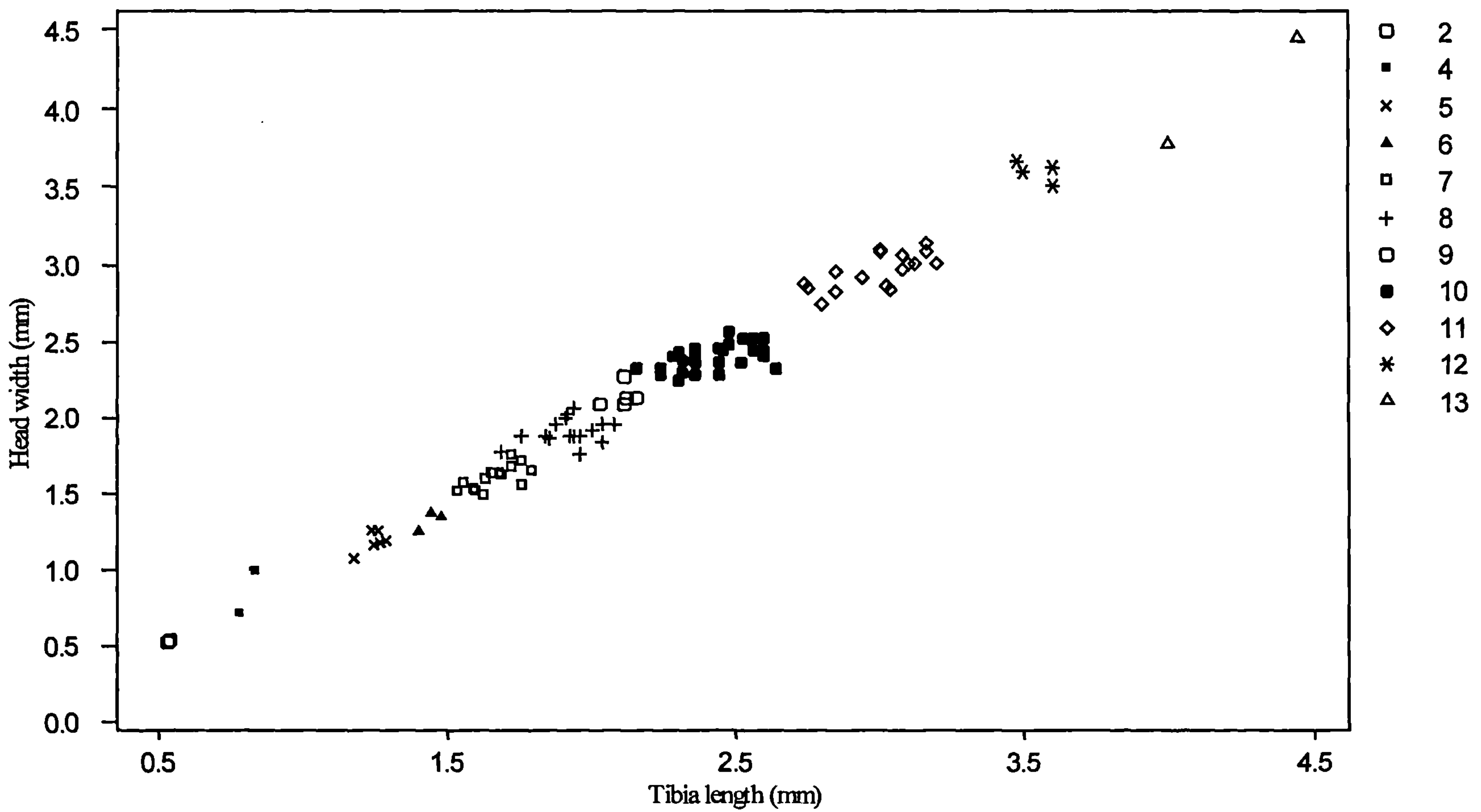


Fig. 4.14 Relationship between head width and tibia length for *P. nymphula* larvae (n=100) of different instar groups (see key).

4.3.4.3 Percentage increase in size dimensions between instars/ instar groups

Percentage size increase between successive instars was calculated for example between A and B as (mean head width B – mean head width A)/ mean head width A. For *P. nymphula,* this was calculated between instars (Fig. 4.17), but also between instar groups as for *C. mercuriale* (Figs. 4.15 - 4.16) for comparison between the two species. Figs. 4.15 and 4.16 show a steady decrease in percentage size increase (in head width and tibia length) as development proceeds in *C. mercuriale* and *P. nymphula.* For wing bud length, percentage size increase is large when they appear (between B and C) but then decreases dramatically as development proceeds. When the percentage size increase for *P. nymphula* is examined in more detail, between successive instars, the same decrease as development proceeds is found for head with and tibia length. For wingbud length, there is considerable fluctuation in percentage size increase as development proceeds.

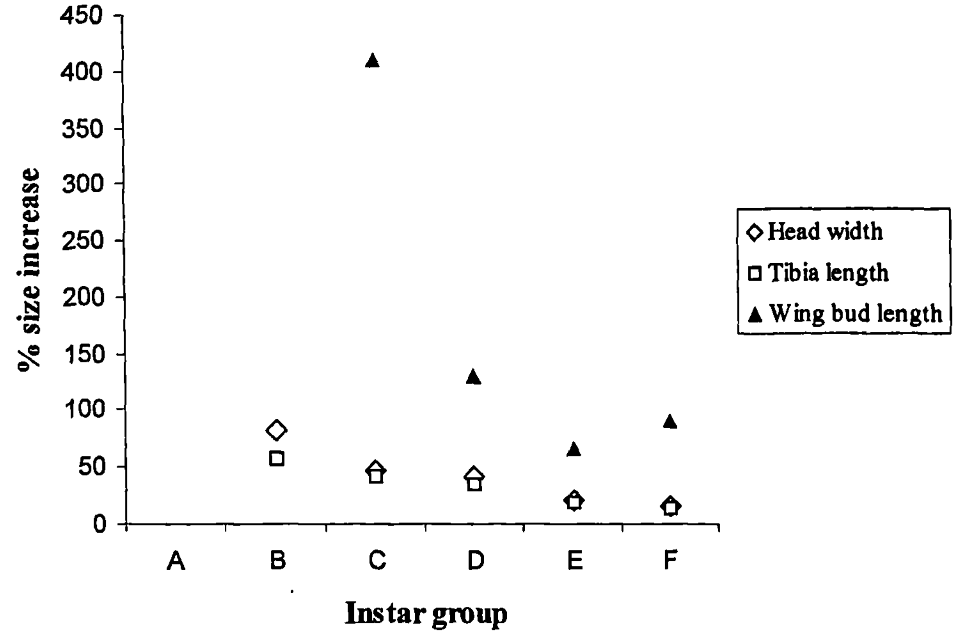


Fig. 4.15 Size increase between instar groups for *C. mercuriale* expressed as the percentage increase in head width, tibia length and wing bud length.

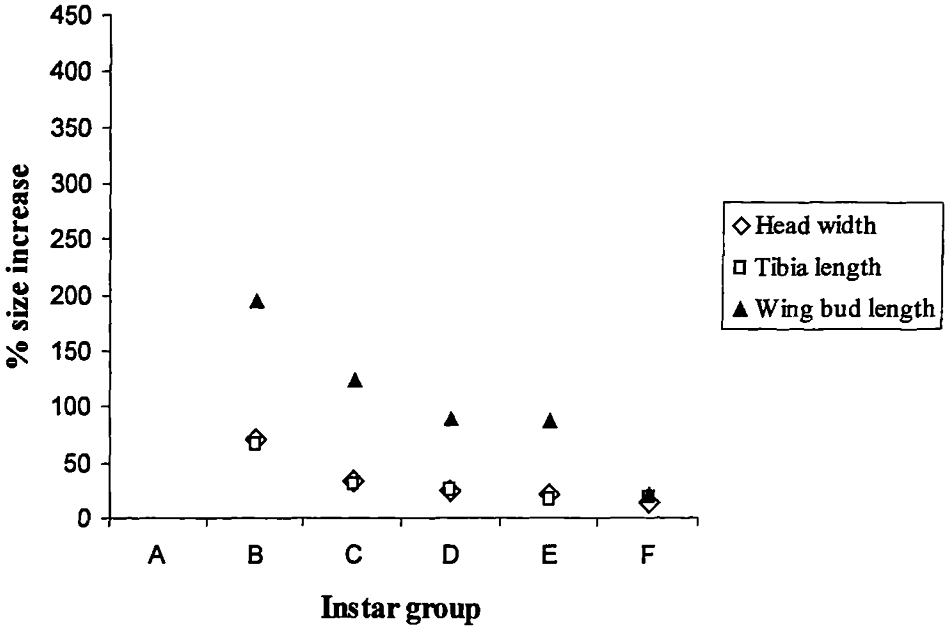


Fig. 4.16 Size increase between instar groups for *P. nymphula* expressed as the percentage increase in head width, tibia length and wing bud length.

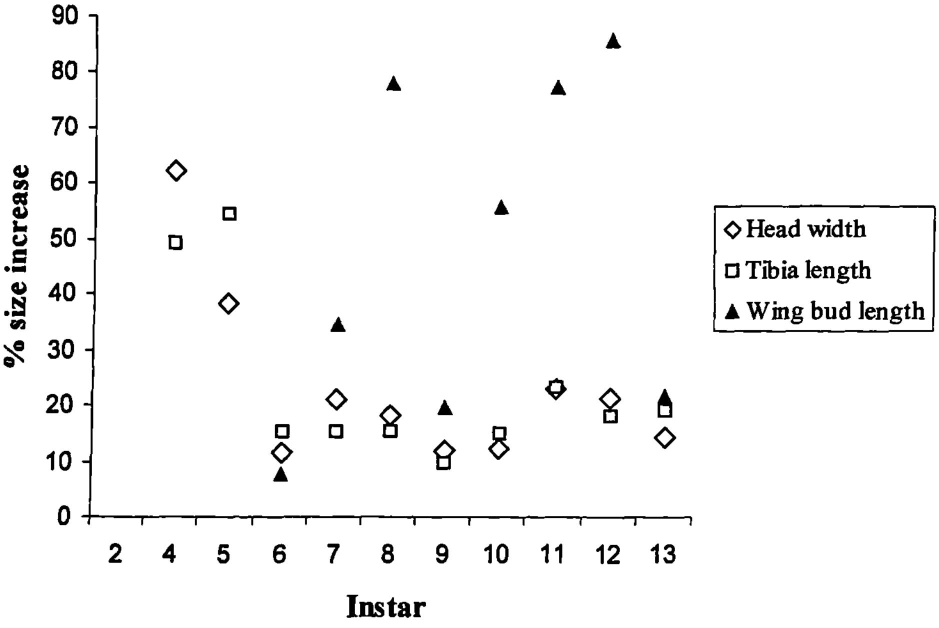


Fig. 4.17 Size increase between instars for *P. nymphula* expressed as the percentage increase in head width, tibia length and wing bud length.

4.3.5 Larval sex ratios and sexual size dimorphism in *C. mercuriale*

Since individuals could only be sexed at head widths greater than or equal to 1.7mm, instars A, B and C were omitted from these analyses. Sex ratio only differs from unity in *C. mercuriale* for instar E (penultimate instar) in which there is a significant excess of females. For *P.nymphula*, there is no evidence that the sex ratio differs from unity, though there are less data available to test this.

Table 4.6 Numbers of males and females in each instar group of *C. mercuriale* (summed across all months) and chi-square tests (Yates corrected) for a difference of the sex ratio from unity.

Instar Group	Males	Females	χ^2	*p-value*
D	134	140	0.091	0.763
E	90	122	4.533	0.033*
F	46	37	0.771	0.379
Adults 1997	71	69	0.065	0.798

Table 4.7 Numbers of males and females in each instar of *P.nymphula* (summed across all months) and chi-square tests (Yates corrected) for a difference of the sex ratio from unity.

Instar	Males	Females	χ^2	*p-value*
8	12	4	3.06	0.08
9	5	0	3.20	0.07
10	13	14	0.00	1.00
11	10	7	0.24	0.63
12	2	2	-	-
13	1	1	-	-

Female are significantly larger than males in head width and tibia length for instars D to F (Table 4.8 - 4.9). For wing bud length, females are larger than males for instars D and E but not in the final instar (Table 4.10). If size specific predation on larvae produces male biased sex ratios, one would predict that the degree of bias in sex ratio towards males would be proportional to the degree of size dimorphism between males and females. This relationship is shown in Fig. 4.18 (for instar-month combinations in which there were more than 5 individuals) but is not significant (Spearman's rank correlation r_s =0.378, p=0.082, n=15).

Table 4.8 T-tests comparing head widths in males and females for instars D to F (*=tests, which do not assume equal variances).

Instar Group	n_m	n_f	$\mu_m \pm$ se	$\mu_f \pm$ se	t	d.f.	p
D*	148	125	2.42 ± 0.01	2.33 ± 0.01	-5.93	268.8	< 0.001
E	94	118	2.93 ± 0.01	3.05 ± 0.01	-6.67	210	< 0.001
F	44	39	3.46 ± 0.02	3.51 ± 0.02	-2.39	81	0.0095

Table 4.9 T-tests comparing tibia lengths in males and females for instars D to F(*=tests which do not assume equal variances).

Instar Group	n_m	n_f	$\mu_m \pm$ se	$\mu_f \pm$ se	t	d.f.	p
D*	148	125	1.76 ± 0.01	1.86 ± 0.01	-5.82	270.8	< 0.001
E	94	118	2.09 ± 0.01	2.22 ± 0.01	-7.37	210	< 0.001
F	44	39	2.39 ± 0.02	2.58 ± 0.02	-5.74	81	< 0.001

Table 4.10 T-tests comparing wing bud lengths in males and females for instars D to F (*=tests which do not assume equal variances).

Instar Group	n_m	n_f	$\mu_m \pm$ se	$\mu_f \pm$ se	t	d.f.	p
D	148	125	1.21 ± 0.02	1.31 ± 0.02	-4.08	271	< 0.001
E	92	117	2.00 ± 0.03	2.16 ± 0.02	-7.37	210	< 0.001
F*	44	39	3.91 ± 0.05	3.96 ± 0.10	-5.01	55.1	0.3095

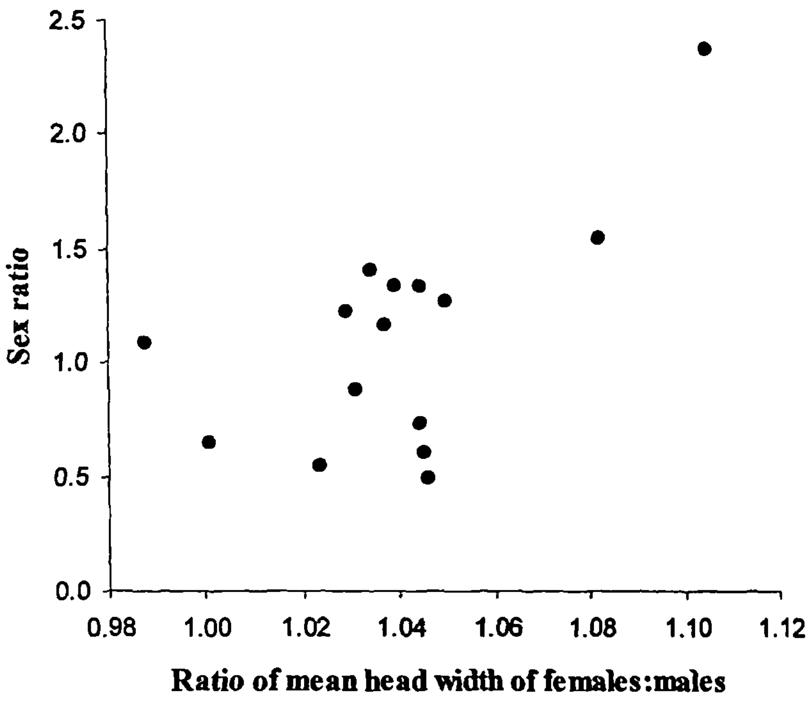


Fig. 4.18 Relationship between sex ratio (males:females) and ratio of mean head width (females:males)

4.3.6 Prey items of *C. mercuriale*

Harris (2000) deduced that the diet of larval *C. mercuriale* sampled at Glan-yr-afon Uchaf in 1999 included *Ephemeroptera, Diptera* (*Chironomidae* and *Simulidae*), and *Gammarus sp.* Whilst a large proportion of prey items could not be identified no parts of *C. mercuriale* were found in samples. Chironomids made up a large proportion of individuals present in sample of invertebrates taken from Glan-yr-afon Uchaf in March 2000 (see Appendix 7).

4.4 Discussion

Here voltinism, growth and diapause in *C. mercuriale* at Glan-yr-afon Uchaf is discussed in the context of core populations of this species and of other odonates. Seasonal regulation of this species is examined in the light of information obtained in Chapter 3. First the tolerance of larvae to variation in habitat factors is described.

4.4.1 Variation in larval abundance and physical stream parameters

Pyrrhosoma nymphula make up a small proportion of the population on this length of stream. At Waun Fawr in Pembrokeshire, Evans (1989) found that where there were high densities of *C. mercuriale* larvae this species did not usually co-occur with other species such as *P. nymphula*. *Orthertrum coerulescens* and *Cordulegaster boltinii* were sometimes found to share the same stream sections (Chapter 2). There was no correlation between the number of *C. mercuriale* and the number *of P. nymphula* in a particular month. This could be due to differences in habitat use by these species or differenced in monthly variation in mortality factors. Low numbers *of P. nymphula* may have made a correlation difficult to detect.

There was considerable monthly variation in width, depth, and flow rate of the small streams in the study area. This produces monthly variation in the efficacy of sampling methods but may also influence development in *C. mercuriale* as discussed in Chapter 2 For example, in mayfly larvae, Sweeney (1978) found that individuals reared in fluctuating temperature regimes had increased development rates compared to those reared in constant temperature regimes. In addition, small, exposed streams have large diel temperature regimes with a rate of temperature increase of up to 3.3 °C per hour. In contrast, the maximum rate of temperature increase in rivers is around 1.17°C per hour (Ward 1982). Such habitats will heat up quickly in summer and allow larval development and emergence to proceed quickly (see Chapter 3). Their presence has been cited as one of the four factors of importance in determining the presence of *C. mercuriale* populations in Germany (Buchwald 1994) and was found to be associated with adult and larval populations in Britain in Chapter 2.

4.4.2 Voltinism and length of the growth period in *C. mercuriale*.

C. *mercuriale* is semivoltine at Glan-yr-afon Uchaf, which is consistent with the work of Corbet (1957b), who carried out monthly samples at 4 British sites (2 in the New Forest, 2 in the Gower), and with single 'snapshot' samples taken in Pembrokeshire (Evans 1989) and Devon (Knights 1983). In mid-European populations (such as those in Baden-Württemburg) 2 years are required to complete larval development (Sternberg *et al.* 1999). However Thelen (1992) found that development could be completed in one year when industrial cooling waters increased the water temperature to over 25°C. This has lead some authors to speculate that univoltinism might be obligate in Mediterranean populations (Sternberg *et al.* 1999) and may also occur in slow running, shallow spring canals (e.g. East Germany), which warm up in summer (Buchwald *et al.* 1989). There are currently no data to support this speculation. In *C. mercuriale* then, there is likely to be regional variation in voltinism depending on temperature and perhaps the productivity of the habitat.

Such regional variation in other odonates has been attributed to a variety of factors including latitude (Thompson 1978b) temperature (Leggott & Pritchard 1985) and increased larval density (Banks & Thompson 1987). For example, *P. nymphula* normally takes two years to develop in Britain (Corbet 1957a; Lawton 1970b; Corbet & Harvey 1989) but some individuals may take three years when there is a large year group (Macan 1964) probably because interference competition reduces growth rate (*cf* Gribbin & Thompson 1990a). Corbet (1957a) found that some individuals were univoltine in Southern England. Given that voltinism changed within one generation in the German population subjected to temperature increase, this would suggest that voltinism is a plastic trait in *C. mercuriale*. In contrast, in *Aeshna cyanea* (Schaller 1962 (cited in Parr 1970)) voltinism is genetically determined, at least in response to temperature. Few odonates show genetic adaptation to temperatures in the temperate zone, despite being insects of tropical origin (Leggott & Pritchard 1985). For example, individuals from three populations of *Argia vivida* from habitats with different thermal regimes showed similar rates of egg and larval development when reared at constant temperature. Whilst this lack of adaptation allows plasticity in response to environmental change, it may also limit the degree to which odonates (including *C. mercuriale*) have expanded into Northern temperate regions. It would be interesting to examine the physical factors that determine voltinism in *C. mercuriale* along a latitudinal gradient and to examine biotic factors at the boundary where semivoltine and univoltine populations co-exist. Whether differences in developmental patterns shown in field populations persist under constant laboratory conditions could be examined.

There was no change in the proportion of the month's sample found in each instar group, between November and late March, suggesting that no growth occurred in this period in *C. mercuriale*. When examined within each cohort (by plotting mean head width versus month), the main period of growth seems to occur between April and September and probably continues into October.

From its distribution it would appear that the primary factor limiting growth in winter in *C. mercuriale* is probably temperature. Lower temperature thresholds for growth have been described in other temperate odonate species (e.g. 10-12°C for *Coenagrion puella* (Waringer, 1984); 8°C for *Ischnura elegans* (Thompson, 1978); 12°C for *Lestes disjunctus* (Duffy, 1994); 11.3°C for *Argia vivida* (Leggott, 1985). The proximate cause of such thresholds may be the profound effect of temperature on activity (and thus the availability) of prey, and on the feeding rate of invertebrate predators, increasing attack rate and decreasing handling time (Thompson, 1978). In *I. elegans* (Thompson, 1978), the onset and termination of growth occurs at the temperature (8°C) at which the attack rate on prey increases sharply.

Sit and wait predation as opposed to active predation is a behavioural correlate of low growth rate and long larval development in coenagrionid species such as *Coenagrion puella* and *Ischnura elegans* (Lawton *et al.* 1980; Johnson 1991). Such species also have the capacity to survive food stress for long periods (Lawton *et al.* 1980). Such behaviour may be important in allowing *C. mercuriale* to persist in low productivity environments on the edge of its range.

Leggott & Pritchard (1985) point out that lower temperature thresholds which permit growth in *odonates* are usually higher than those for temperate zone Ephemeroptera and Plecoptera. Species of the latter orders often develop at temperatures below 5°C. The existence of a high lower temperature threshold for growth may constitute one of the ultimate factors determining the south-western distribution of *C. mercuriale* in Britain and Europe and its selection of thermally advantageous microclimates at a broad scale (Chapter 2).

4.4.3 Location of diapause

Seasonal regulation is described in Chapter 3 and, in particular, how the range of instars in which *C. mercuriale* overwinters in the second year accounts for its asynchronous emergence curve. Asynchrony is evident in the larval population at the point at which emergence begins (i.e. May in most British populations of *C. mercuriale* (Chapter 3, Jenkins 1995; Hold 1997). If we examine the May sample, it can be seen that, by the time emergence begins in the population, 67% of the second year larvae are still in the antepenultimate and penultimate instars. Similarly, Corbet (1957b) found that 50% of the age group had not entered the final instar by the time metamorphosis began. By June, 86% of the population were in the final instar and most had emerged by July.

With regards to the location of diapause, this study provides further evidence that there is no egg diapause in *C. mercuriale* (*cf* Corbet 1957b). Having hatched, individuals passed rapidly through instars A, B (99% of cohort in July) and C (83% of cohort in September) between June and September.

As soon as growth resumed in Spring, individuals passed from the antepenultimate instars into the penultimate (D to E) and final instars(E to F) rapidly. Later, in May, emergence from the final instar began. If there were a rising series of lower temperature thresholds for entry into successive larval instars (Corbet 1957b), transitions from E to F would begin after transitions between D and E. It may be that the temperature threshold for emergence from the final instar is higher than that for the preceding two larval transitions or the later appearance of this larval stage may be due to the low number of individuals in the final instar when growth resumed in Spring. These data are inconsistent with a series of rising temperature thresholds that synchronise development in Spring. However, they are not inconsistent with the existence of a facultative Autumn diapause in the penultimate instar (Corbet 1957b). This could be induced by decreasing photoperiod, such that larvae entering the penultimate instar in September and October would tend to remain there for winter but in March and April (when water temperatures are probably similar), ante-penultimate instar larvae would pass through the penultimate and final instars in quick succession. In this study in that second year individuals over-winter mostly in the antepenultimate and penultimate instars with only 4 % at maximum of individuals overwintering in the final instar (indicating the facultative nature of the diapause). Further experimental work (e.g. Lutz 1974) is required to determine the precise effect of temperature and photoperiod on diapause in this species.

4.4.4 Size distribution of larval cohorts, habitat use by different cohorts and the consequences for intraspecific interference competiton and predation.

Voltinism affects the size structure of the population and, therefore, the type and intensity of population interactions (such as competition and predation) that can occur in different stages (Butler 1984). In semivoltine populations, second year individuals co-occur with first year conspecifics. Wissinger (1988a) found that for two species of libellulids (*Libellula lydia* and *L. luctuosa)* some intraspecific predation always occurred when co-existing larvae differed by two or more instars. This predation increased in intensity as a function of the size difference between instars. In *C. mercuriale*, in most months, instar groups A and B coexisted with groups D to F thus there was at least two instars difference between the smallest and largest groups. The ratio of body size between co-existing cohorts ranged from 1.65 to 6.16. This is similar to the range of ratios for odonates in which intraspecific predation has been found to occur (e.g. *Libellula lydia*; 3.0-11.8, *L. luctuosa*; 1.6-6.9, *Epitheca cynosura 1.0-2.4*). Although there is the potential for intraspecific predation, within larval populations of *C. mercuriale,* there are several zygopterans in which it does not occur despite this potential (e.g. *Pyrrhosoma nymphula* - Lawton 1970a; *Ischnura elegans* - Thompson 1978a). No remains of *C. mercuriale* larvae were found in a limited sample of prey obtained from faecal pellets of *C. mercuriale* (Harris 2000) suggesting cannibalism is rare. However interference can occur in the absence of intraspecific predation. In the laboratory, Gribbin (1990a) found that interference suffered by small instars in presence of large conspecifics (i.e. due to aggressive exclusion from the best feeding perches) resulted in reduced growth rates, doubled mean development time and reduced mean head widths over the period of one instar.

A further consequence of interference competition may be differential habitat use between age groups. Instar groups A and B were not sampled consistently through the winter months, making up 0-4% of the population in January and February and then re-appearing to make up 22% of the population in March. A similar ‘winter disappearance’ of small instars has been noted in other populations of *C. mercuriale*, occurring from November to May in the New Forest (Corbet 1957b) and is widespread in other odonate populations (Corbet 1957a; Bennett & Mill 1993). In both univoltine (Johannsson 1978) and semivoltine (Corbet 1957c; Macan 1964; Lawton 1970b) odonate populations this has been attributed to the spatial separation of large and small instars between different microhabitats. For example *Anax imperator* hatches in *Potamogeton*, moves to *Litorella* for the first year of larval development and then to *Hypericum* for the second year.

All instars of *C. mercuriale* were found in the perennial plant substrate and no larvae were found in the peat layer on the base of the stream. In addition, the shallow, narrow streams at Glan-yr-afon are very finely divided into microhabitats that are unpredictable in terms of location and abundance. Therefore, spatial separation is probably achieved by large and small instars occupying different portions of the water column rather than by separation into different microhabitats. Small instars probably retreat further towards the base of the submergent vegetation (*Pyrrhosoma nymphula* Bennett (1993); Lawton (1970a)). Thelen (1992) found all instars in submerged vegetation and found larvae associated with plants that are available during the oviposition period (such as *Sium erectum*, *Nasturtium officinale*, *Phalaris arundinacea* and *Carex* sp.). He concluded that the larval developmental period is spent entirely in the vicinity of the oviposition site and that the perennial plant substrate is the most important component of the micro-habitat for *C. mercuriale* larvae. In contrast, Corbet, (1957b) observed that second year *C. mercuriale* larvae used patches of vegetation (such as *Hypericum* and *Eleogiton*) in shallow rapids over gravel, whilst the first year larvae were found in the organic silt amongst plant roots. However, the stratification of the sampling regime employed by Corbet, (1957b) was fairly crude.

The larval population of *C. mercuriale* shows more variation in size dimensions than that of *P. nymphula*, both within the age group and when divided into the same instar groups. This is due to differences in modes of seasonal regulation between these two species. *Coenagrion mercuriale*, being a summer species (Chapter 3), has a long emergence and thus oviposition periods. Adult emergence, mating and oviposition are well-synchronised in *P. nymphula* since it is a spring species (Corbet 1960). From eight emergence curves for *P. nymphula* in the literature (Lawton 1970b; Gribbin & Thompson 1991; Bennett & Mill 1993), it has been deduced that the duration of emergence ranges from 18 to 45 days in this species. EM_{50} (i.e. the number of days in which 50% of the population had emerged) was 6 days for the 1967 population and 17 days for the 1968 population (Lawton 1970b) which is similar to values obtained for other spring species. The duration of emergence in *C. mercuriale*, in contrast, is around 60 days and EM_{50} is 22 days. Thus the length of the hatch period will be greater for *C. mercuriale* and this coupled with differential growth in larvae will produce broader size distributions even within year groups (Johnson 1991) in comparison to *P. nymphula*. Wide within year class variation in larval size dimensions has been noted in previous studies on *C. mercuriale* (Corbet 1957b; Evans 1989). The consequences of this for interference competition have been discussed above.

Variation in head width seems to decrease as development proceeds through the last three larval instars of *C. mercuriale*. This may be due to the synchronising action of the diapause in the penultimate instar. Percentage size increase (in head width and tibia length) also decreases as development proceeds (D-F) in *C. mercuriale* and *P. nymphula*. This may occur because the efficiency with which food is assimilated (and is thus available for growth) decreases with increasing larval size (Lawton 1970a). Measurement of head width increases between instars in the field can be used to indicate field feeding rates (Pickup & Thompson 1990) when compared to head width increases of larvae fed at a maximum rate in the laboratory. In *Pyrrhosoma nymphula*, if the feeding rate falls below a maximum (for a particular temperature), size increases between instars are sacrificed in order to achieve more rapid development. (Lawton 1970a) By the same token, a comparison of head width increases between instars across field populations should indicate the relative extent to which one field population is food limited. Extent of food limitation could be compared between edge of range populations and core populations for *C. mercuriale*.

4.4.5 Larval sex ratio and sexual dimorphism

As with many other invertebrates, the sex determination mechanism in odonates predicts a sex ratio of unity in the zygote (Kiauta 1969). Thus any imbalances in sex ratio at emergence can be attributed to differential mortality of eggs or larvae which may arise due to sex-linked differences in form, activity or response to environmental factors. In common with other zygopterans (Corbet & Hoess 1998), an excess of males was found at emergence for *C. mercuriale* (see Chapter 2). Size selective predation on larger female larvae has been postulated as a mechanism by which mortality could have a disproportionate effect on females. It has been shown to operate when the predator is given a choice of instars which vary widely in size e.g. *Ischnura verticalis* by the pumpkin seed sunfish, *Lepomis gibbosus* (Dixon & Baker 1988).

Whilst female *C. mercuriale* larvae were significantly larger than males for the last three larval instars, the sex ratio in these instars and in the adult population from 1997, was not male-biased. The degree of male-bias in sex ratio, within an instar group, was not proportional to the degree of dimorphism (i.e. extent to which females are larger than males) in the group. Dimorphism may not have produced size selective predation since the differences in body dimensions between males and females were small despite their significance and may not be detectable by predators. Instead Baker (1992), having found sex-linked differences in activity and development rate of late instar larvae in *Ischnura verticalis,* suggested that higher predation pressure on the more actively foraging sex may produce biased sex ratios.

Despite male biased sex ratios at emergence, sex ratios in larval populations of other zygopterans have been found to be close to unity (Lawton 1972; Garrison & Hafernik 1981; Pickup *et al.* 1984; Baker *et al.* 1992; Duffy 1994). If sex-linked differences in activity or development arise only in late instar larvae, it may be difficult to detect differences in sex ratio before emergence.

In conclusion, *Coenagrion mercuriale* is semi-voltine and growth is prevented in winter in a population on the Northern edge of its range. A facultative Autumn diapause in the penultimate instar is the most likely mode of seasonal regulation in this species. The overlap of size distributions (and thus diet) within and between cohorts which result from this growth pattern may lead to intraspecific interference that may further increase mortality or decrease the rate of growth in edge-of-range populations.

Chapter 5 Habitat selection for emergence, oviposition and egg hatching by adult *Coenagrion mercuriale.*

5.1 Introduction

Habitat was described in Chapter 2 as an autecological concept that emphasises the interaction between a species and the physical structure of its environment (Samways 1994). For organisms to persist they must select habitat that meets the ecological needs of all the stages of their life cycle and habitat use is determined by selection on survival and reproduction, arising from differential fitnesses between habitats (Boyce 1999). Investigation of the proximate cues to which animals respond during habitat selection can help to elucidate features of the habitat that are required by the species (ultimate factors). These cues may have either a direct or indirect relationship with such habitat features i.e. either they are the features required or they indicate the presence of those features. In this chapter, the cues used for selection of habitat for oviposition and emergence are investigated for *C. mercuriale* and then related, where possible, to ultimate factors.

Whilst in some odonates, adults home to the water body from which they emerged (Uterzi *et al.* 1984), it is widely accepted that most adult odonates carry out active habitat selection (Corbet 1999). Wildermuth (1994) has suggested that odonate species respond to the features of their habitat in a hierarchical manner as indicated in the following scheme: Adults respond to the biotope at a large scale when flying at decimetres above the habitat (e.g. wet heathland/valley mire for *C. mercuriale*). At 0.5-5m above the habitat, they respond to cues features of the larval water body (small stream or runnel for *C. mercuriale*) whilst at 0-0.5m above the water they respond to the features of the oviposition site. More general cues are likely to be detected visually and while tactile or thermosensory cues will be used only at the final stages of the hierarchy. For example, Steiner (1948) found that *Leucorrhina dubia* distinguished between peat-bog water and other types of water by means of chemoreception.

As in other Zygoptera, *C. mercuriale* oviposits endophytically, i.e. females lay eggs *directly into the stems of submerged plants* by curving their abdomens onto the plant surface and making incisions in the plant wall with their ovipositor through which eggs are inserted. This study investigates the cues used by *C. mercuriale* at the ultimate stage of the hierarchy, by measuring the utilisation of a stem for oviposition once a pair has landed during caged and natural pair focals. Site utilisation for oviposition is then related to a variety of habitat variables that may be used as proximate cues and thus may relate to ecological requirements.

As discussed in Chapter 2, vegetation is used at all stages of the odonate life cycle (Buchwald 1992) and macrophytes are likely to feature highly among the proximate cues used for habitat selection. Even pioneer species such as *Orthetrum cancellatum* and *Libellula depressa* that live in habitats with little or no vegetation need areas with a minimum cover of submerged vegetation for some activities (e.g. roosting in unfavourable weather). Thus among the proximate cues investigated in *C. mercuriale*, many aspects of plant structure were included as well as other non-vegetative cues found to be important for oviposition site selection in other odonates (such as flow, shelter, water depth, temperature).

During habitat selection for oviposition, cues may indicate ultimate factors required by the larval stage, the egg stage and the adult stage. There is strong selection pressure for the female to select oviposition sites with habitat features that maximise the growth and survival of offspring (Buskirk & Sherman 1984; Ubukata 1984). There are a number of reasons for this. Firstly, there is no parental care in odonates so females can only influence offspring survival through the provisioning and placement of eggs. Secondly, the aquatic stage of odonates suffers an estimated 99 % mortality (Benke & Benke 1975) and survival and growth during this stage is strongly influenced by factors such as the amount of food, conspecific density, shelter and temperature (see Crowley *et al.* 1987 for a review and references in Chapter 4). Finally, the egg stage is immobile and movement during the larval stage is likely to be limited especially during early instars (Corbet 1962).

Females may select habitat features that minimise the costs of oviposition itself as well as attempting to maximise the subsequent benefits to their offspring. These costs may be the energy expended during oviposition; the loss of time and energy due to harassment by male conspecifics (Ubukata 1984; Waage 1987); and due to predation (Fincke 1982; Fincke 1986b; Michiels & Dhondt 1990). In particular, the latter directly influences longevity which is the primary determinant of mating success in a number of odonates (Fincke 1982; Banks & Thompson 1985b; Banks & Thompson 1987a; Koenig & Albano 1987; McVey 1988).

Previous oviposition habitat selection experiments have focused on territorial (Ubukata 1984; Waage 1987; Alcock 1990; Meek & Herman 1991; Wingfield Gibbons & Pain 1992; Tsubaki *et al.* 1994; Siva-Jothy *et al.* 1995), rather than non-territorial odonate species (Martens 1989; Michiels & Dhondt 1990; Martens 1992; Martens 1999, Rehfeldt 1990). In the former, oviposition does not usually occur in tandem and males guard patches of suitable oviposition habitat and, in doing so, gain access to mates (resource defence polygyny). Thus female choice of oviposition location is likely to be influenced strongly by the location and behaviour of conspecifics as well as by oviposition site quality. *C. mercuriale* in contrast is non-territorial and oviposition usually occurs in tandems which are rarely broken up by conspecific males (pers. obs) and thus oviposition site quality is likely to have an overriding influence on oviposition habitat selection.

Whilst this study focuses on microhabitat use by *C. mercuriale*, the aspects of a pair's oviposition behaviour that may be influenced by the species ecological requirements were also observed. To investigate how cues used for oviposition relate to the ecological requirements of the egg stage, egg-hatching success was measured in stems from focals carried out in natural conditions. Most studies have estimated egg mortality and larval mortality together or have tried to estimate egg mortality from the difference between egg input and density of early instar larvae (Macan 1964; Lawton 1970b). Since the latter are notoriously difficult to sample it is better to examine egg mortality from plant material left in situ until after the hatch period (Bennett & Mill 1995a). In this study, this technique was developed in an attempt to quantify possible sources of egg mortality in *C. mercuriale.*

During habitat selection for emergence, cues are only likely to indicate habitat features required by the teneral adult, to minimise the risk of predation and competition and for emergence to proceed quickly. In Chapter 3, daily variation in emergence was attributed to both time in season and duration of sunlight on the day before emergence. In this study, spatial variation in emergence between cages in relation to a number of habitat variables is investigated. Again, the 'plantscape' is likely to be important at this life stage, and the differential use of various plant species for emergence is examined.

Identifying the common features that constitute ecological requirements of a species and which cues are used by individuals to recognise them is particularly important in a rare species such as *C. mercuriale*. The availability of such features or cues may determine the distribution of adults between habitats within a site and may influence the distribution of populations across a species range. In addition, *C. mercuriale* occupies different habitats in different parts of Europe (Buchwald 1989) and Britain and it is interesting to consider to what extent ecological requirements are similar in different parts of its range.

5.2 Materials and Methods

5.2.1 Study site

This study was carried out at Upper Crockford. See Chapter 3 for a description of the study site.

5.2.2 Oviposition site selection

This experiment took place in June and July 1999 on a marked population of adults at Upper Crockford (see Chapter 3 for mark-release-recapture protocol). Focals were performed on marked ovipositing pairs. The duration and number of oviposition bouts on each stem were recorded as measures of the utilisation of an oviposition site. Two types of focals were carried out:

- Natural focals were carried out when pairs came to the stream to oviposit after copulation. Stems into which eggs had been laid were marked with coloured plastic pegs and covered with wire to prevent further oviposition. The location of the stem on site was marked with a flag.

- Caged focals were carried out on pairs found in tussocks (*in copula* or before copulation) or at the stream before oviposition. The pairs were placed into cages (see Chapter 3 for cage design and location) that had been in place since the beginning of the flight period, and thus contained vegetation that had not been used previously for oviposition. Stems were removed immediately after the focal for dissection ensuring data on egg deposition rate (whereas some stems from natural focals were not recovered after the hatch period). Given the difficulty encountered during natural focals in tracking pairs across boggy habitat, caged focals permitted the entire oviposition period of pairs to be observed without disturbance.

As well as recording the duration and number of oviposition bouts into a stem, a number of habitat variables were measured for each stem. Firstly, the time of day and temperatures (water and air) were recorded during each bout. The plant species, length of stem above water and vegetation patch size were recorded (patch size code was 1 for a single stem, 2 for a small patch containing between 2 and 10 stems and 3 for a large patch containing more than 10 stems). It was not possible to detect the small differences in flow found in the oviposition sites using the meters available (Chapter 4). Thus the importance of flow was measured by recording the distance of the stem from the nearest discernible area of flow and similarly, the importance of shelter was measured by recording the distance of the stem from the nearest tussock. In addition, the depth of water by the stem was measured. Observations were made on submerged oviposition and the presence of conspecifics and predators where appropriate.

5.2.3 Egg hatching success and egg deposition rates

Marked stems from natural focals were removed after 4 weeks, 1 week longer than the hatching period in captivity (Corbet 1955). After egg deposition (caged stems) or retrieval after the hatch period (natural stems) the plant material was put into tap water for 2-6 days. It was the transferred to a mixture of concentrated acetic acid and 96% ethanol in a 2:1 ratio for 24 hours. It was then cleaned in 96% ethanol before being preserved until dissection in 70% ethanol. Stems were dissected to remove the eggs (using micropyles protruding from the leaf surface as a guide to their location). The size and appearance of eggs change between oviposition and hatching. When they are laid, they are transluscent or white with a transparent chorion. Fertilised eggs then darken to become yellowish partly due to the tanning of chorion that occurs soon after oviposition (Waage 1978). When the eggs of *C. mercuriale* were then examined under a dissecting microscope, four forms were observed which corresponded to four types of development. Type 1 eggs had hatched successfully before stem removal and consisted of split yellow chorions, lacking in micropyles. Type 2 eggs consisted of segmented embryos with eyespots (at the end nearest the micropyle) and were heathly eggs in a late stage of development that would have been ready to hatch shortly after stem removal. Type 3 eggs had a yellow chorion with a milky interior and were heathly eggs in an earlier stage of development than type 2. Type 4 eggs had died during development before stem removal and were either translucent or blackened. Thus for each stem, the total number of eggs; the number of eggs in each developmental type, the plant species, the stem diameter (mean from 5 measurements of the area containing eggs) the total stem length and the length of stem covered by eggs, were recorded.

For each stem removed after caged focals, the total number of eggs, the plant species, the stem diameter (mean from 5 measurements of the area containing eggs) the total stem length and the length of stem covered by eggs, were recorded.

5.2.4 Emergence perch use

To determine, how perch preferences differ between species and sexes and whether perch preferences reflect the abundance of plant species in the cages, vegetation in each cage was searched for exuvia at the end of the study. Exuviae were removed and preserved in alcohol and the following was recorded; plant species, cage number, whether the stem was in an area of discernible flow and height of the exuvia above and below the water surface. Exuviae were sexed and then identified to species (see Chapter 4 for larval keys).

5.2.5 Description of vegetation communities used for emergence and oviposition

To survey the type of habitat used by emerging *C. mercuriale* and *C. tenellum*, the area of water enclosed by each cage was treated as a quadrat. Within each quadrat, the following variables were measured - percentage cover of each plant species; peat and water depths (mean of measurements at five positions); flow rate (using an electromagnetic flow meter) where depth was sufficient.

To survey the type of habitat used for oviposition, 1m x 1m quadrats were placed around each oviposition site and the percentage cover of each plant species within each quadrat was estimated. For comparison, the same procedure was carried out within quadrats placed at random in the stream habitat. Quadrats were classified according to the National Vegetation Community classifications (Rodwell 1991) and the European Community Corine System by inputting the percentage cover data into Tablefit version 1.0. This is an algorithm for computerised diagnosis of vegetation types that measures the goodness-of-fit between samples of vegetation and the expected species composition of each vegetation type (Hill 1989).

5.2.6 Review of plant species and communities used by *C. mercuriale* in other parts of its British and European range.

Literature on British and European *C. mercuriale* populations was surveyed for observations of a particular plant species or habitat feature being used for oviposition for emergence. Since some authors reviewed the observations of preceding authors, only observations made in a population and at a time that differed from other observations were considered to be discrete. Due to the paucity of references containing information on the use of plant species for emergence, only the observations of use of plant species for oviposition were tabulated.

5.3 Results

5.3.1 General oviposition behaviour

Only focals in which the entire oviposition period, from after copulation until the pair split up, were included in the subsequent analysis. Due to the difficulty of tracking pairs, of the 80 attempted, only 39 focals (19 caged and 20 natural) were completed. After copulation in tussocks next to the stream, pairs flew towards the stream and landed repeatedly on plant substrates. Females settled on the substrate while males either hovered upright on the prothorax of the female or perched on vertical structures above the female. Upon landing the female would curve her abdomen to bring her ovipositor in contact with the plant substrate. Often this contact lasted less than five seconds before the abdomen was held out straight again or rapid probing movements were performed with the ovipositior in a variety of positions until a 'suitable' position was found. Thus an oviposition bout was defined as a period in excess of five seconds when the female's ovipositor was in contact with the plant stem. Pairs usually oviposited in several stems (Fig. 5.1) with several bouts of oviposition (Fig. 5.2). Most pairs oviposited into one plant species during the oviposition (Fig. 5.3). The mean total duration of oviposition behaviour was 670.8 ± 49.4 seconds (*n*=36) and ranged from 244 to 1471 seconds. Due to loss of or damage to stems before dissection, total number of eggs laid on all stems used during the oviposition focal was only available for 13 pairs. The mean number of eggs laid by a pair was 90.5 ± 22.3 eggs and ranged from 23 to 337 eggs. These data, together with those described in Chapter 6, may suggest that females of *C. mercuriale* do not lay their entire clutch of eggs in one visit to the breeding stream. The female submerged to oviposit always up to her wings but submerged completely in 15.4% (6/39) of ovipositions. When the female submerged completely the male broke the tandem and flew to the nearest perch above the water where oviposition was taking place. The male usually left before oviposition was completed. In three focals, oviposition was terminated when the female was caught in sundew. Only 5% (2/39) of *C. mercuriale* pairs were affected by predators during oviposition. In one focal the female was caught (but released) by a water strider and in another, killed by a water spider. Whilst conspecifics did fly up to ovipositing pairs, this did not result in a change in oviposition behaviour.

Two sample t-tests were performed to investigate whether the focal pair's environment (i.e. caged or natural) had any influence on oviposition behaviour (Table 5.1). There was no difference between caged and natural focals in the total number of stems used, total number of oviposition bouts, total duration of oviposition, total number of eggs laid, mean duration of oviposition bouts and mean number of eggs laid in a bout. There was no difference between caged and natural focals in the number of plant species used (χ^2=2.82, 1 d.f., p = 0.093).

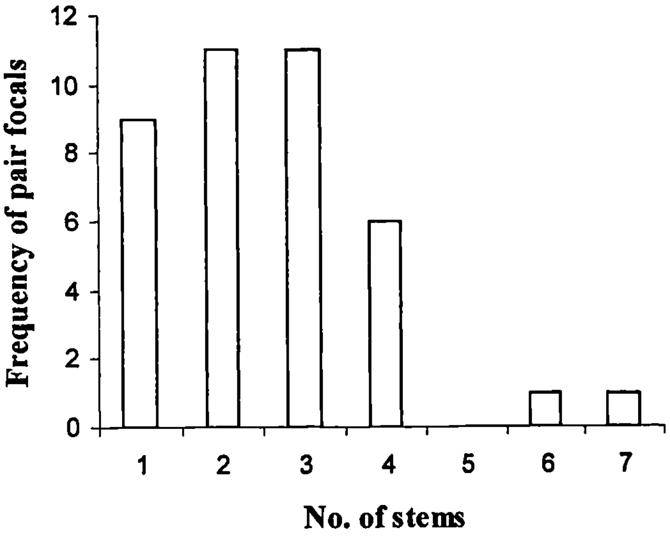


Fig. 5.1 Frequency distribution of the number of stems used by pairs during the oviposition period (*n*=39).

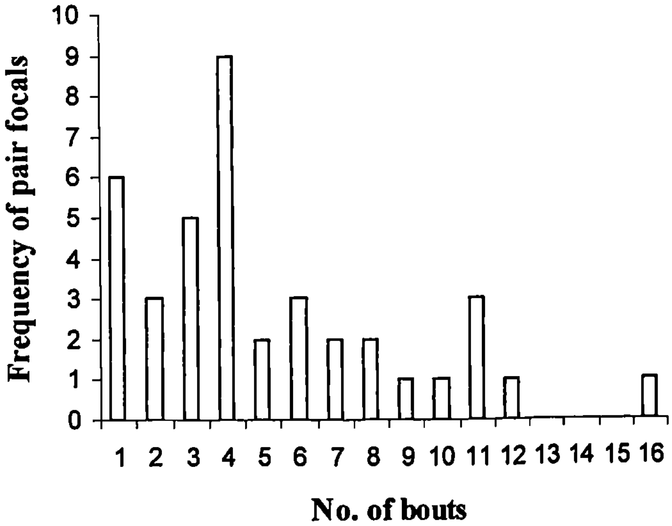


Fig. 5.2 Frequency distribution of the number of bouts of egg laying by pairs during the oviposition period (*n*=39).

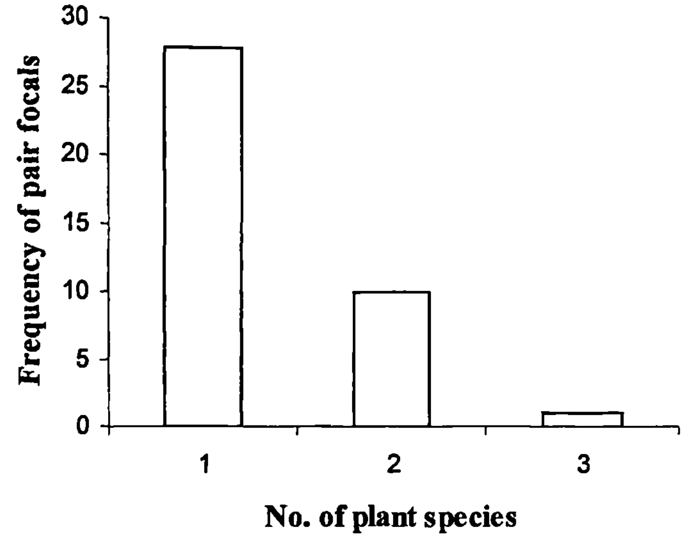


Fig. 5.3 Frequency distribution of the number of plant species used by pairs during the oviposition period (*n*=39).

Table 5.1 Two sample t-tests comparing the number of stems used, number and duration of oviposition bouts and eggs laid between caged and natural focals.

	Caged		Natural		t-tests		
Variable	*n*	$\mu \pm$ s.e	*n*	$\mu \pm$ s.e	*t*	d.f	*p*
Total number of stems used	20	2.80 ± 0.38	19	2.37 ± 0.90	0.997	29	0.33
Total number of oviposition bouts	20	5.70 ± 0.92	19	4.58 ± 0.69	0.965	37	0.34
Total duration of oviposition	20	650.05 ± 56.37	19	692.68 ± 83.68	-0.426	37	0.67
Total eggs laid (square-root transformed)	8	57.02 ± 12.50	18	83.94 ± 17.61	1.237	24	0.23
Mean duration of oviposition bouts	20	304.31 ± 34.69	19	322.26 ± 41.50	-0.333	37	0.74
Mean number of eggs laid in a bout	8	65.93 ± 13.74	18	40.71 ± 8.13	1.692	24	0.10

5.3.2 Measures of site utilisation for oviposition

Mean total duration of oviposition on a stem was 247.3 ± 21.9 seconds (n=195) and ranged from 10 to1073 seconds. Mean total number of eggs laid on a stem was 44.12 ± 8.39 eggs (n=30) and ranged from 0 to 353 eggs. Mean deposition rate (calculated from 29 stems into which one bout of oviposition occurred) was 14.06 ± 2.66 eggs per minute and ranged from 3 to 65.81. Site utilisation for oviposition was quantified at the level of the stem. 47 stems were used during the 19 caged focals and 62 stems were used during 20 natural focals. In some cases, several bouts of oviposition occurred on the same stem (Fig. 5.4). Thus two potential measures of site utilisation could be calculated for each stem- total duration of oviposition per stem (i.e. the sum of the duration of all bouts of oviposition on a stem) and total number of eggs laid into the stem.

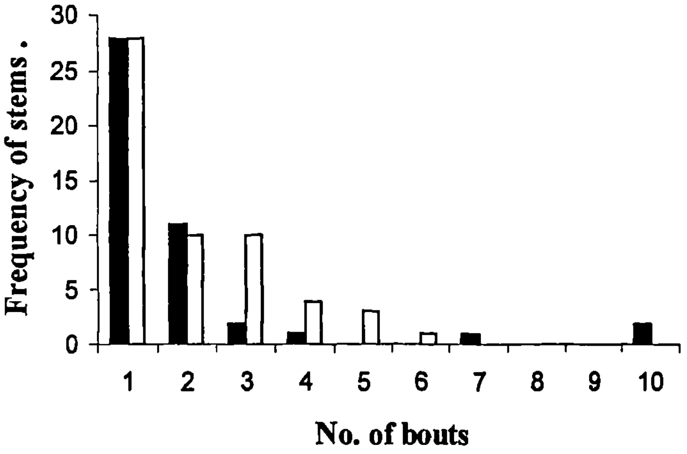


Fig. 5.4 Frequency distribution of stems on which different numbers of bouts of egg laying were performed, from caged (closed bars, n=45) and natural (open bars, n=56) focals.

However, in other zygopterans, eggs are not deposited during short initial periods of abdominal contact e.g. around 40 seconds in *Platycnemis pennipes* (Martens 1992). The duration of these non egg-laying 'test' bouts in *C. mercuriale* can be predicted from the y-intercept of a regression of the total duration of oviposition against the number of eggs laid (Fig. 5.5), for stems with only one oviposition bout. Since both these variables were measured accurately, use of a model I regression is permitted (Sokal & Rohlf 1995). There was no difference between stems from caged (c) and natural (n) focals with regards to total number of bouts into each stem (χ^2=5.58, 2 d.f., p=0.0314), total duration of oviposition (Wilcoxon two sample test; median_c=195.0, n_c=45; median_n=178.0, n_n=60; W=2986.0, p=0.209) and total number of eggs laid (Wilcoxon two sample test; median_c=31.0, n_c=40; median_n=28.5, n_n=22; W=1209.0, p=0.453). Thus both caged and natural stems could be amalgamated for the regression analysis.

Fig. 5.5 shows the value of the y intercept to be 8.819 with a 95% confidence interval of between 6.738 and 10.90. Thus the duration of non egg-laying 'test' bouts is predicted to be 77.8 seconds with a 95% confidence interval of between 45.4 and 118.8 seconds. Given that a substantial number of bouts in which eggs were laid fall below the y-intercept on Fig. 5.5, the length of a non-egg laying test bout is likely to lie close to the lower limit of the 95% confidence interval.

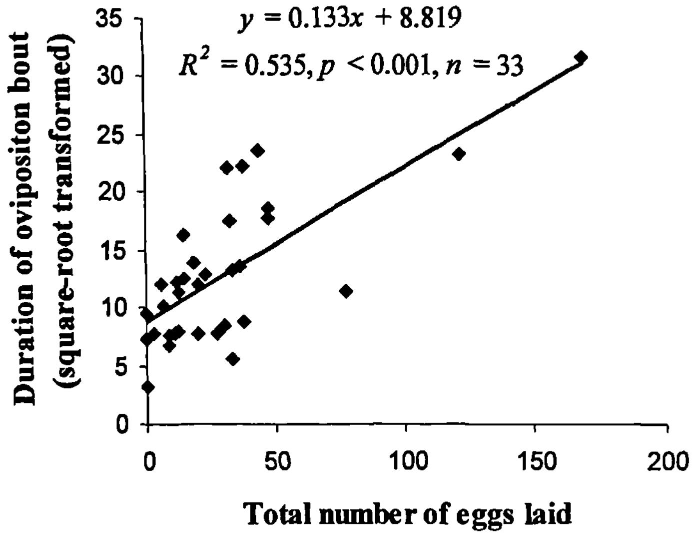


Fig. 5.5 Relationship between duration of an oviposition bout on a stem (in seconds) and the total number of eggs laid into it – for stems where only one bout of oviposition was recorded.

Almost 30% of all oviposition bouts observed were less than 50 seconds (i.e. near the lower limit of the 95% confidence interval – Fig. 5.6), suggesting that many bouts are non-egg laying 'test' bouts. This may lead to an over-estimation of the total duration of oviposition on some stems.

There was a significant positive relationship between total duration of oviposition on a stem and total number of eggs laid on a stem (Fig. 5.7) indicating that total duration of oviposition could be used as measure of site suitability for oviposition. An additional measure of site suitability was required since some stems were decomposed or lost before dissection such that the total number of eggs was not available for all stems. Total duration of oviposition was calculated with all bouts (uncorrected) and again without bouts that lasted for less than 40 seconds (corrected) in an attempt to remove 'test' bouts. However, although a substantial proportion of all bouts were less than 40 seconds (see above), for the 58 stems for which total eggs laid was available, performing the correction resulted in a different value of total duration of oviposition for only six stems. Thus corrected total duration of ovipositon did not differ from the uncorrected variable in its relationship with total number of eggs laid and thus was not a better measure of site utilisation for oviposition.

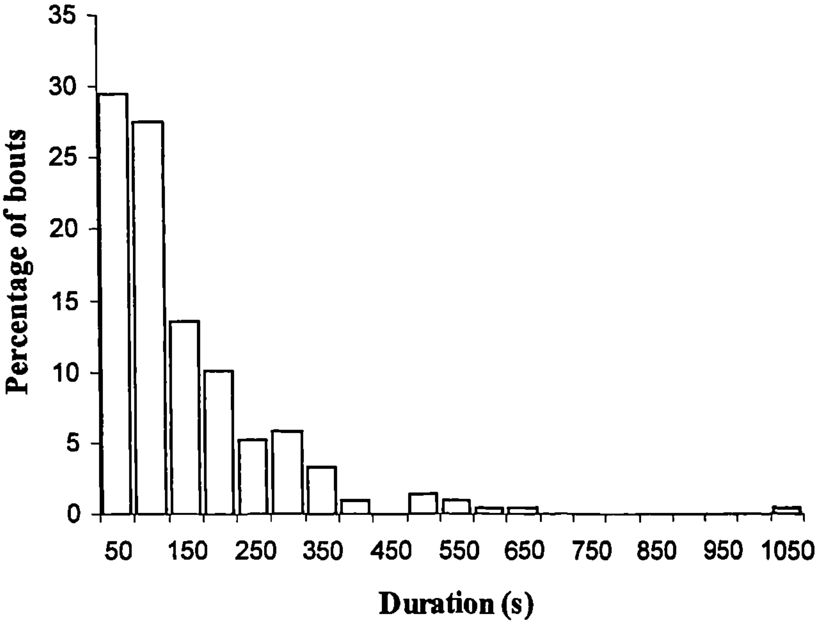


Fig. 5.6 Percentage distribution of duration for all bouts (n=207; bar labels indicate the upper limit of the class interval).

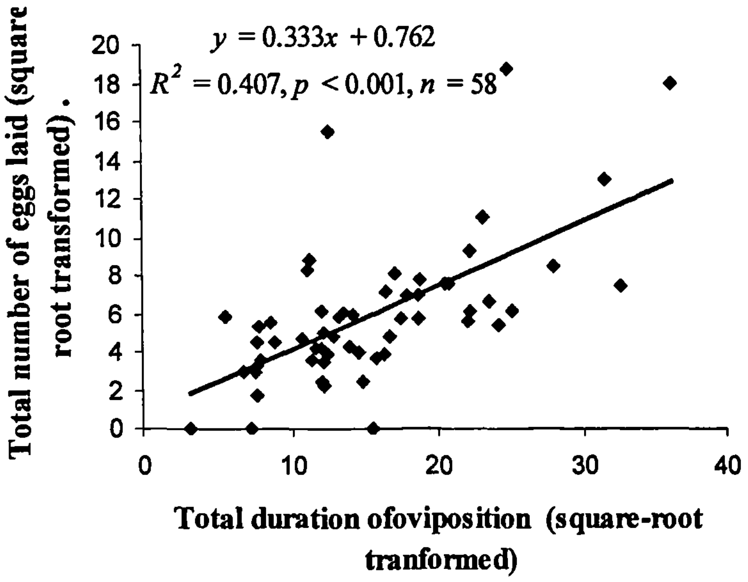


Fig. 5.7 Relationship between total number of eggs laid and total duration of oviposition on a stem (all stems).

5.3.3 Effect of habitat variables on site utilisation for oviposition

Two multiple stepwise regression analyses were performed (Stepping Method Criteria; probability of F-value = 0.05 for entry and probability of F-value = 0.10 for removal) with total duration of oviposition (square-root transformed) and number of eggs laid on a stem (square-root transformed) as the dependent variables. The following continuous predictor variables were available for these analyses; air temperature (10cm above water surface), water temperature (5cm below water surface), pH, water depth, distance from discernible flow (square-root transformed), distance from nearest tussock (i.e. shelter), length of emergent stem (square-root transformed), diameter of stem. When either of the two dependent variables was considered, none of the predictor variables was added to the model.

Three coded binary variable were created for total duration of oviposition. Stepwise logistic regression analyses were performed (Stepping Method Criteria; probability of F-value = 0.05 for entry and probability of F-value = 0.10 for removal) including continuous and categorical predictor variables. Continuous variables were: air temperature, water temperature, pH, length of emergent stem (square-root transformed), diameter of stem, water depth. Categorical variables were: distance from discernible flow (1=0cm, 2=1-50cm, 3=more than 50cm), distance from nearest tussock (1=0-50cm, 2=51-100cm, 3=more than 100cm), patch size (coded as above), and plant species. Again, none of the predictor variables was added to the model. Thus, the habitat use for oviposition can only be qualitatively described.

Table 5.2 Binary variables created for total duration of oviposition

Variable	Code	Definition
Duration^{50}	0	where 50 seconds of ovipositon or less occur on a stem
	1	where more than 50 seconds of ovipositon occur on a stem
Duration^{100}	0	where 100 seconds of ovipositon or less occur on a stem
	1	where more than 100 seconds of ovipositon occur on a stem
Duration^{median}	0	where 195 seconds of ovipositon or less occur on a stem
	1	where more than 195 seconds of ovipositon occur on a stem

Oviposition behaviour occurred at air temperatures of between 13.8 and 28.5 °C (μ=23.05 ± 0.36) and at water temperatures of between 18.1 and 29.9 (μ=24.96 ± 0.30). The pH of water in which oviposition occurred ranged from 5.5 to 7.9 (μ=6.67 ± 0.05). Whilst the depth of the water in which oviposition occurred ranged from 1.5 to 25 cm (μ=8.19 ± 0.55), 75% of ovipositions occurred at depths of 9cm or below. The distance from discernible water flow ranged from 0 to 4m (μ=62.1 ± 10.1) but 75% of ovipositions occurred within 80 cm of flow. The distance from the nearest tussock ranged from 0 to 2m (μ=61.4 ± 6.6). In addition oviposition always occurred on areas of stream with a dark brown peat rather than gravel substrate.

With regards to the features of the stem itself, oviposition occurred in stems with diameters of between 0.74 and 4.78 mm (μ=1.99 ± 0.10) and, in 75% of stems, only 4cm of the stem protruded above the surface of the water (μ=2.91 ± 0.37). The maximum distance (below water) between where eggs were placed on the stem and the surface of the water ranged from 0.9 cm to 8.7 cm (μ=3.8 ± 0.54, *n*=16), reflecting the distances attained when females submerge to oviposit. The distance along the stem covered by the egg clutch ranged from between 3mm to 52mm (μ=18.7 ± 0.17, *n*=38). 43% of stems used for oviposition occurred singly whilst 28% were positioned within a small patch (2-10 stems) and 29% were positioned within a large patch of vegetation (> 10 stems, *n*=97). The plant species and communities used for oviposition are discussed in sections 5.3.5 and 5.3.6.

5.3.4 Egg hatching success

Data on developmental types were available for eggs from only 20 stems from 10 ovipositions. The mean proportions of eggs from each stem that were of each developmental type are presented in Table 5.3. After these stems were removed (four weeks after oviposition), although 65% of eggs had hatched on average, 21% were healthy but in stages of development before hatching. This suggests that the hatch period of eggs can last considerably longer than four weeks in their natural environment. Since the stems were removed before healthy eggs had hatched and due to the low sample size of stems it was not possible to investigate, in detail, the effect of habitat variables on egg hatching success. Given the regular pattern of egg placement along stems it was possible to deduce that none of the stems considered had been used previously for oviposition.

Table 5.3 Mean proportion of eggs of each development type in stems after 4 weeks

Development types	Proportion of eggs laid into stem μ ± s.e.
1 – Hatched	0.656 ± 0.101
2 – Eye spot	0.093 ± 0.052
3 – Stages of development before eye spot	0.116 ± 0.060
4 – Deceased	0.136 ± 0.047

5.3.5 Frequency of plant use for oviposition

Coenagrion mercuriale used the following plant species (and parts) for oviposition at Upper Crockford; *Carex sp.* (petiole), *Cirsium dissectum* (stem), *Drosera rotundifolia* (stem), *Hypericum elodes* (stem), *Juncus articulatus* (stem), *Mentha aquatica* (stem), *Molinia caerulea* (stem), *Potamogeton polygonifolius* (petiole and central leaf surface). A preference for a plant species for oviposition could be inferred if it is chosen more frequently than expected from its abundance in the habitat and an avoidance of a plant species could be inferred if it is chosen less frequently than its abundance. Thus chi-squared tests were used to compare the frequency of plant use with plant abundance. In caged focals 47 stems of 4 plant species were used. The mean percentage cover across cages used for oviposition focals (Fig. 5.8a) was computed for all plant species and was multiplied by 47 to generate the expected frequency that each plant species would be used for oviposition. In natural focals, 62 stems were used of 7 plant species. The mean percentage cover across all quadrats placed around oviposition sites (Fig. 5.8b) was computed for each plant species and was multiplied by 62 to generate expected frequencies of plant use.

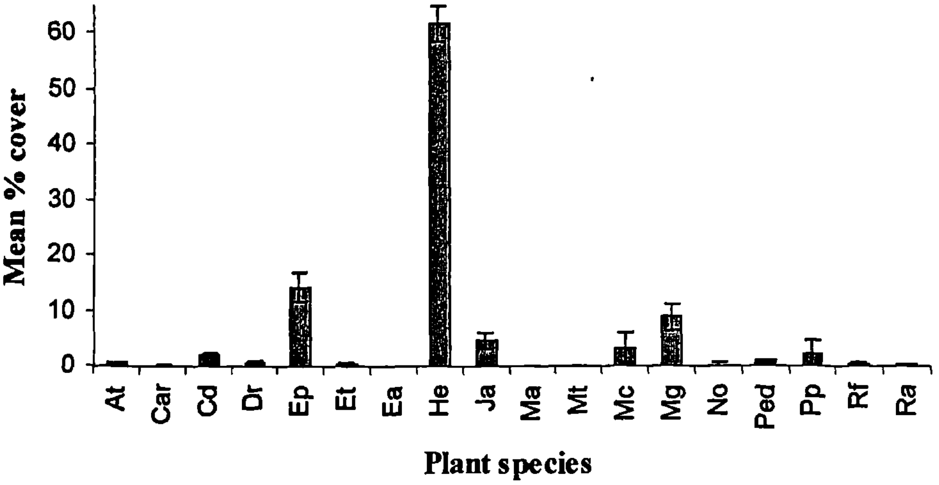


Fig. 5.8a Mean (± s.e.) percentage cover of plant species in cages used for focals.

Fig. 5.8b Mean (± s.e.) percentage cover of plant species in natural oviposition site quadrats.

Plant species key for Figs. 5.8, 5.9, 5.10 and 5.11: At - *Anagalis tenella*; Car - *Carex panicea* or *C. echinatum*; Cd - *Cirsium dissectum*; Di - *Drosera intermedia*; Dr - *Drosera rotundifolia*; Ep – *Eleocharis palustris*; Et - *Erica tetralix*; Ea – *Eriophorum*; He - *Hypericum elodes*; Ja - *Juncus articularis*; Jb - *Juncus bulbosis*; Mc - *Molinia caerulea*; Mg - *Myrica gale*; No - *Narthecium ossifragum*; Ped - *Pedicularis sp*; Pp - *Potamogeton polygonifolius*; Rf - *Ranunculus flaminula*; Ra - *Rhynchospora alba*.

For stems from caged focals, Fig. 5.9a shows observed and expected frequencies of use of each plant species for oviposition in cages. There is a significant difference between the observed (O) and expected (E) use of five plant species (χ^2=21.26, 4 d.f., $p < 0.001$; including only those species for which expected frequency of use was two or more). Table 5.4 shows that *Hypericum elodes* and *Eleocharis palustris* contribute to the chi-squared value. *Hypericum elodes* was used more often than expected from its abundance in cages whilst *Eleocharis palustris*, *Myrica gale* and *Molinia caerulea* were used less often than expected. For stems from natural focals, Fig. 5.9b shows observed and expected frequencies of use of each plant species for oviposition. Again, there is a significant difference between the observed (O) and expected (E) use of six plant species (χ^2=128.20, 5 d.f., $p < 0.001$; including only those species for which expected frequency of use was two or more). *Hypericum elodes*, *Potamogeton polygonifolius* and *Juncus articulatus* were used for oviposition more often than expected from their abundance whilst *Eleocharis palustris*, *Myrica gale* and *Molinia caerulea* were used less often than expected.

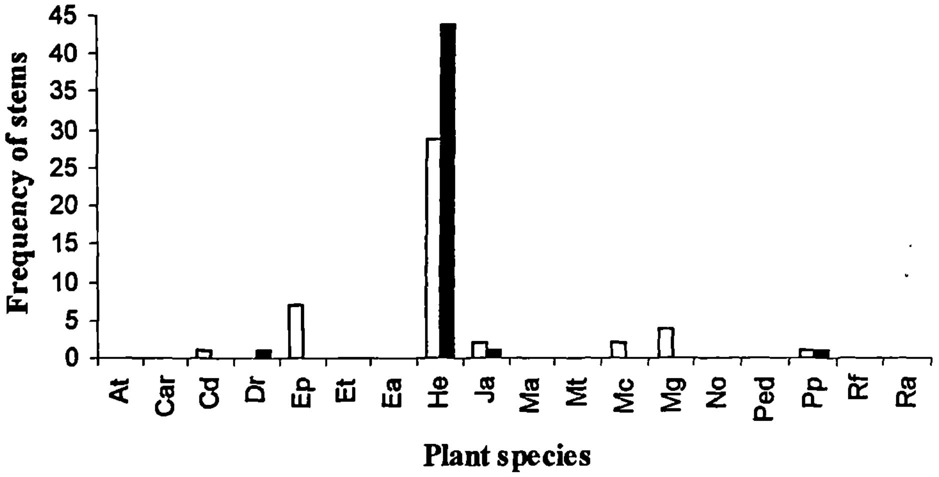


Fig. 5.9a Observed (closed bars) and expected (open bars) frequency of plant use for oviposition for caged focals.

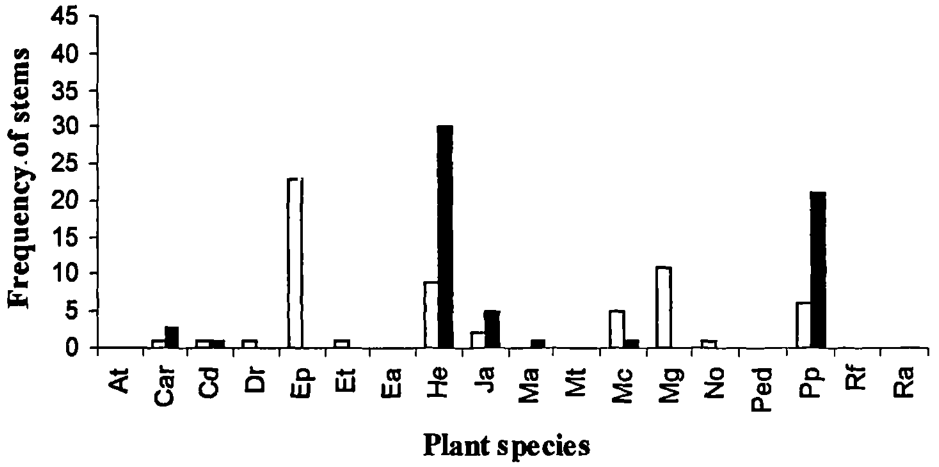


Fig. 5.9b Observed (closed bars) and expected (open bars) frequency of plant use for oviposition for natural focals.

Table 5.4 Chisquare test of difference between observed and expected use of plant species for oviposition.

	Frequency of stems from					
		Caged focals			Natural focals	
Species	E	O	$(O-E)^2/E$	E	O	$(O-E)^2/E$
Ep	7	0	7.00	23	0	23.00
He	29	44	7.76	9	30	49.00
Ja	2	1	0.50	2	5	4.50
Mc	2	0	2.00	5	1	3.20
Mg	4	0	4.00	11	0	11.00
Pp	-	-	-	6	21	37.50
		$\chi^2=$	21.26		$\chi^2=$	128.20

5.3.6 Plant communities used for oviposition

The abundance (percentage cover) of eight plant species (i.e. those species which covered more than 1% of a quadrat on average) were compared between quadrats around oviposition sites and quadrats positioned at random in the stream. Wilcoxon two samples tests (Table 5.5) were used since it was not possible to normalise the percentage cover variables using arcsine transformations. Oviposition and stream quadrats only differed significantly in the percentage cover of *Myrica gale*, which was higher in ovipositon quadrats. This probably reflects the presence of tussocks in 18 out of 25 oviposition quadrats.

Table 5.5 Wilcoxon two samples test for difference in % cover of particular plant species between oviposition quadrats (n=25) and all stream quadrats (n=22).

Plant species	Median$_{ovip}$ % cover	Median$_{stream}$ % cover	W	p
Carex sp.	2.57	1.52	605.5	0.099
Drosera sp.	0.38	0.54	537.5	0.838
Eleocharis palustris	48.5	39.6	596.5	0.147
Hypericum elodes	5.68	2.69	511.0	0.724
Juncus articulatus	3.12	0.00	609.0	0.072
Molinia caerulea	0.93	2.34	487.0	0.372
Myrica gale	4.60	15.00	380.0	0.002*
Potamogeton polygonifolius	3.87	4.95	469.0	0.207

The most common NVC plant community in both oviposition and stream quadrats was S19, or *Eleocharis palustris* swamp. Table 5.6 shows a similar distribution of oviposition and stream quadrats between a range of communities.

Table 5.6 Plant communities of oviposition and stream quadrats.

NVC Community	Name of community	No. of Oviposition quadrats	No. of Stream quadrats
S19, S19a, S19b	*Eleocharis palustris* swamp	11	13
M15, M15a	*Scirpus cespitosus-Erica tetralix* wet heath	6	3
M21b	*Narthecium ossifragum-Sphagnum papillosum* valley mire	0	1
M25a	*Molinia caerulea– Potentilla erecta* mire	2	0
M29	*Hypericum elodes – Potamogeton polygonifolius* soakways	6	5

5.3.7 Frequency of plant use for emergence

For both *C. mercuriale* (83.8% i.e. 62/74) and *Ceriagrion tenellum* (98.6% i.e. 69/70), exuviae were found in areas of discernible flow. The mean height of exuviae above water level was 3.64 ± 0.36 cm (n=74) for *C. mercuriale* and 2.35 ± 0.18 cm (n=68) for *C. tenellum.*

As for oviposition (Section 5.3.5), chi-squared tests were used to compare the frequency of plant use for emergence with plant abundance. The mean percentage cover across emergence cages was computed for all plant species (Fig. 5.10) and was multiplied by the total number of exuviae (70 for *C. mercuriale* and 64 for *C. tenellum*) to generate the expected frequency that each plant species would be used for emergence by each species.

For both species, the difference between observed and expected perch use (Fig. 5.11a-b) was significant (Table 5.7; *C. mercuriale*; χ^2=285.84, 7 d.f., $p < 0.001$; *C. tenellum*; χ^2=106.90, 7 d.f., $p < 0.001$). For both species *Eleocharis palustris*, *Juncus articulatus* and *Hypericum elodes* contribute most to the total chi-squared value. The former two are used more often than expected and the latter is used less often than expected for both species.

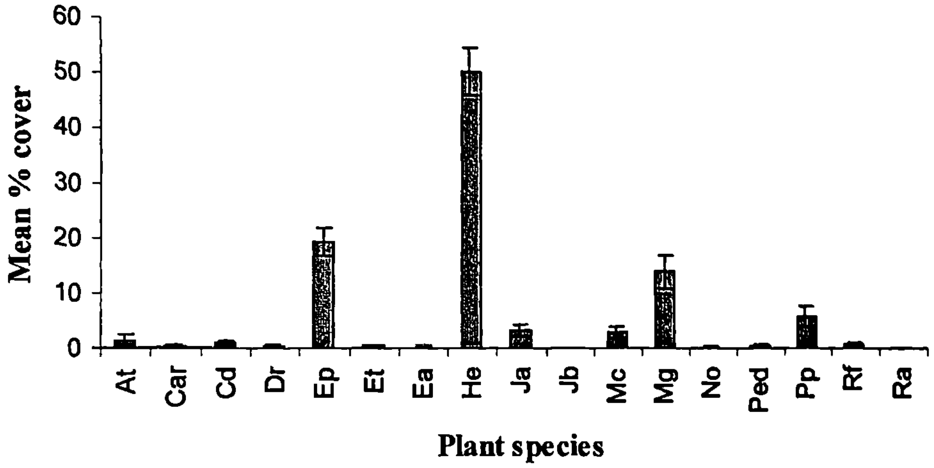


Fig. 5.10 Mean (± s.e.) percentage cover of each plant species in all emergence cages.

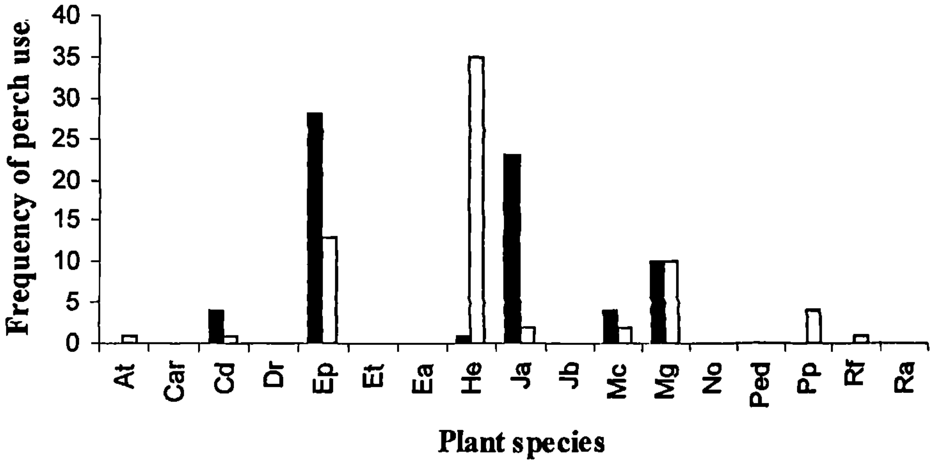


Fig. 5.11a Observed (closed bars) and expected (open bars) frequency of perch use by *C. mercuriale.*

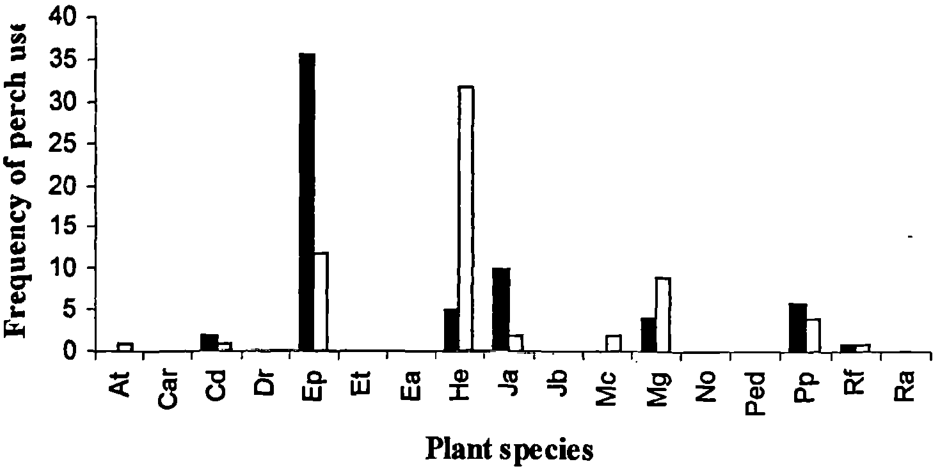


Fig. 5.11b Observed (closed bars) and expected (open bars) frequency of perch use by *C. tenellum*.

Table 5.7 Chisquare test of difference between observed and expected use of plant species for emergence.

	Frequency of perch use					
	C. mercuriale			*C. tenellum*		
Species	E	O	$(O-E)^2/E$	E	O	$(O-E)^2/E$
Cd	1	4	9.00	1	2	1.00
Ep	13	28	17.31	12	36	48.04
He	35	1	33.03	32	5	22.78
Ja	2	23	22.05	2	10	32.04
Mc	2	4	2.00	2	0	2.00
Mg	9	10	0.11	9	4	2.78
Pp	4	0	4.00	4	6	1.00
		χ^2=	285.84	χ^2=	106.90	

The frequency with which plants were used as perches was compared between *C. mercuriale* and *C. tenellum* using a chi-square test including only the five plant species used by both plant species (to eliminate the problem of low expected values). *C. mercuriale* and *C. tenellum* were significantly different in their use of these five plant species (χ^2=11.429, 4 d.f., p=0.002). *C. mercuriale* used *Juncus articulatis and Eleocharis palustris* most frequently whilst *C. tenellum* used *Eleocharis palustris* (Fig. 5.11a-b).

5.3.8 Literature review of habitat use for oviposition and emergence in *C. mercuriale*

Table 5.8 lists the 23 plant species that have been used for oviposition by *C. mercuriale* at Upper Crockford (UC), in other British heathland (BH) populations, in British chalk stream (BC) populations and in European (E) populations (limestone streams and calcareous spring mires). The number of observations (on distinct occasions in distinct populations) is given and the frequency of use in this study for comparison. In addition, the growth form, season and plant group are given for each species. The majority of species are soft stemmed herbs and are submerged or semi-emergent. Most are perennial i.e. live for at least three seasons and many are evergreen or semi-evergreen.

In addition, more than two authors stated that the importance of the following in oviposition sites; unshaded, open stream areas, lack of canopy, lack of dense or tall emergent vegetation, abundant submerged vegetation, and low or no water flow.

The use of specific plant species for emergence features in only two papers. In south west Germany, exuviae were found on *Schoenus* sp., *Juncus subnodulosus*, *J. alpinis*, and *Carex* sp. (Buchwald 1989) and, in Germany as a whole, *Sium erectum*, *Solanum dulcamara*, *Mentha aquatica* and *Nasturtium officinale* were also used (Sternberg et al. 1999). In Britain, Winsland (1997a) states that any suitable emergence support is used including the stems of grasses and rushes.

Table 5.8 Growth form, season and plant group of species used for oviposition by *C. mercuriale* in Britain and Europe.

		No. of Observations				
Plant species	Plant type	UC	BH	BC	E	Sources of Observations
Monocotyledons						
Grasses						
Molinia caerulea	Tussock-forming perennial with flat greyish leaves	1 (1%)				
Phalaris arundinacea	Tall stout creeping, emergent, evergreen perennial				2	Burbach 1997; Sternberg 1999
Sedges						
Carex sp.	Grass-like, emergent with solid stems		1	1		Hold 1997; pers. obs.
Eleocharis palustris	Creeping, emergent evergreen that forms small tufts				1	Grand 1996
Schoenus nigricans	Tufted, emergent stems up to 60 cm tall		3			Merritt 1983; Knights 1983; pers. obs.
Rushes						
Juncus sp. *(J. articulatus)*	Slender emergent herbs with cylindrical stems and hairless leaves	6 (5%)	3			Evans 1989; Knights 1983; Merritt 1983
Horsetails						
Equisetum fluviatale	Emergent, perennial with hollow ridged and jointed stems, dies down in winter		1			Woodman 1999
Dicotyledons						
Alisma plantago aquatica	Semi-emergent, hairless, perennial deciduous herb				1	Burbach 1997
Apium nodiflorum	Semi-emergent, creeping hairless, perennial herb		3	1		Merritt 1983; Cowley 1953; Strange 1999; Sage 1957
Apium inundatum	Semi-emergent, creeping hairless, perennial herb	1				Winsland 1997
Berula erectum	Semi-emergent, hairless, perennial herb				3	Burbach 1997; Martens 1999; Lunau 1934
Callitriche sp.	Submergent, creeping herb with slender stems				3	Martens1999; Burbach 1997; Grand 1996

Table 5.8 continued.

Plant Species	Plant Type	No. of Observations UC	BH	BC	E	Sources of Observations
Dicotyledons contd.						
Drosera sp.	Small, semi-emergent perennial evergreen herb, leaves covered with sticky red tipped gland-bearing hairs	1 (1%)				
Elodea canadensis	Semi-emergent, perennial aquatic herb				1	Grand 1996
Glyceria maxima	Semi-emergent, perennial herb			1	1	Hold 1997; Grand 1996
Hypericum elodes	Semi-emergent, creeping, grey hairy perennial herb	72 (64%)	2			Merritt 1983; Winsland 1997a
Mentha aquatica	Semi-emergent, creeping, downy, perennial herb	1 (1%)	0		2	Burbach 1997; Robert 1958
Nasturtium officionale	Semi-emergent, creeping hairless perennial				2	Burbach 1997; Grand 1996
Potamogeton sp. *(P. polygonifolius)*	Submergent, perennial herb with floating leathery leaves	32 (28%)	4		1	Evans1989; Merritt 1983; Winsland 1997a; Burbach 1997; pers. obs.
Rorippa nasturtium aquaticum	Semi-emergent, hairless creeping perennial herb			1		Strange 1999
Scrophularia sp.	Emergent, erect, hairless, perennial semi-evergreen herb				1	Burbach 1997
Solanium dulcamaria	Semi-emergent, downy, woody, perennial herb				1	Burbach 1997
Sparganium erectum	Semi-emergent, erect, branched, hairless perennial				1	Burbach 1997
Veronica sp. *(V. beccabunga)*	Semi-emergent, hairless, creeping perennial herb			1	1	Burbach 1997; Strange 1999

5.3.9. Distribution of *C. mercuriale* and *C. tenellum* between cages.

Mean and range of total density (through season) per cage for *C.meruriale* and *C. tenellum* is shown in Table 5.9.

Table 5.9 Mean and range of total density per cage through the season.

Species	No. of cages	$\mu \pm$ s.e. (m^2)	Range (m^2)
C. mercuriale	10	52.20 ± 10.80	6.90 - 122.20
C. tenellum	15	21.57 ± 5.35	2.78-80.56

To investigate whether emerging individuals are distributed at random through space, the index of dispersion was calculated (as in Section 3.2.2) using the total number of individuals emerging in each cage (cages 1-15 between 9th June and 2nd August, Table 5.10). For both species, I^D is well above the critical value of $\chi^2_{0.05}$ and the variance:mean ratios are larger than one (Table 5.11). Therefore, individuals of *C. mercuriale* and *C. tenellum* are not distributed at random between cages and it is necessary to investigate factors affecting emergence from a particular cage.

Table 5.10 Total number of individuals emerging, % of total emergence, and mean daily emergence in each cage between 9th June and 2nd August for *C. mercuriale* and *C. tenellum*.

	C. mercuriale		*C. tenellum*	
Cage no.	Total no. of individuals (%)	Mean (± s.e.) daily emergence	Total no. of individual (%)	Mean (± s.e.) daily emergence
1	33 (9.3)	0.60 ± 0.11	2 (0.86)	0.04 ± 0.03
2	48 (13.6)	0.87 ± 0.18	6 (2.58)	0.12 ± 0.05
3	4 (1.1)	0.07 ± 0.04	58 (24.89)	1.12 ± 0.27
4	32 (9.0)	0.58 ± 0.13	3 (1.29)	0.06 ± 0.03
5	18 (5.1)	0.33 ± 0.09	3 (1.29)	0.06 ± 0.03
6	63 (17.8)	1.15 ± 0.22	16 (6.87)	0.31 ± 0.09
7	8 (2.3)	0.15 ± 0.06	8 (3.43)	0.15 ± 0.07
8	2 (0.6)	0.04 ± 0.03	28 (12.02)	0.54 ± 0.16
9	24 (6.8)	0.44 ± 0.13	4 (1.72)	0.08 ± 0.04
10	13 (3.7)	0.24 ± 0.06	15 (6.44)	0.29 ± 0.07
15	15 (4.2)	0.27 ± 0.08	20 (8.58)	0.39 ± 0.11
16	27 (7.6)	0.49 ± 0.11	4 (1.72)	0.08 ± 0.11
17	29 (8.2)	0.53 ± 0.14	20 (8.58)	0.39 ± 0.10
18	3 (0.9)	0.06 ± 0.03	30 (12.88)	0.58 ± 0.14
19	35 (9.9)	0.64 ± 0.14	16 (6.87)	0.31 ± 0.08

Table 5.11 Index of dispersion for total number of *C. mercuriale* and *C. tenellum* in each cage.

	C. mercuriale	*C. tenellum*
Mean	23.60	15.53
Variance	301.02	222.90
Variance:mean ratio	12.755	14.353
n-1	14	14
I^D	178.57	200.94
Critical value of $\chi^2_{0.05, n-1}$	23.685	23.685

Table 5.12 shows habitat variables for each cage and 'suitability' of each cage for emergence of *C. mercuriale* and *C. tenellum*. Emergence cages were designated as 'suitable' or 'unsuitable' according to whether more (suitable, coded as 1 on Table 5.12) or less (unsuitable, coded as 0 on Table 5.12) than the mean proportion of emergence occurred within the cage. For *C. mercuriale*, the mean proportion of emergence across cages was 0.067 ± 0.013, for *C. tenellum*, it was 0.298 ± 0.014. Tables 5.13 and 5.14 show Wilcoxon two sample tests comparing suitable and unsuitable cages for *C. mercuriale* and *C. tenellum* respectively with regards to a variety of habitat variables. Suitable cages for *C. mercuriale* emergence had a higher percentage cover of *Hypericum elodes* than unsuitable cages (W=36, p=0.021). For *C. tenellum*, suitable cages had a higher percentage cover of vegetation than unsuitable cages (W=54, p=0.029). There was no correlation between the mean daily number of *C. mercuriale* and that of *C. tenellum* emerged each day (Spearman's rank correlation $r_s = -0.496, p = 0.060, n=15$).

It is possible to qualitatively describe suitable emergence habitat. Mean water depth (across cages) was 6.73 cm ± 6.70cm and mean peat depth was 22.93 cm ± 8.24cm. The national vegetation community in 13 cages was M29 i.e. *Hypericum elodes-Potamogeton polygonifolius* mire which is also defined as acid shallow fringe (CORINE biotope 22.313) though the goodness-of-fit was poor (Table 5.12). The other two cages contained S19a and S19b which is *Eleocharis palustris* swamp (CORINE biotopes c53.14 and c22.312 respectively). Broadly, suitable emergence habitat consisted of semi-submerged communities of *Hypericum elodes* (mean % cover is 50% ± 4.4%), *Potamogeton polygonifolius* (mean % cover is 5.8% ± 1.9%), *Eleocharis palustris* (mean % cover is 19.2 ± 2.6%), *Juncus articulatus* (mean % cover is 3.2% ± 1.1%) and *Carex* sp..

Table 5.12 'Suitability' and habitat variables in each emergence cage.

Cage No.	% vegetation cover	% of vegetation cover made up by			Peat Depth	Water Depth	NVC (goodness of fit)	CORINE biotope	Suitability for *C. mercuriale*	Suitability for *C. tenellum*
		Hypericum elodes	*Juncus articulatus*	*Eleocharis palustris*						
1	65	53.2	0	31.9	-	4.67 ± 1.67	M29(38)	c22.313	1	0
2	50	28.3	0	37.7	23.40 ± 5.50	7.33 ± 1.59	M29(50)	c22.313	1	0
3	95	14.3	0	21.4	-	2.67 ± 0.54	M29(32)	c22.313	0	1
4	60	51.7	0	17.2	-	7.33 ± 2.38	M29(49)	c22.313	1	0
5	60	25.3	2.5	19	30.20 ± 1.83	8.33 ± 1.01	M29(46)	c22.313	0	0
6	90	64.5	10.8	16.1	16.80 ± 1.24	8.00 ± 1.39	M29(43)	c22.313	1	1
7	70	50.6	0	25.3	-	6.17 ± 0.82	M29(59)	c22.313	0	0
8	60	47.1	0	11.7	-	5.33 ± 0.97	M29(48)	c22.313	0	1
9	90	68	2.9	19.4	-	3.50 ± 1.35	S19b(47)	c22.312	1	0
10	60	52.6	0	10.5	-	10.01 ± 1.25	S19a(39)	c53.14a	0	0
15	90	56	0	24	17.80 ± 1.02	10.83 ± 1.59	M29(55)	c22.313	0	1
16	30	60.6	6.1	15.2	8.20 ± 2.42	9.33 ± 1.74	M29(28)	c22.313	1	0
17	90	74.8	9.4	0	41.20 ± 5.09	8.83 ± 1.91	M29(46)	c22.313	1	1
18	80	36.5	7.3	31.2	-	5.00 ± 2.88	M29(58)	c22.313	0	1
19	80	66	9.4	7.6	-	6.83 ± 2.83	M29(55)	c22.313	1	1

Goodness of fit numbers calculated using Tablefit version 1.0; 0 – 49=very poor; 50-59=poor, 60-69=fair, 70-100=good

Table 5.13 Wilcoxon two sample tests comparing suitable (s) and unsuitable (us) emergence cages for *C. mercuriale.*

Variable	n_{us}	n_s	Median$_{us}$	Median$_s$	W	p
% vegetation cover	7	7	70.00	65.00	16	0.620
Water depth	7	8	3.17	7.33	48	1.000
% cover of *Eleocharis palustris*	7	8	21.43	16.68	59	0.613
% cover of *Hypericum elodes*	7	8	47.06	62.57	36	0.021
% cover of *Cirsium dissectum*	7	8	0.00	0.24	48	0.397
% cover of *Juncus articulatus*	7	8	0.00	4.48	43.5	0.152
% cover of *Molinia caerulea*	7	8	1.04	0.00	57.5	0.463
% cover of *Potamogeton polygonifolius*	7	8	19.91	17.65	52	0.185

Table 5.14 Wilcoxon two sample tests comparing suitable (s) and unsuitable (us) emergence cages for *C. tenellum.*

Variable	n_{us}	n_s	Median$_{us}$	Median$_s$	W	p
% vegetation cover	8	6	60.00	85.00	54	0.029
Water depth	8	7	7.33	6.83	28.5	0.867
% cover of *Eleocharis palustris*	8	7	19.20	16.13	47	0.336
% cover of *Hypericum elodes*	8	7	52.18	56.00	60	0.694
% cover of *Cirsium dissectum*	8	7	0.00	0.80	57	0.463
% cover of *Juncus articulatus*	8	7	0.00	7.29	52.5	0.189
% cover of *Molinia caerulea*	8	7	0.97	0.00	51.0	0.613
% cover of *Potamogeton polygonifolius*	8	7	1.61	4.00	24	0.281

5. 4 Discussion

In this study the proximate cues used by *C. mercuriale* to select habitat for oviposition and emergence were identified, focusing on the final stage of the hierarchy proposed by Wildermuth (1994). Most previous authors have inferred these cues from the microgeographic distribution of adults (Corbet 1980) and from the geographic distribution of a species across sites (Chapter 2). Here, the proximate cues used at the smallest scale by *C. mercuriale* are compared with information (where available) on the habitat features required at the within site and between site scale in this species. In particular, phytosociological studies on odonates have focused on the relationship between species distribution and aspects of the vegetation structure at sites (for *C. mercuriale* Buchwald 1983; Buchwald 1989; Buchwald *et al.* 1989; Buchwald 1992; Buchwald 1994; Roske 1995). Thus the use of the plantscape by *C. mercuriale* is compared with the use of the plantscape by other odonates.

5.4.1 General oviposition behaviour

Pairs usually oviposited in several stems with several bouts of oviposition on each stem (*cf* Rehfeldt 1990; Tsubaki *et al.* 1994; Bennett & Mill 1995a). Most pairs used stems of the same plant species throughout the focal. Whilst, changes in position between stems could be a strategy for distributing eggs between several sites, especially in populations which are heavily predated either during the egg stage or during oviposition (Buskirk & Sherman 1984; Rehfeldt 1990), they most probably occur in *C. mercuriale* after unsuccessful attempts at oviposition.

In *C. mercuriale*, as in some other zygopterans (Okazawa & Ubukata 1978; Martens 1992), eggs were not deposited during short initial periods of abdominal contact with a stem. These non egg-laying bouts were predicted to last between 45 and 118 seconds (95% confidence interval). Almost 30% of all oviposition bouts observed during focals were less than 50 seconds in duration and probably did not involve egg laying. Similarly, in a French population of *C. mercuriale*, Martens (1999) found that 54.9% of oviposition bouts lasted less than 20 seconds and that females touching the substrate for up to 77 seconds laid no eggs. In *Platycnemis pennipes*, no eggs were laid when the abdomen was in contact with the substrate for less than 40 seconds (Martens 1992).

Explanations for oviposition behaviour without egg laying include the suggestion that egg flow stops during oviposition, that females are checking for the presence of predators near the stem (Rehfeldt 1990) or that some attempts at oviposition are unsuccessful (Martens 1992). Martens (1992) rejected the first explanation having found a constant increase in egg number laid with oviposition duration in *Platycnemis pennipes*. The proportion of *C. mercuriale* pairs affected by predators during oviposition behaviour was lower than that found for other odonates (Fincke 1982; Fincke 1986b; Michiels & Dhondt 1990). Thus the presence of predators is unlikely to account for the termination of bouts before egg laying seen in many pairs. Thus, in *C. mercuriale*, non egg-laying bouts probably reflect unsuccessful attempts at oviposition due to the physical properties of the environment. When several bouts occurred on one stem, the female often terminated one short bout of oviposition by shifting her ovipositior relative to the stem before performing another oviposition bout. Often several rapid probing movements were performed with the ovipositior in a variety of positions until a 'suitable' position was found. The same movements were often performed after the last bout of oviposition on a stem before a pair flew to another stem. Such unsuccessful attempts at oviposition would necessitate the frequent changes between stems seem in *C. mercuriale*. Since oviposition behaviour is performed without egg laying in *C. mercuriale* the duration of oviposition may not be an accurate measure of reproductive success (*cf.* Fincke 1986a; Banks & Thompson 1987a; Fincke 1988) in this species or in others that show discontinuous oviposition behaviour. In addition, when monitoring *C. mercuriale* across its range only those plant species on which oviposition is performed for more than 50 seconds should be considered suitable for oviposition.

Females of *C. mercuriale* always submerged to oviposit up to their wings and submerged completely in 15.4% (6/39) of ovipositions. This behaviour has been observed in other British (Evans 1989; Jenkins 1997; Woodman 1999) and European populations (Burbach 1997; Kuhn 1998; Martens 1999) of *C. mercuriale*. It is found in a range of endophytic dragonflies (e.g. Sawchyn & Gillott 1975; Fincke 1986b) and may allow the female to avoid harassment by males during oviposition (Ubukata 1984; Waage 1987). However, in *C. mercuriale*, where oviposition occurs in tandem, harassment of a pair by conspecific males rarely appeared to alter the female's behaviour. Females of *C. mercuriale* would be hidden from males (and so avoid harassment) if they descended to a short distance below the water surface (e.g. females at a distance of 5cm were hidden from males in *Enallagma hageni* - Fincke 1986b). However, they commonly descend further, up to a depth of 10cm and eggs were placed up to 8.7cm below the water surface suggesting that this behaviour serves to place eggs far down in the water column. This behaviour increases the area of suitable stem available to a female and allows more continuous bouts of oviposition to occur. Most importantly, it decreases the likelihood of desiccation of eggs as water levels drop during the summer (Fincke 1986b). In *E. hageni*, Fincke (1986b) found that no eggs hatched from exposed sedge stems whilst 96.3% of eggs hatched from submerged stems. Drying out of oviposition sites may constitute a significant risk to *C. mercuriale* since this species utilises shallow water bodies that are subject to considerable fluctuations in dimensions (Chapter 2). For example, at Upper Crockford in 1999, the width of the stream reduced by some five metres in places during June and July.

The mean number of eggs laid by a pair during an oviposition was less than the mean initial clutch size of females elucidated in Chapter 6. These data, together with those presented in Chapter 6, suggest that females of *C. mercuriale* do not lay their entire clutch of eggs in one visit to the breeding stream. Since females have been observed ovipositing alone in this species, they do not require a male to facilitate oviposition and thus do not need to lay all their eggs while the male is contact guarding them on the day of mating. The mean duration of continuous oviposition for a female was 11.2 minutes but varied considerably between females. This is shorter than oviposition duration in another coenagrionid *Pyrrhosoma nymphula* (Bennett & Mill 1995a), in which females oviposited for 22.8 minutes, and may reflect the fact that females of *C. mercuriale* do not always lay their entire egg clutch in one oviposition episode. Clutch size and partitioning by *C. mercuriale* are discussed in more detail in Chapter 6 together with the consequences for sperm competition.

There was a positive relationship between the total duration of oviposition on a stem and the number of eggs laid on it, for both stems where only one oviposition bout had been performed and for stems where several bouts of oviposition had occurred. Frequent non egg laying bouts due to unsuccessful oviposition is probably partly responsible for the scatter around this relationship in *C. mercuriale*, especially for stems where more than one oviposition bout occurred. Similarly, Martens (1992) attributed large variation of egg deposition rate on a particular plant species to the fact that actual oviposition proceeds discontinuously relative to oviposition behaviour in *Platycnemis pennipes*.

The mean rate of egg deposition (14.06 ± 2.66 eggs per minute) for *C. mercuriale* was among the highest noted for zygopterans. Other species with high mean deposition rate include *Pyrrhosoma nymphula* (10.76 eggs per minute Bennett & Mill 1995a) and *Enallagma hageni* (13 eggs per minute Fincke 1986b). However, most zygopterans deposit less than 10 eggs per minute. Bick *et al.* (1976) found a range of 1.3 to 5.5 eggs deposited per minute for 5 zygopteran species, *Platycnemis pennipes* deposits 6.4-9.4 eggs per minute (Martens 1992) and *Enallagma cyathigerum* deposits 4-8 eggs per minute (Doerksen 1980). Oviposition rate varies between individuals of the same species due to the temperature of the water (Fincke 1986b) and the suitability of the substrate (Waage 1978, Martens 1992). As mentioned above, given that it is impossible to distinguish between actual oviposition and a non egg-laying bout in most species, it is difficult to measure oviposition rate accurately. There are obvious differences in the magnitude of the deposition rate between endophytic and exophytic species, with the later depositing hundreds of eggs per minute. However differences between zygopteran species probably reflect the peculiarities of the study environment or measurement error rather than constituting functional differences between species. For example, in *C. mercuriale* at Upper Crockford, the mean egg deposition rate was considerably higher than that of a French population of this species (3.66 or 5.08 eggs per minute - Martens 1999).

Oviposition behaviour was unaffected by the presence of a cage, reflected in the similarity between caged and natural focals in a number of respects (the number and duration of bouts, the number of plant species used and the number of eggs laid). The similarity of oviposition behaviour in situations where conspecific males and other odonates were present (i.e. natural focals) and absent (i.e. caged focals) may indicate that these factors do not influence habitat selection for oviposition substantially. However, it is probable that pairs of *C. mercuriale* aggregate during oviposition. Martens (1999) found that pairs were attracted to oviposition sites containing other pairs over those that contained no pairs.

5.4.2 Hatching success, duration and mortality of hatch period

After four weeks of development in stream conditions, eggs of *C. mercuriale* had suffered 14% mortality on average. Of the remaining eggs, 75% had hatched but 13% were in a stage of development before eye spot development. Thus while *C. mercuriale* eggs can hatch in four weeks, a substantial proportion require a longer hatch period and hatching is not well synchronised within each clutch. In captivity, the hatch period is shorter, taking only 21 days (Corbet 1955). Another coenagrionid, *Pyrrhosoma nymphula,* suffered a similar level of mortality (25% failed to hatch) but hatching was highly synchronised within clutches (Bennett & Mill 1995a). The length of the hatch period of *C. mercuriale* was within the range for other species with direct egg development i.e. between 5 and 40 days. Eggs of species with indirect development (i.e. with a diapause stage) can take between 80 and 320 days to hatch (Corbet 1980).

In addition to desiccation (Macan 1964; Fincke 1986b; Bennett & Mill 1993), possible sources of egg mortality in endophytic species include infertility, unhatchability, predation, parasitism (e.g. by Hymenoptera - Bennett & Mill 1995a) and over-use of stems (Waage 1978). Although further oviposition into stems after natural focals was not permitted, no previous clutches were found in the stems from before the focal was carried out. This suggests that stems are not over-used to a large extent in this population of *C. mercuriale* and thus eggs will not be susceptible to being punctured during repeated oviposition on the same stem. In addition, there was no evidence of predation on or parasitism of eggs whilst in stems. Thus the 14% mortality was attributed to infertility and unhatchability (*cf* Bennett & Mill 1995a).

Whilst none of the stems used for natural focals were found exposed due to drops in water level, the stream margin did retreat considerably during the flight season leaving areas that had been used for oviposition exposed. Thus while none of the eggs dissected had died due to desiccation, this could still be a significant mortality factor in such a shallow water environment. Further quantitative investigation is necessary to determine the factors that influence egg mortality and egg hatching success in *C. mercuriale.* The method elucidated in this study of dividing the eggs into developmental stages could be employed in such investigations (*cf* Siva-Jothy *et al.* 1995).

5.4.3 Proximate cues for oviposition

In multiple and logistic regression analyses, none of the measured habitat variables could be used to predict the duration of oviposition or the number of eggs laid. There are number of possible explanations for this. Firstly, difficulties in tracking pairs and recovering stems resulted in a low sample size of stems. With both multiple and logistic regression models a solution is only possible if the number of observations is at least one greater than the number of independent variables. Much larger sample sizes are desirable to obtain a good estimate of population parameters (Sokal & Rohlf 1995). Secondly, these variables may be unimportant in determining the amount of oviposition that occurs once a pair has landed on a stem but may influence the decision of whether to land at all i.e. they act earlier in the hierarchy of decisions described by Wildermuth (1994). Most of these factors could probably be assessed visually before landing and thus may constitute more general cues. For example, the fact that 43% of stems used for oviposition were within a patch containing only one stem suggests that plant stems can be detected visually before landing to a high degree of accuracy. The fact that oviposition was possible at a range of values of variables such as water depth, distance to flow, vegetation patch size, degree of shelter and temperature provides evidence that these variables may define suitable emergence habitat only at a broad scale.

The time spent ovipositiong having landed is most likely to be determined by the physical properties of the stem. Martens (1992) pointed out that the structure of water plants and their resulting usefulness to damselflies for oviposition varies greatly. With regards to the plant species used for oviposition by *C. mercuriale*, *Hypericum elodes*, *Potamogeton polygonifolius* and *Juncus articulatus* were used for oviposition more often than expected from their abundance whilst *Eleocharis palustris*, *Myrica gale* and *Molinia caerulea* were used less often than expected. This is in contrast to the findings of Sternberg (1999) in Europe where the use of plant species by *C. mercuriale* was not significantly different to the abundance of each species in the habitat and to the suggestion of Winsland (1997) that *C. mercuriale* oviposited in the submerged bases of rushes and sedges in Britain.

It is necessary to confirm that these plant species are being used as direct cues for oviposition due to (physical) properties required by *C. mercuriale* rather than constituting indirect cues that merely indicate the presence of other required properties of the habitat. The plant species that were used more often for oviposition have similar physical properties. They are herbaceous and soft stemmed with thin cuticular layers that lack collenchyma cells but have spongy parenchyma cells that may protect the eggs during development. Plant species that were used less often than expected for oviposition had strengthening layers in the stem that would impede the insertion of eggs into the stem. Strengthening layers took the form of a tough cambium layer in *Myrica gale*, a woody species, whilst stems of *Molinia caerulea* and *Eleocharis palustris*, there is a subcuticular layer of collenchyma cells. Stems of *Hypericum elodes*, *Juncus eleocharis* and *Potamogeton polygonifolius* were also wider (at around 2mm) than those of other soft-stemmed herbs that were used rarely if at all for oviposition such as *Drosera rotundifolia*, *Anagallis tenella* and *Carex* sp. The stems and petioles of *Hypericum* and *Potamogeton* extend laterally under the water surface and have systems of side shoots which may facilitate their use for underwater oviposition in particular.

The review (Section 5.3.8) of plant species in which *C. mercuriale* has been noted to oviposit in other parts of its range is consistent with the hypothesis that plant species are used as direct cues due to their physical properties. Although a range of plant species is used for oviposition, the majority are also soft stemmed herbs and are submerged or semi-emergent. In addition, they share similar temporal properties. Most are perennial i.e. live for at least three seasons and a few are evergreen or semi-evergreen. Plants with the latter two characteristics would provide a permanent cover of vegetation for larval development. However, the plants in which Thelen (1992) found larvae, although evergreen, do not correspond directly to those chosen for oviposition. For example whilst all larval instars occurred between herbs such as *Berula erecta*, *Nasturtium officinale*, *Phalaris arundinacea* and *Carex* species, few larvae were found under the leaves of *Callitriche* sp, which has been selected for oviposition in some studies. In several odonate species, larvae move from the oviposition site to a different sub-habitat having passed through the early larval instars (e.g. Corbet 1957c; Macan 1964; Duffy 1994) and similarly *C. mercuriale* larvae may be capable of at least a limited degree of movement. Thus the proximate cues used for oviposition habitat selection at the final stage of the hierachy may relate most closely to the habitat features required for egg development and efficient oviposition rather than indirectly indicating the permanence of habitat for larval development (Chapter 2). The failure of eggs to hatch out of tougher stems has been cited as a possible cause of variation in egg mortality in another coenagrionid, *Pyrrhosoma nymphula* (Bennett & Mill 1995a) and illustrates the importance of physical stem properties.

There are no particular habitat properties that are indicated by all the plant species used for oviposition such that they could not act as indirect cues. They indicate a range of different conditions. Some species are clump-forming and accumulate silt (*Alisma plantago aquatica, Callitriche* sp., *Elodea canadensis, Rorippa nasturtium aquaticum, Veronica beccabunga*) which may important for creating habitat for early instar larvae, some are shade intolerant (*Veronica beccabunga)* whilst others (*Callitriche* sp. and *Sparganium erectum*) are shade tolerant (Haslam 1978). These species also differ widely in their water level requirements (Newbould & Mountford 1997).

Given the importance of their physical properties and the observation of behaviours such as repeated probing of stems with shifts in oviposition position, it is likely that they are selected after landing, at the final stage of the hierarchy, rather than being assessed visually beforehand. This is consistent with Zimmermann's (1975 cited in Martens 1999) suggestion that *C. mercuriale* pairs search for useful plants for oviposition by trial and error.

Examples of physical properties of plants influencing oviposition behaviour can be found in other odonates. In *Platycnemis pennipes* the relative duration of oviposition on two plant species depends on their physical properties (Martens 1992). Short bouts of oviposition are permitted on *Myriophyllum spicatum*, the stems of which are narrow, irregularly shaped and interrupted by many filamentous leaves. Long bouts of oviposition are carried out on *Nuphar lutea* that has wider stalks without many leaves and thus presents a larger surface area for oviposition. In addition, plant surfaces covered by water–repelling layers such as the floating leaves of *Potamogeton natans* are probed but left unused by *P. pennipes*. Another example is where pairs of *Coenagrion pulchellum* oviposit preferentially in *Nuphar* and *Nymphaea* leaves that have holes in them made by the beetle *Donacia crassipes* over leaves that do not contain holes (Martens 1989) since such holes may provide better access to the fleshier leaf parts.

Odonates are linked to vegetation in different ways. Some species are linked with one particular plant species e.g. *Aeshna viridis* predominantly oviposits in *Stratiotes aloides*. Others are associated with a few types of plant community e.g. *Lestes sponsa* is associated with rush stands or reedbeds. The degree of specificity of preferences expressed during oviposition habitat selection probably reflects the length of time spent in the immobile egg stage. For example, Sawchyn & Gillott (1974a) stated with reference to three species of *Lestes* that species that overwintered as eggs in temperate or sub-artic regions had particularly specific requirements for oviposition. Not only do *Lestes disjunctus, L. unguiculatus* and *L. congener* only oviposit into *Scirpus* stems they select different types of stems according to the developmental requirements of the egg (Sawchyn & Gillott 1974a; Sawchyn & Gillott 1974b). *Lestes disjunctus* and *L. unguiculatus* lay thin-walled desiccation prone eggs early in the season and need moisture to complete pre-diapause development before August. They oviposit in green stems (for moisture) in small stem groups or at the border of large stem groups and they seal the incisions. These stems collapse early in late autumn storms and are snow covered and insulated relatively early. *L. congener* has thick walled, desiccation resistant eggs and oviposits later in dry stems that are bent or broken in the centre of stem groups. Diapause occurs earlier here and broken stems are wetted early in spring to allow embryogenesis to be completed quickly.

In comparison to these species, *C. mercuriale* spends a short time immobile in the oviposition site, and while particular physical plant properties are used as cues plant species use is much less specific. It may be that very few odonates with direct development rely on one particular plant species for oviposition (see Bick *et al.* 1976 for some examples). The association of adult populations of *C. mercuriale* with perennial herbaceous vegetation suggests that such plants are indeed selected as indirect cues to the permanence of flow and larval habitat (Chapter 2). However such selection does not occur at oviposition but probably elsewhere in the adult stage (than oviposition) such as in the choice of display or rendezvous locations by males. As well as using a range of plant species, *C. mercuriale* used a range of plant communities for oviposition at Upper Crockford including *Eleocharis palustris* swamp (S19, S19a, S19b); *Molinia caerulea–Potentilla erecta* mire (M25a*)*, and *Hypericum elodes – Potamogeton polygonifolius* soakways (M29). Although some quadrats were found to be *Scirpus cespitosus-Erica tetralix* wet heath (M15, M15a), this community is not widespread in Southern Britain and *Scirpus cespitosus* was not abundant on the site. This consistent with the association of adult populations of *C. mercuriale* with a range of plant communities (Chapter 2).

To confirm which physical properties of plant stems influence oviposition behaviour in *C. mercuriale*, it would be advantageous to carry out choice experiments (*cf* Waage 1987; Martens 1989; Martens 1992; Martens 1999). Here a limited number (usually two) of alternative oviposition substrates (which differ in some physical property) are offered to pairs and the duration of oviposition and number of eggs laid on each substrate are recorded. Given the highly variable structure of plant mats used by *C. mercuriale*, the cages used in this study provide an ideal choice chamber in which two (or more) distinct oviposition sites can be isolated from the rest of the habitat.

Many of the other habitat features used for oviposition at this small scale were consistent with broad scale features associated with adult populations in Britain and Europe (Chapter 2). Oviposition behaviour occurred in unshaded, open areas of water without dense or tall emergent vegetation (*cf* Hold 1997; Sternberg *et al.* 1999) but with abundant submerged aquatic vegetation. At Upper Crockford, oviposition also occurred near to tussocks for shelter. Since *Myrica gale* is not used for oviposition, the higher percentage cover of this species near oviposition sites compared to general stream habitat also supports the suggestion that pairs require the shelter of tussocks for oviposition. Such shelter probably improves the accuracy of probing and oviposition movements and allows oviposition to proceed quickly. Oviposition occurred at a range of air temperatures, water temperatures and pH, in stems that were at least 1mm in diameter and where only 4cm of the stem protruded above the surface of the water.

Whilst in Europe oviposition occurred where water currents were between 0 and 0.05 m/s (Sternberg *et al.* 1999), in British Chalkstream populations oviposition required discernible flow of not less than 0.029 m/s (Strange 1999). In the heathland population in this study oviposition similarly occurred in shallow, (usually less than 10cm), unshaded, open areas in locations near to discernible flow (between 0.01 and 0.3 m/s). A requirement for flow has been found in other odonates (e.g. *Calopteryx maculata* - Wingfield Gibbons & Pain 1992; Siva-Jothy *et al.* 1995). The existence of flow preferenda has been attributed to a few factors. Siva-Jothy (1995) found a reduction in the build up of algal matter on the surface of stems in fast flow. Such a build up could reduce the rate of oxygen supply to the eggs or prevent hatchlings from leaving the stem. Increased flow also reduces the boundary layer of still water around the egg, allowing oxygen to diffuse into it more rapidly (Fox 1937). Halverson (1983) speculated that egg mortality and rate of embryogenesis in field populations of *Aeshna tuberculifera* could be attributed to variation in dissolved oxygen concentrations in the field and thus to flow. As discussed in Chapter 2, a requirement for flow could occur in *C. mercuriale* in the larval stage since it has a relative small gill area for oxygen diffusion compared to species such as *Ceriagrion tenellum* which commonly live in standing water (Sternberg *et al.* 1999).

In addition, oviposition always occurred in areas of stream with a dark brown peat substrate rather than light gravel substrate. Whilst such a substrate may be preferred if it permits the existence or particular vegetation types, Sternberg (1995) describes how another shallow bog pool species, *Somatochlora arctica*, prefers to lay on *Sphagnum* over dark brown peat due to sunlight absorption by the peat. The latter can produce temperatures of up to 20°C in bog waters. A similar mechanism may occur in the shallow waters occupied by *C. mercuriale* and may allow processes such as oviposition and emergence to proceed quickly. Again adult populations of *C. mercuriale* are associated with dark-coloured organic substrates.

5.4.4 Habitat use for emergence

Coenagrion mercuriale and *Ceriagrion tenellum* both emerge in an upright position usually in the morning. Final instar larvae of *C. mercuriale* leave the water by ascending emergence vegetation in shallow water rather than by walking onto shore as has been seen in some other zygopterans. The mean perch heights for *C. mercuriale* and *C. tenellum* are consistent with those of other zygopterans i.e. 5-10cm of the water surface (e.g. Cordero 1988 cited in Corbet 1999) and the finding of exuvia at 15cm above the water in Badem-Wurttemburg (Leinsinger cited in Sternberg *et al.* 1999).

C. mercuriale and *C. tenellum* differed in the plants chosen as emergence perches. *Eleocharis palustris* was used most frequently but *C. mercuriale used Juncus articulatus* as well. *Hypericum elodes* was the most abundant plant but was rarely used as an emergence perch, whilst *Eleocharis palustris* and *Juncus articulatus* were used frequently despite their low abundance. As described above, the former species is soft stemmed, with thin cuticular layers lacking in collenchyma and is thus less able to resist movement due to wind and water flow. The large leaves probably represent obstructions to soft-bodied tenerals. The latter species make effective perches since they have rigid upright stems (with collenchyma) which resist movement. The existence of common physical properties shared by plant species used for emergence suggests that the species are used as direct cues in habitat selection. In south-west Germany, exuviae were found on *Schoenus* sp. *Juncus subnodulosus, J. alpinis,* and *Carex* sp. (Buchwald 1989). However, on European sites, emergence perches for *C. mercuriale* include semi-emergents such *as Berula erecta, Solanum dulcamara, Mentha aquatica* and *Nasturtium officinale* (Sternberg et al. 1999) rather than being restricted to rigid emergents.

C. mercuriale, C. tenellum and *Orthetrum coerulescens* all emerged from the same stream habitat, in contrast to suggestions by local naturalists (Winsland 1993) that although the range of *C. mercuriale* overlaps with that of other odonates, it seldom uses the same stretches of stream. The mean density of individuals emerging from one square metre through the season was 52.2 ±10.8 for *C. mercuriale* and 21.6 ± 5.35 for *C. tenellum*, indicating that *C. mercuriale* is the dominant species on this site. Estimates of density for both species are considerable higher than estimates for other Zygoptera e.g. 4.7-8.7/m^2 for *Pyrrhosoma nymphula* (Gribbin & Thompson 1991) and 2.1/m^2 (range 0-5) for *Lestes disjunctus disjunctus* (Duffy 1994). Whilst these species may exist in higher density populations, the estimates may be high for purely methodological reasons (e.g. collection of individuals from a small area of suitable habitat as opposed to collection from large area containing some unsuitable habitat as well).

Both species were distributed non-randomly between cages and this distribution differed between the two species. Although 'suitable' cages for *C. mercuriale* emergence contained a significantly higher percentage cover of *Hypericum elodes* than 'unsuitable' cages, since this species is not important as an emergence perch this result must be an artefact of the low sample size of cages. The absence of a correlation between the mean daily number of *C. mercuriale* in a cage and that of *C. tenellum* suggests that the two species differ in habitat use for emergence. In order to investigate seasonal and daily emergence patterns in *C. mercuriale* (Chapter 3), the emergence cages were all placed in habitat that was presumed to be suitable for emergence to obtain as many emerging individuals as possible. To explicitly test the effect of habitat variables on emergence a large number of cages would be positioned in a wide range of habitats.

Habitat that was broadly suitable for emergence of *C. mercuriale* was unshaded, shallow, open, and slow flowing (between 0.01 and 0.30m/s) and had floating mats of *Hypericum elodes, Potamogeton polygonifolius, Eleocharis palustris, Juncus articulatus,* and *Carex* sp. (corresponding to M29 – *Hypericum elodes-Potamogeton polygonifolius* mire). This community is often found in wet heath-valley mire transitions in situations of fluctuating water levels (Newbould & Mountford 1997).

In conclusion, this investigation of the proximate cues used for habitat selection revealed several habitat features to be required by *C. mercuriale* for oviposition and emergence in

Britain. Open, unshaded stream sections that are shallow and slow flowing with some areas of peat substrate are required. Such sections should contain abundant aquatic vegetation communities including both herbaceous, soft-stemmed, perennial (and evergreen) submergent or semi-emergent species for oviposition and rigid emergent species for emergence. Tussocks provide sheltered areas for oviposition and emergence. Features used at a small scale for these processes are consistent with those that determine the distribution of adults within and between sites (Chapter 2).

Chapter 6 Reproductive behaviour, lifetime mating success and survivorship in a natural population of the damselfly, *Coenagrion mercuriale.*

6.1 Introduction

Variation in lifetime reproductive success (LRS) can be generated by several, non-exclusive processes; sexual selection, natural selection and/or random processes (Koenig & Albano 1986). Sexual selection arises from competition between conspecifics for access to mates or fertilisations whilst natural selection refers to all other forms of selection (Andersson & Iwasa 1996). If LRS is mostly due to foraging success or predator avoidance and due to timing of weather events then reproductive success will be combination of chance and natural selection (Fincke 1986a; Koenig & Albano 1986; Michiels & Dhondt 1991).

To examine the relative opportunity for sexual versus natural selection, many studies have partitioned the variance in LRS into variation in mating or fertilisation efficiency versus components such as adult lifespan, oviposition efficiency (Stoks 2000). The action of selection on LRS may even occur during the larval stage, for example there was selection for large body size in male larvae of *P. nymphula* – a species which is territorial in both the adult and the larval stage (Harvey & Corbet 1985). However, for an evolutionary response to either type of selection to occur, a correlate must be found between one of these components and a heritable phenotypic character (Arnold & Wade 1984b; Fincke 1986a).

In previous studies of LRS there has been an emphasis on female choice and male contests whilst other mechanisms of sexual selection such as scramble competition for mates have been poorly investigated (Andersson & Iwasa 1996). Odonates have frequently been used as model organisms in studies of LRS, but stream-dwelling species have been understudied (Fincke *et al.* 1997). Here the factors influencing lifetime mating success (LMS) in *C. mercuriale*, a non-territorial, stream-dwelling species are examined. In scrambling species, factors such as the timing and location of mating may be more important to females than choice of mate based on male phenotype although stabilising selection on body size has been shown in some species (Fincke 1982a; Banks 1985). This may particularly apply to *C. mercuriale* in Britain, where it often occurs in small populations and oviposition sites may be patchily distributed.

The timing and location of mating activity will also be influenced by stochastic processes such as weather (Thompson 1990). Fincke (1997) pointed out that weather can be a major constraint on sexual selection in odonates, with much of the variance in male and female reproductive success being explained by environmental conditions. Thus a weather component should be included in a partitioning analysis of LMS. Ideally LRS rather than LMS should be examined since it provides a more direct measure of the importance of potential selection pressures. However, components such as the number of eggs laid are difficult to measure for all females in the population unless all suitable breeding habitat can be monitored simultaneously. For *C. mercuriale*, such habitat is diffuse and overgrown in places making such measurements difficult. Observations were made on aedegus morphology, clutch size and partitioning in some individuals to allow inferences about components of reproductive success other than those involved with mating.

Longevity has been found to account for a major component of LRS for both males and females in many odonates regardless of the male mating system (Fincke *et al.* 1997). More generally, there has been a paucity of work on a phenomenon known as endurance rivalry where mating opportunities increase with time spent at a site and the ability to remain reproductively active for long periods of time is favoured (Andersson & Iwasa 1996). Since longevity also directly determines the amount of time the individual is present at the breeding site, the factors influencing the probability of survival were also examined in this population. Recent theoretical advances in mark-recapture models allow the separation of recapture and survival probabilities (Lebreton *et al.* 1992). Studying survival in a small isolated population will minimise the underestimation of survival that arises due to emigration. For comparison, Chapter 7 examines survival in a larger population in which emigration does occur. Again, it is necessary to investigate whether there are phenotypic correlates of survival (such as sex or body size) or whether survival is mainly dependent on stochastic processes such as weather. In particular, sex differences in survival in the mature adult population has been postulated as one mechanism by which a male-biased sex ratio could be produced in this stage (Stoks 2001b).

Apart from its relationship to LRS or LMS, it is interesting to investigate survival during the mature adult stage of odonates in the context of survival through other stages of the complex odonate life cycle. Chapter 5 discusses mortality during the egg stage in *C. mercuriale* whilst Chapter 3 refers to mortality at emergence and in the pre-reproductive period. It is also interesting to compare survival in an edge of range population of mature adult *C. mercuriale* with mature adult survival in core populations and with that in other odonates. More generally, in insect species of epidemiological and conservation importance, investigation of the climatic determinants of survival (or more properly mortality) at a local scale have provided possible predictors of distribution at larger scales (e.g. Randolph 2000; Thomson & Connor 2000).

It is also important to investigate the mated proportion of the population in small populations of rare species such as *C. mercuriale*. In small populations, genetic problems (e.g. inbreeding depression, loss of evolutionary potential for adaptation to environmental change) may arise through loss of genetic variation due to the joint action of natural selection and genetic drift. The rate of loss due to genetic drift depends on the effective population size (N_e) i.e. the size of the 'genetically idealised' population to which the actual population (N) is equivalent in genetic terms. Crudely speaking, N_e is equal or less than the number of breeding individuals but is usually much less for a variety of reasons. In general, N_e is close to N/2 (range N/4 – 3/4N) but a number of factors such as variation in female fecundity (and thus presumably also variation in mating success) can substantially reduce N_e (Nunney 1996). Thus investigation of the mated proportion of the population in *C. mercuriale* sheds light on the maximum probable effective population size and whether mate searching behaviour or population density may be producing an allée effect in this species (i.e. where fitness components are (usually directly) proportional to the number of conspecifics present - Stephens & Sutherland 1999).

Therefore, in this Chapter, the factors influencing lifetime mating success and survival are investigated in a small isolated population of a non-territorial, stream-dwelling species on the edge of its range with emphasis on the role of stochastic factors such as weather. In addition, aspects of the reproductive behaviour of *C. mercuriale* are considered.

6.2 Methods

6.2.1 General reproductive biology of *C. mercuriale*

6.2.1.1 Duration and timing of reproductive behaviours

As described in Chapter 5, focals were carried out on pairs under caged and natural conditions at Upper Crockford in 1999. Where focals could be carried out from before copulation in the morning to the point at which the pair split after oviposition it was possible to determine what proportion of time pairs spent in each stage of reproductive behaviour. Where such continuous focals were not possible, copulation was timed. At Aylesbeare in 1998, similar observations were made where possible, though at this site, the observation of all matings was of prime concern. In addition, at Upper Crockford, hourly censuses were carried out, on eight days, along a 50m stretch of stream noting the number of unpaired males and females, the number of paired individuals and the temperature and time of day.

6.2.1.2 Clutch size, egg size in relation to body size and oviposition behaviour

Females were collected from Upper Crockford in 1999 (1) before copulation in the morning, (2) after copulation and (3) after ovipositon. All females were retained in 70% ethanol. In the laboratory, head width (x 20 magnification) and the length of a portion of the left forewing (between the pterostigma and the point of attachment with the body) (x 10) were measured under a binocular dissecting microscope calibrated using a slide micrometer and eye-piece graticule. The spermatheca and bursa were first removed from each female by gently prising apart the two prongs of the ovipositor. These translucent sperm storage organs were placed on a slide and observed under the microscope to score sperm presence (visible as a grey mass) inside them. The ovaries of the female were then dissected, and the total number of mature eggs counted. Mature eggs could be distinguished from immature eggs by their larger size and lighter colouration. In addition, immature eggs tended to be concentrated towards the anterior of the ovarioles. Where available, ten eggs were selected at random from the mature eggs retrieved from each female and measured under a dissecting microscope as above (x 30). With regards to ovipositon behaviour at Aylesbeare, observations were made on the number of times females oviposited entirely alone or instances where contact-guarding by males did not continue throughout oviposition. Any effect of predation or weather conditions on oviposition behaviour was noted. These are compared to similar observations made at Upper Crockford in 1999.

6.2.1.3 Aedegus Morphology

Aedegi were removed from several males of *C. mercuriale* using fine forceps, and freeze-dehydrated, coated with gold palladium and mounted according to the method of Veltkamp *et al.* (1994). They were then examined under a scanning electron microscope.

6.2.2 Mark-recapture protocol and lifetime mating success study

The mark-recapture exercises were conducted from June to August 1998, on Aylesbeare Common, East Devon (SY055907). The colony of *C. mercuriale* occupies a south-facing slope with a basic flush system, running through an acid dry heath (Kerry 1994).

Study of adults began on 6th June and continued until the end of the flight season in early August. The first adults were marked on 7th June. Individuals seen for the first time were scored as being one day old, age referring to the age of sexually mature individuals. Since the site had been searched for several days before 7th June, the ages of the individuals initially present were also scored by this method. A sexually mature individual is here defined as one with adult colouration (tenerals are pale brown in colour developing to pale blue-grey). The mark-recapture exercise began at 9.00h, before the first males arrived at the streams, and ending at 17.00h when most of the individuals had left the breeding area. All *C. mercuriale* found were uniquely marked by writing a number on the forewing with an indelible pen and placing a dot of paint on the dorsum of the thorax. Time of capture, position on the site (in terms of distance from the stream and vegetation type of patch), activity of the individual, forewing length, age, morph (for females) and sex were recorded for each individual. Mark-recapture exercises were carried out on every day that weather permitted the presence of odonates on the breeding site i.e. for 44 days between 7th June and 2nd August.

By slowly walking around the site (following a defined route) on average, twice every hour, the presence of all the individuals was recorded. It can be assumed that all matings occurring at the stream on a day were observed because (1) the average mated pair spends more than an hour in tandem (this chapter) (2) the same individual was often seen several times on any given day. If individuals were not present at the stream they were dead or roosting inside tussocks. Since the site was searched on average every 30 minutes, it is unlikely that even tandems of short duration that did not result in oviposition were overlooked. If biased in this way, the data would tend to overestimate the percentage of males in the population since females are only conspicuous when in tandem. Tandem pairs were captured unless both male and female had already been marked. The difficulty of keeping captured pairs in tandem during marking resulted in an abnormal excess of single females at the water, and may have artificially increased the number of matings per day (see results).

The majority of studies have partitioned lifetime mating success using the methods of Arnold & Wade (1984a & b) or that of Brown (1988) which are based on the relationship between the variance in LMS and the variance and covariances of its components. Stoks (2000) pointed out that these two approaches both require that the components of LMS are multiplicative which may produce spurious covariations between them and also assume direct effects, ignoring any causality in relationships between components. Instead this author used path analysis (Wright 1920 cited in Stoks 2000) to test hypotheses about causal relationships using a series of multiple regressions and correlations structured by an *apriori* hypothesis, (including unmeasured variables). Due to the small number of individuals in the population and the narrow range of frequencies of number of mates obtained, my dataset were not amenable to the latter type of analysis. Thus stepwise logistic regression analysis between mated and unmated individuals was used to test hypotheses about causal relationships between components of LMS (*cf* Carchini *et al.* 2000) since this accounts for multicolinearity between components. Stepwise logistic regression analyses are also used in this chapter to investigate the probability that mating occurred on a particular day (Section 6.3.1.1) and are used in other chapters. This merits some explanation at this stage into the use of such analyses. Maximum likelihood methods are used to fit these models to the data since least squares regression is inappropriate when the data has a binomial error structure. Likelihood ratio tests were used to assess the significance of parameters in explaining the variation in the dependent variable. These are preferable to Wald Tests (based on the ratio of the parameter estimate to its standard error). They are more reliable for use with small samples, perform better with non-linear constraints and because likelihood ratios are the fundamental measure on which the initial model fitting is based (Hosmer 1989; Trexler & Travis 1993). The G-statistic was computed for each for each parameter as – twice the differences in log-likelihood ratio between the model with a given parameter and the model without a given parameter. This statistic has a chi-square distribution with one degree of freedom and tests the null hypothesis that the excluded parameter is equal to zero. In the stepwise logistic regressions in this thesis, variables must have a significance of less than 0.05 for this score statistic to be entered into the model and a significance exceeding 0.10 to be removed. The stepwise nature of this procedure accounts for multicolinearity among variables. A G-test is presented for each variable and for the final model (Model χ^2 in tables where degrees of freedom are equal to the number of covariates in the model). The exponential of the coefficients (B) for each variable in the model are given (e^B), *since this represents the amount of change in the* dependent variable per unit change in the independent variable. Thus if e^B is greater than one, the odds of an event (e.g. mating) increase whilst if e^B is less than one, the odds of mating decrease.

6.2.3 Methods for analysis of survival and recapture probabilities

6.2.3.1 Background to survival analysis

There were 44 days on which weather permitted mark-recapture exercises to take place between 7th June and 2nd August. 217 adults were marked, only 24 of which were marked as teneral adults and 193 of which were marked as mature adults. The length of the immature period is only approximately known in this species (Chapter 3) and tenerals spend this maturation period roosting and feeding in vegetation away from the breeding site where they will have a lower probability of recapture (*cf* Van Noordwijk 1978). These reasons coupled with the low sample size of marked tenerals (45.8% of which were recaptured) necessitate the restriction of this analysis to survival and recapture probability during the mature adult lifespan. In addition it was restricted to those 111 mature adults (42 females and 69 males) for which body size measurements were available. Of these individuals, 32.4% were recaptured. Using these 44 encounter occasions, capture histories were constructed for each individual, coded as a series of 1s and 0s depending on whether the individual was sighted or not on a given occasion. Individuals were divided by sex into 2 attribute groups and for each, the covariate of body size was included. Since body size decreased with day of entry to the marked population for males in this dataset and for males and females in Chapter 3, day of entry was not considered in this analysis. The unequal intervals between recapture occasions were also specified in the model.

Capture-recapture estimates of survival of a dispersive species suffer from an unknown bias (downwards) due to permanent emigration from the study area (Frederiksen & Bregnballe 2000). Whilst inter-population dispersal has been observed in *C. mercuriale* (Chapter 7) up to a distance of 1.06km, the population on Aylesbeare Common (SY055907) and the nearest neighbouring population of *C. mercuriale* at Colaton Raleigh Common (SY050868) were separated by 3.85km. Thus permanent emigration was unlikely to constitute a source of bias in estimates of survival in this study. However, the last observation of an individual may still not represent death due to chance or biological reason such as the behaviour of roosting in vegetation in days intervening visits to the breeding stream. When data consists purely of resightings, two types of parameter are estimated - the probability that a marked animal survives from one occasion to the next (survival probability ϕ) and the probability that a surviving marked animal that has not emigrated permanently is observed in the study area (recapture probability p). The product of these two parameters (β, - Lebreton *et al.* 1992) is estimated for those dates when survival and recapture probabilities cannot be estimated separately (for instance for the last sample).

The Cormack-Jolly-Seber model (CJS model) was used which assumes a multinomial distribution of the observed number of individuals sharing a particular recapture history. The goodness-of fit of field data to this model was assessed using the two tests provided by RELEASE (Burnham, 1987). These two tests assess the goodness of fit of the classical CJS model i.e. with temporal variation only. The analysis was carried out in MARK (Cooch, 1999) which estimates model parameters iteratively by maximum likelihood methods and provides facilities for goodness-of fit testing and model selection.

6.2.3.2 Model selection (and notation): comparison between groups and effects of individual and external covariates

Survival and recapture probabilities were expected to be dependent on sex and body size (in light of previous studies on odonates) and were also expected to vary with time. A global model including the main effects of and interactions between sex, size, time and a temperature and rain variable would have 438 parameters. Since the effective sample size (i.e. the total number of releases) of this dataset is 469 such a model is not applicable since low sample size relative to the number of parameters to be estimated would result in low precision for the parameters of interest. Given this and the huge number of possible models that would arise from these variables, an *a priori* selection of models was carried out on the basis of biological assumptions on what could be important ecological factors (*cf.* Yoccoz *et al.* 1998). Given the widespread finding in previous studies that males are more likely to be recaptured (and possibly more likely to survive) than females, all 16 possible models involving sex and time (and their interaction) were fitted to the data first. Since the finding of a body size effect on survival in odonates is slightly less widespread, this individual covariate was added at the next stage to the best of the sex and time models. Finally, recapture probabilities and then survival probabilities were constrained by external covariates (weather variables) to see if they improved the model. Given that mark-recapture exercises were only performed when weather condition permitted the adults to fly, it was difficult to model the explicit effect of weather variables on recapture and survival probabilities, but these analyses at least give an indication of the importance of stochastic weather variables on these probabilities. Recapture probabilities were constrained by the value of weather variables on the day of recapture. Survival probabilities were constrained by the value of weather variables between t and t-1. Given that the data were obtained over unequal time intervals, a logit (log odds) link function was used to model both survival and recapture probabilities (Lebreton *et al.* 1992).

To select between these models at each stage and estimate precision, Akaike's Information Criterion (AIC_c: Akaike 1985) was used. This quantity is defined as;

$$AIC_c = -2 \ln L + 2 \times np$$

where *np* is the number of parameters of the model.

This is an information-theoretic measure that ensures a good balance between under and over fit when the most general model does not fit the data (Anderson *et al.* 1994). The reliability of the results provided using AIC's is not influenced by the number of tests performed. Since the absolute value of AIC_c is uninformative, ΔAIC_c is presented i.e. the difference in AIC_c between the model in question and the model with the lowest AIC_c. Differences between models of the order of 1 or 2 in the values of AIC_c are, customarily, not considered significant (e.g. Lebreton *et al.* 1992; Yoccoz *et al.* 1998). Model notation used here is based on Lebreton *et al.* (1992) using the subscripts given in Table 6.1 and with plus signs indicating that the model includes only main effects while an asterisk indicates that it includes interaction terms.

Table 6.1 Model subscripts used in the analyses.

Subscript	Meaning
t	Time-dependence (day-to-day variation)
s	Sex-effect
Individual covariate	
b	Body size (left forewing length (mm))
External covariates	
Maxt	Maximum temperature in 24 hours (°C)
Mint	Minimum temperature in 24 hours (°C)
Meant	Mean temperature in 24 hours (°C)
Rain	Amount of rain (mm)

6.3 Results

6.3.1 General reproductive biology of *C. mercuriale*

6.3.1.1 Description of the reproductive behaviour of *C. mercuriale*

Duration of reproductive behaviours

In both Aylesbeare (n=15) and Upper Crockford (n=22), copulations occurred in tussocks of vegetation near the stream rather than in areas of open water. There was no difference between copula duration in caged versus natural conditions at Upper Crockford (two sample t-test, t=1.05, p=0.31, 20 d.f.). Thus caged and natural copulations were amalgamated for the following partial correlation analyses. There was no effect of temperature on copula duration controlling for time of day (partial correlation coefficient r_p = -0.104, p=0.662, n=18). There was no effect of time of day on copula duration controlling for temperature (r_p = -0.273, p=0.244, n=18). As for other odonates, it was possible to distinguish three stages of copulation in *C. mercuriale*. The mean duration of the insemination stage (Stage 2) was 12.39 ± 1.58 minutes.

Table 6.2 Mean (± s.e) and range of total copula duration (minutes) for pairs from Aylesbeare and Upper Crockford.

		n	μ ± s.e.	Range
Aylesbeare		2	19.46 ± 0.63	-
Upper	All	22	23.13 ± 1.63	14.22 – 44.98
Crockford	Caged	15	21.96 ± 1.63	15.00 – 40.00
	Natural	7	25.64 ± 3.80	14.22 – 44.98

Since pairs usually went into tandem in tussocks focals began when pairs arrived at the breeding site rather than at the beginning of the tandem. Thus only 5 pairs at Upper Crockford were observed from the point at which they formed a tandem until the point at which they split after oviposition. For these pairs, the mean duration of the tandem was 69.92 ± 15.95 minutes (ranging from 43 to 130.37 minutes).

Thus when investigating the distribution of a pair's time between different reproductive behaviours, the period between the beginning of copulation and the end of oviposition will be considered here. This information was available for nine pairs from Upper Crockford. This period can be divided into 1) copulation, 2) tandem between copulation and oviposition, and 3) searching for oviposition sites and oviposition itself. The mean and range of the duration of each of these reproductive behaviours and for the whole period are given in Table 6.3. The mean percentage of the total period spent in each behaviour is shown in Fig. 6.1. The total period of a pair's reproductive activity (as defined above) lasted just over an hour. Copulation and oviposition (or searching for oviposition sites) each made up around 40% of a pair's time whilst 20% of it was spent in tandem in between copulation and oviposition (Fig. 6.1). Of the time spent in behaviour 3), the mean percentage time spent actually ovipositing rather than searching for sites was 50.07 ± 8.45% (ranging from 23.49 to 100%).

Table 6.3 Mean ± s.e. and range (in minutes) of time spent in different reproductive behaviours for 9 pairs from Upper Crockford 1999.

Time period	μ ± s.e.	Range
Total period	67.98 ± 8.53	39.60 – 102.63
1) Copulation	24.17 ± 2.43	15.00 – 40.00
2) Tandem between copulation and oviposition	13.35 ± 3.50	3 – 38.95
3) Oviposition or searching for oviposition sites	30.47 ± 5.53	8.25 – 58.00

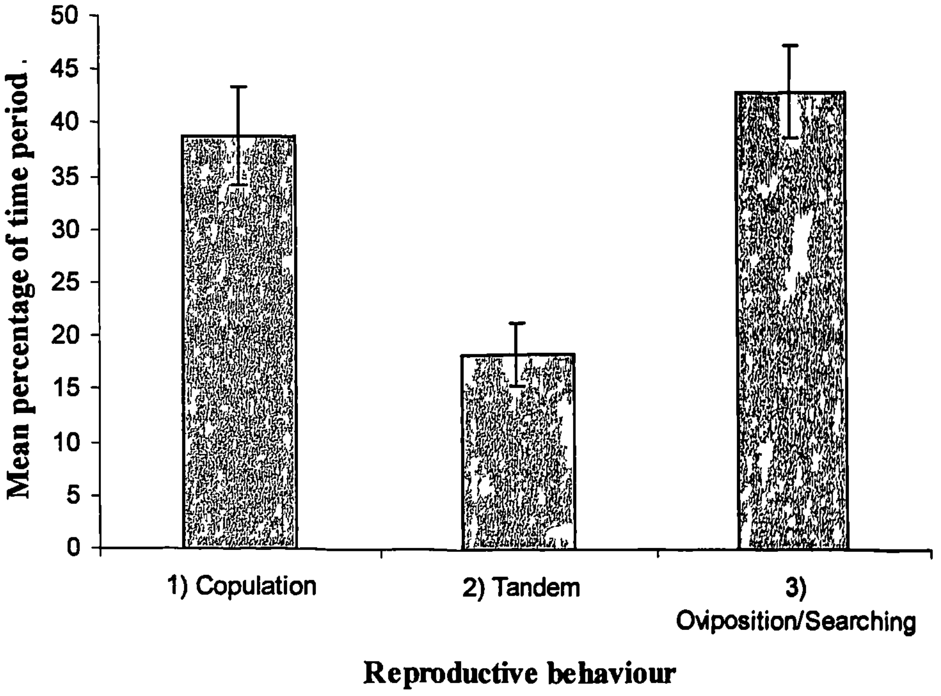


Fig. 6.1 Mean percentage (± s.e.) of the total time period spent in each reproductive behaviour.

There was a peak of damselfly activity (in terms of number and percentage of individuals present) in the middle of the day (Figs. 6.2 and 6.3) at Upper Crockford. A peak in reproductive activity also occurred in the middle of the day (i.e. paired individuals on Fig. 6.4). Females are seen more often in tandem than unpaired. Although mean temperature also peaked in the middle of the day (Fig. 6.5), it tended to remain high through the afternoon whilst damselfly numbers and reproductive activity decline through the afternoon.

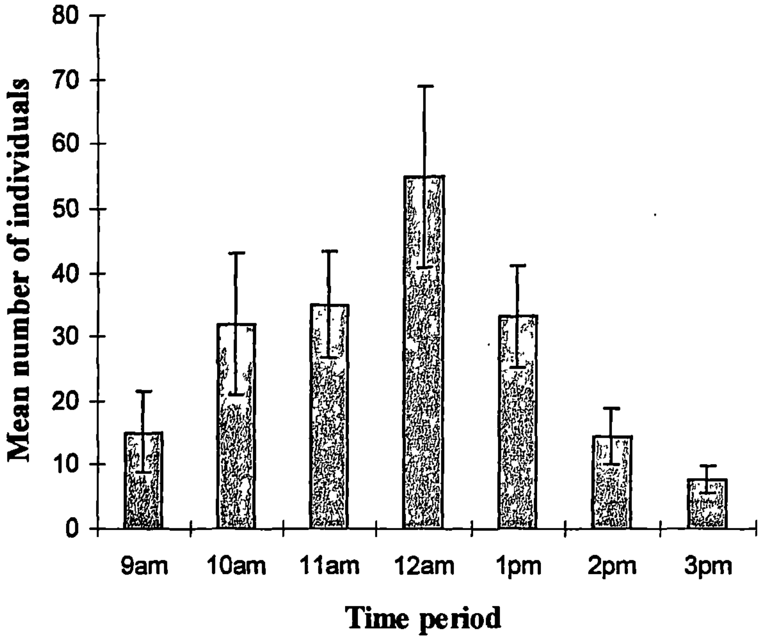


Fig. 6.2 Mean number of individuals (± s.e.) present in each time period (*n*=8 days).

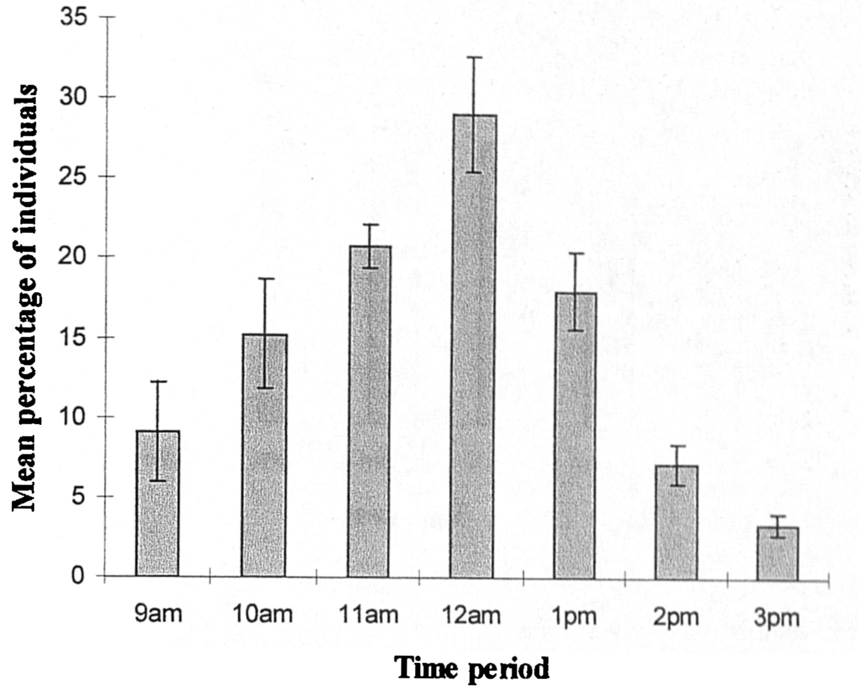


Fig. 6.3 Mean percentage of day's individuals (± s.e.) present in each time period (*n*=8 days).

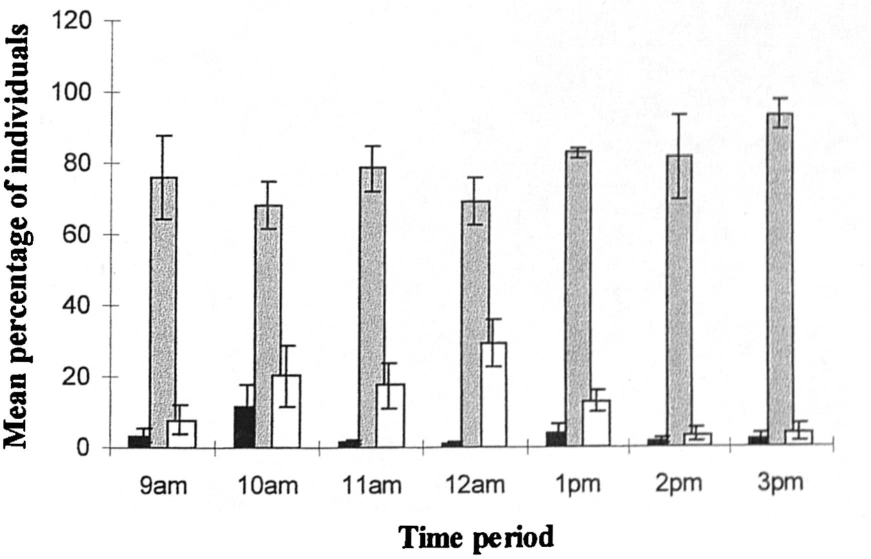


Fig. 6.4 Mean percentage of individuals (± s.e.) that are unpaired males (grey bars), unpaired females (black bars) and paired (open bars) in each time period (*n*=8 days).

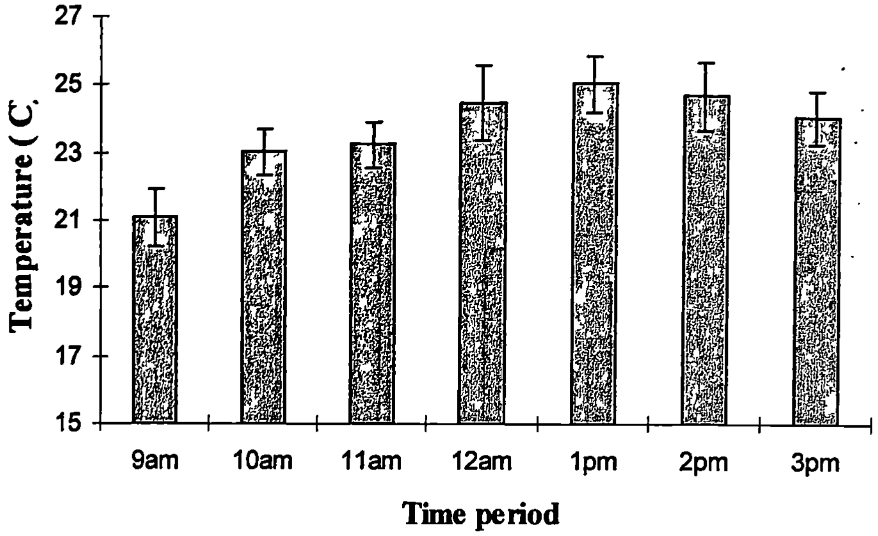


Fig. 6.5 Mean temperature (± s.e.) in each time period (*n*= 8 days).

Daily variation in damselfly activity was examined in relation to weather variables and season using the Aylesbeare dataset. Such examination is justified since only a fraction of the individuals known to be alive on a given day (due to subsequent recapture) were actually present on site (Fig. 6.6a). Since mark-recapture exercises had only been performed when damselflies were present on site, this analysis investigates how weather variables and season effect the activity of odonates, given that weather permitted odonates to be present at all. The sum of hours spent by all individuals present at the breeding site on a day was used as a measure of damselfly activity, for 42 days when atleast one damselfly was seen. Thus, this measure incorporates both the number of individuals present and the time they spent on site. The daily sex ratios at the stream varied from 6:1 to 1:1 (males:females – Fig. 6.6b. Males exceeded females in the number of individuals present (paired t-test, t=-8.036, p<0.001, 49 d.f. – Table 6.4 and Fig. 6.6b); the sum of the hours spent at the breeding site by all individuals (paired Wilcoxon signed ranks test, Z=-5.150, p<0.001 – Table 6.4). Thus the analysis of the effect of weather on activity was performed separately for males and females. The sum of hours spent by all males at the breeding site on a day was square-root transformed and is hereafter referred to as MACTIVITY whilst the measure for females did not require transformation and will be referred to as FACTIVITY.

Table 6.4 Mean (± s.e.) of the number of individuals present and the sum of the hours spent at the breeding site by all individuals.

Variable (per day)	n	Males $\mu \pm$*s.e.*.	Females $\mu \pm$*s.e.*.
Number of individuals present at the breeding site	50	10.14 ± 1.23	3.86 ± 0.61
Sum of the hours spent at the breeding site by all individuals	51	20.20 ± 3.61	6.49 ± 1.03

The following weather variables (with their variable name in parentheses) were obtained from a British Atmospheric Data Centre climate station in Exmouth 10km away from Aylesbeare (SY027819); rainfall (in mm) over 24 hours (RAIN); sunlight in 0.1 hours (SUN) and average daytime temperature in 0.1 °C (TEMP). A partial correlation between day of season (DAY) and TEMP controlling for SUN was found to be significant (partial correlation coefficient r_p=0.449, p=0.001, n=48) as was a partial correlation between TEMP and SUN controlling for DAY (r_p=0.257, p=0.036, n=48). There was no significant partial correlation between SUN and DAY controlling for temperature (r_p =-0.135, p=0.351, n=48). Given this multicollinearity among variables, a stepwise multiple regression procedure was used (Stepping Criteria: Probability of F = 0.050 to enter a variable into the model; Probability of F = 0.100 to remove a variable from the model) to determine which variable accounted for most of the daily variation in damselfly activity (i.e.the sum of the hours spent at the breeding site by all individuals - square root transformed). This procedure tests the parameter associated with each variable in the presence of all the variables already in the model (Mendenhall & Sincich 1996; Trexler & Travis 1993).

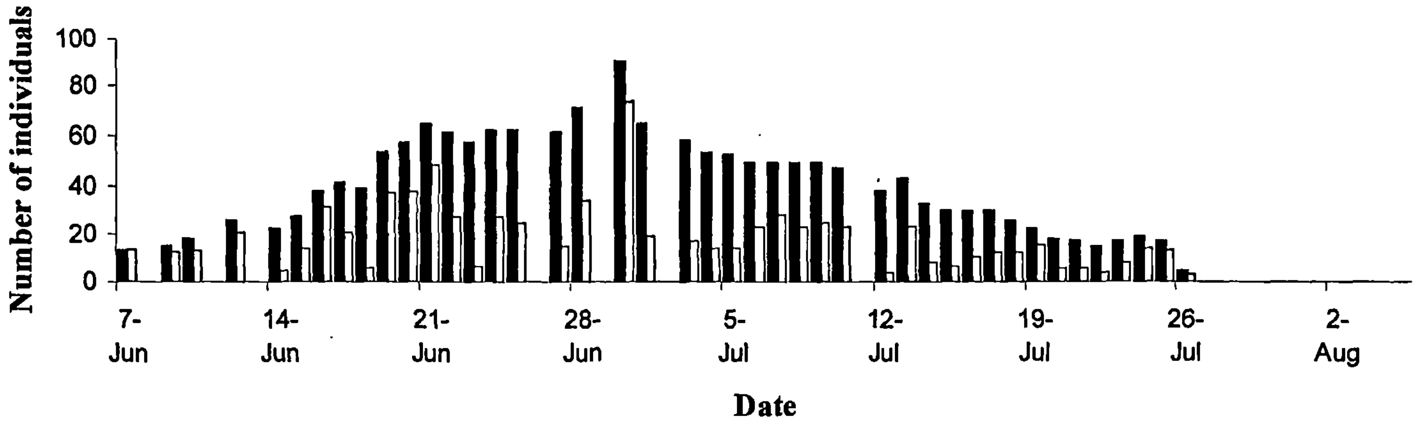


Fig. 6.6a The number of individuals alive (closed bars) and the number of individuals present at the breeding site (open bars) on each date (for days when mark-recapture took place).

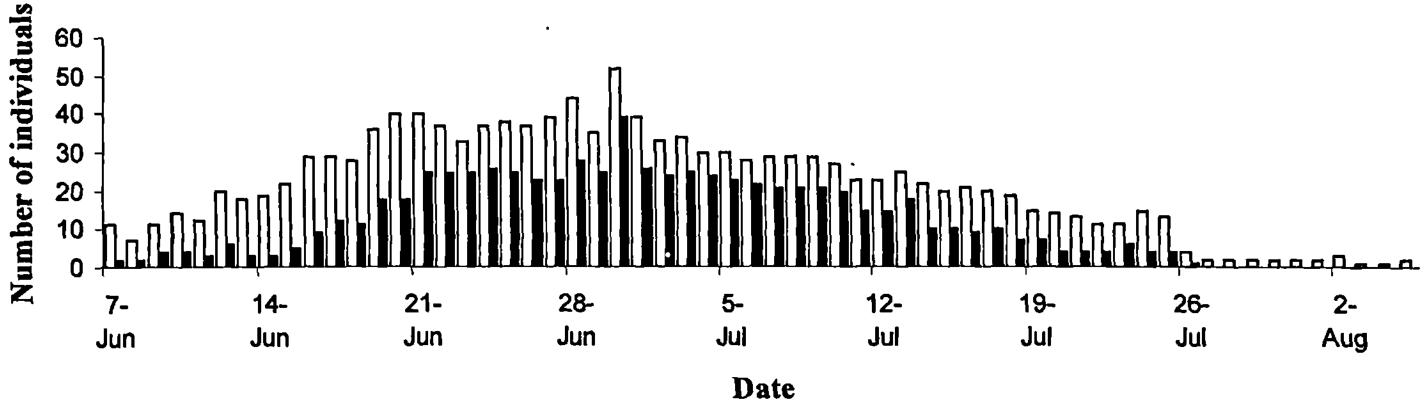


Fig. 6.6b The number of males (open bars) and females (closed bars) present at the breeding site on each date.

For females (Table 6.5a), only SUN was added to the model and had a positive relationship with FACTIVITY but only explained 9.9% of the variation in female activity. For males (Table 6.5b), SUN was added first to the model followed by TEMP and DAY, with significant changes in F-ratio with the addition of each new variable. This model explained 44.6% of the variation in MACTIVITY. Thus male activity increased with the duration of sunlight and temperature but declined as the season progressed. The same explanatory variables were chosen by a stepwise regression when number of individuals is substituted as the dependent variables for both males and females. These data may suggest that weather variables and season may have a greater effect on the activity of males compared to females and thus may affect the LMS of the two sexes to different degrees.. However due to the low recapture rate of females outside tandems it is difficult to draw conclusions about their activities from this dataset.

The probability that mating activity will occur on a particular day (given that damselflies are present at the breeding site) is also influenced by weather variables. To investigate this, a stepwise logistic regression procedure was used to compare days when mating occurred to days when it did not occur. SUN was added as a significant predictor of the probability that mating occurred on a day given that damselflies were present (Table 6.6). In view of this, a weather component was incorporated into the subsequent LMS analysis - the proportion of days in an individual's lifespan on which mating was not possible for any damselflies present at the breeding site.

Table 6.5a Stepwise multiple regression analysis for the sum of hours spent by females at the breeding site on each day.

Model FACTIVITY= SUN + C	d.f.		*Mean square*	F	*p*
Regression	1		174.34	4.39	0.043
Residual	40		39.72		
Total	41				
$R^2 = 0.099$					
Coefficients	B	*s.e..*	β	*t*	*p*
Constant	4.17	1.72		2.43	0.02
SUN	0.05	0.02	0.31	2.10	0.043

Table 6.5b Stepwise multiple regression analysis for the sum of hours spent by males at the breeding site on each day.

Model MACTIVITY=SUN + DAY + TEMP +C	d.f.		*Mean square*	F	*p*
Regression	3		25.76	10.21	<0.001
Residual	38		2.52		
Total	41				
$R^2 = 0.446$					
Coefficients	*B*	*s.e.*.	*β*	*t*	*p*
Constant	-3.55	3.32		-1.07	0.291
SUN	0.02	0.01	0.43	3.44	0.001
DAY	-0.05	0.02	-0.38	-3.00	0.005
TEMP	0.05	0.02	0.31	2.38	0.023

Table 6.6 Logistic regression analysis of the probability that mating will occur on a particular day (given that damselflies are present at the breeding site).

	B	*s.e.*.	Likelihood ratio (LR)	d.f.	G	*p*	n_0	n_1	*exp(β)*
Constant	-1.84	0.72							
SUN	0.03	0.01	-29.07	1	13.30	0.0003	20	22	1.03

Model χ^2=13.30, p< 0.0011 d.f.

Visiting patterns to the stream and residency duration

In total, 116 males were marked and 86 (74.1 %) were recaptured and were termed 'residents'. There was no difference between the proportion of males that did not return to the stream after their first visit (30/116) and those that did not return after their second visit (19/86) $\chi^2 = 0.20$, p=0.651, 1 d.f., (Yates correction). This suggests that there is no effect of marking on recapture probability of males. The duration of residency at the breeding site was calculated as the interval between the first and last capture of an individual. Hereafter this will be referred to as residency duration, rather than lifespan, to distinguish it from survival as estimated by MARK. As shown above, individuals are not present at the breeding site throughout their lifetimes such that residency duration also differs from the total hours or days at the breeding site. Mean residency duration was 10.09 days ± 0.81 for all males, and was 13.26 days ± 0.86 for male residents only.

In total, 77 females were marked and 45 (58.4%) were recaptured and were termed 'residents'. Males and females differed significantly in recapture proportion ($\chi^2 = 17.86$, $p < 0.0001$, 1 d.f.). The proportion of females that did not return to the stream after their second visit (5/45) was smaller than those that did not return after their first visit (32/77) $\chi^2 = 11.07$ $p < 0.0001$, 1 d.f. (Yates corrected). This may indicate a significant effect of marking on females although no trap dependency was found in the subsequent survival analysis (as indicated by Test 2 of RELEASE). Trap dependency is where the probability of capturing an individual on occasion t+1 is positively or negatively related to the probability of capturing the same individual on occasion t. The mean residency duration was 7.91 days ± 1.06 for all females, and was 12.82 days ± 1.41 for female residents only.

Male and female residents did not differ in residency duration (Fig. 6.7a)., Komolgorov-Smirnov Z=0.74, p=0.453, n_m=86, n_f=45). A difference was found when all males and females were considered (Fig. 6.7b), Komolgorov-Smirnov Z=1.39, p=0.023, n_m=116, n_f=74;) but only due to the higher proportion of females with a lifespan of 1 day (see above). Males spent significantly longer at the breeding site during their lifetime than females (Table 6.7) though the mean duration of visits did not differ between males and females.

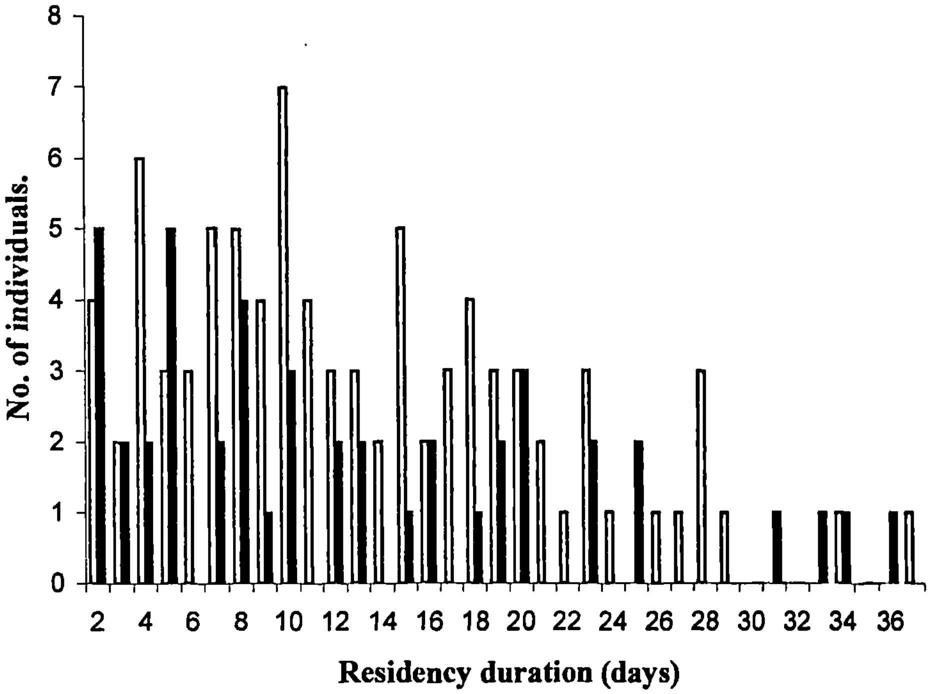


Fig. 6.7a Residency duration of male (white bars, n=86) and female (black bars, n=45) residents.

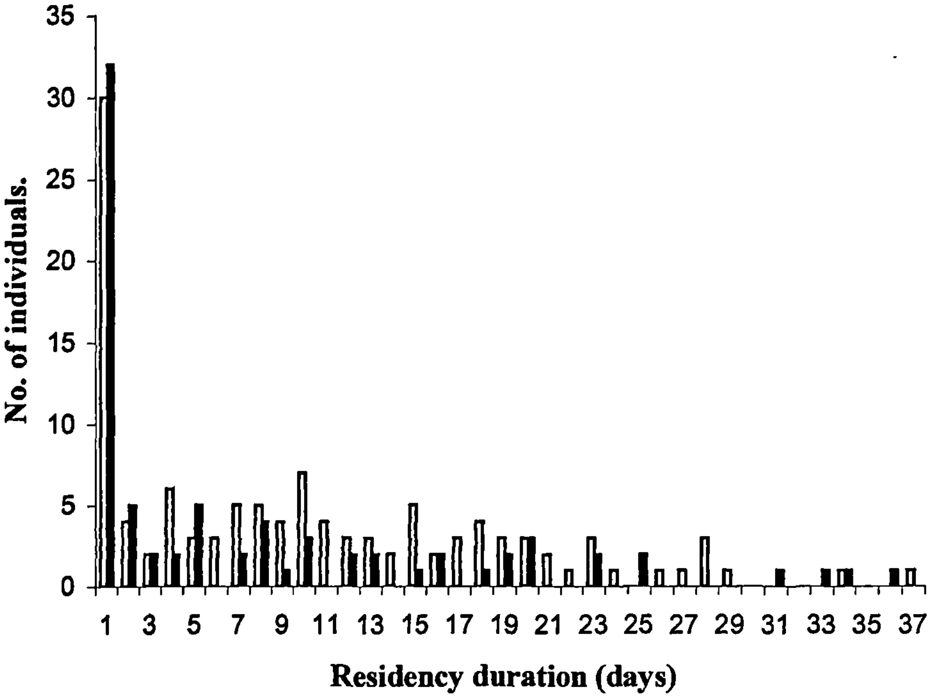


Fig. 6.7b Residency duration of all males (white bars, *n*=116) and females (black bars, *n*=77).

Table 6.7 Mann-Whitney tests between males and females for total hours spent at the breeding site in their lifetime and mean duration of visits to the breeding site (with mean (± s.e.) and range).

Variable	Sex	$\mu \pm s.e.$.	Range	Mann Whitney U	*p*	*n*
Total hours spent at breeding site in lifetime	Male	4.46 ± 0.35	1 – 20	3073.5	<0.001	115
	Female	2.59 ± 0.23	1 – 9			75
Mean duration of visits to breeding site	Male	1.55 ± 0.08	1 – 7	3785.5	0.08	115
	Female	1.40 ± 0.09	1 – 4			76

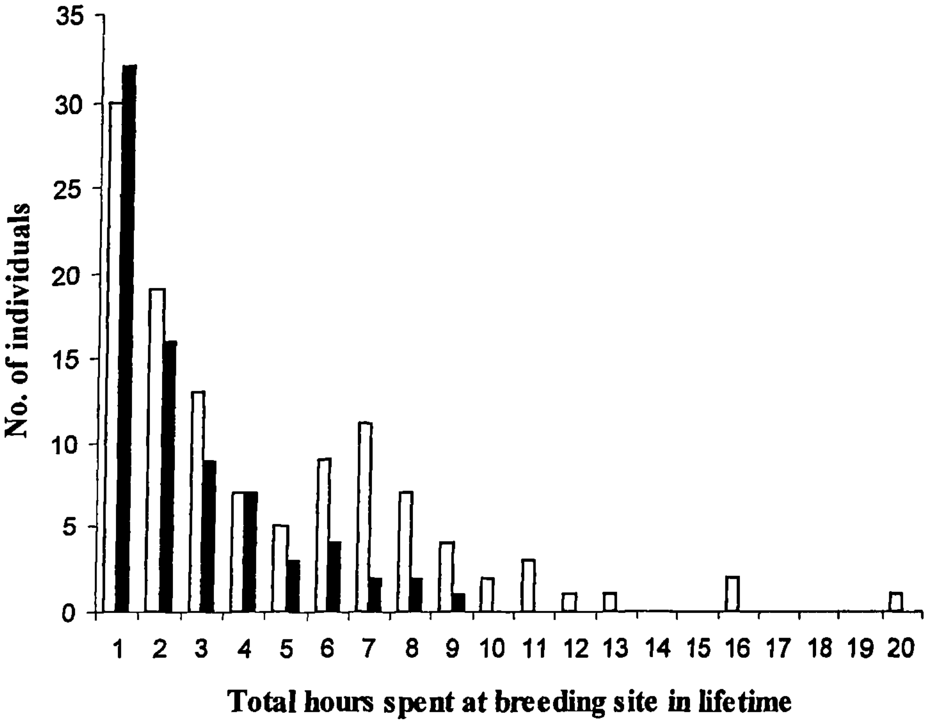


Fig. 6.8 Frequency distribution for males (open bars, n=115) and females (closed bars, n=76) of the total hours spent at the breeding site in their lifetime.

Interval between consecutive matings

Data on the interval between consecutive matings was available for 33 individuals and 50 intervals. The intervals between the 22 days on which weather conditions permitted mating activity ranged from 1 to 4 day with a mean of 2.19 ± 0.25 days. There was a lack of continuously suitable conditions for mating such that the interval between consecutive matings is likely to depend largely on stochastic variation in weather conditions rather than on behavioural decisions on investment in reproductive and other activities. For example, it is not possible to determine explicitly the time required to mature a clutch of eggs by female *C. mercuriale*. However, the fact that some females had an interval of one day between matings (5/21) suggests that it is possible to mature eggs in one day in good weather conditions.

However, males and females did not differ in the mean interval between matings calculated for an individual, or in the interval between matings when the 50 intervals were classified as male or female (some individuals were represented more than once in the latter data).

Table 6.8 Wilcoxon two-sample tests, F-test for homogeneity of variance between males and females for mean interval between matings per individual and interval between matings (with mean (± s.e.) and range).

Variable	n	Sex	$\mu \pm s.e.$.	Range	W	p
Mean interval between	17	M	4.55 ± 0.77	1 - 12	247	0.133
matings*	16	F	7.81 ± 1.46	1 - 18		
Interval between	29	M	4.00 ± 0.55	1 – 9	664	0.134
matings*	21	F	7.57 ± 1.65	1 – 30		

*square root transformed for F-tests, M=male, F=female.

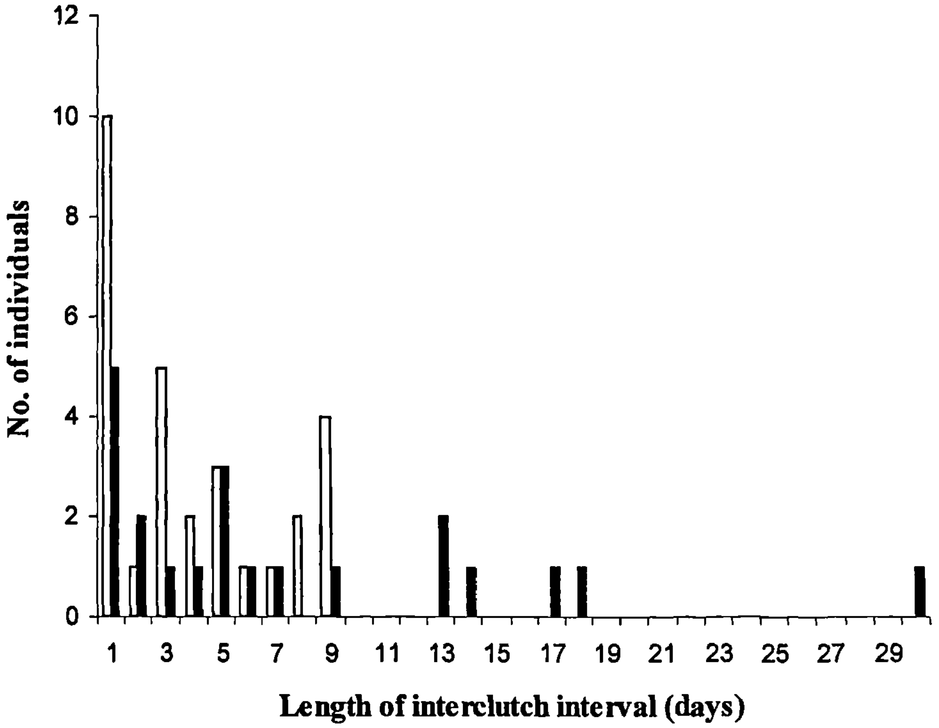


Fig. 6.9 Frequency distribution of the interval between consecutive matings for males (open bars, n=29) and females (closed bars, n=21).

6.3.1.2 Clutch size and oviposition behaviour

In Aylesbeare, 15 oviposition episodes were observed. There were 11 episodes where all oviposition behaviour occurred in tandem, two (13%) where the females oviposited entirely alone and two (13%) where oviposition began in tandem but ended with the female ovipositing alone. Oviposition behaviour was not preceded by mating on the same day in the two lone ovipositions. Two ovipositions in Aylesbeare were prevented (having begun) by wind conditions whilst three were terminated in Upper Crockford when one member of a pair became stuck in sundew (see Chapter 5).

Fig. 6.10 shows the frequency distribution of the total eggs contained by females collected in the morning before oviposition at Upper Crockford. The mean of this total was 146.1 ± 16.0 and ranged from 7 to360 eggs. The frequency distribution of number of eggs found inside females after oviposition is shown in Fig. 6.11. Whilst the mean number of eggs left after oviposition was 12.67 ± 4.94, two individuals had more than 70 eggs remaining. This indicates that a small proportion of females may not lay all their eggs during one oviposition episode but may divide than between two. This is supported by the fact that a substantial portion of females observed in pair focals (Chapter 5) laid 50 eggs or less in an oviposition episode.

Whilst there is no positive linear relationship between clutch size before oviposition and head width (F=1.80, p=0.197, R^2=0.091, 19 d.f.), maximum clutch size may be limited by body size i.e. large clutch sizes (>200 eggs) only occurred in individuals with large head widths (>4mm). Mean egg length was 0.981 ± 0.003mm (ranging from 0.833-1.133, n=325). There was a positive relationship between mean egg length and head width (Fig. 6.14, F=7.82, p=0.009, R^2=0.207, 31 d.f.).

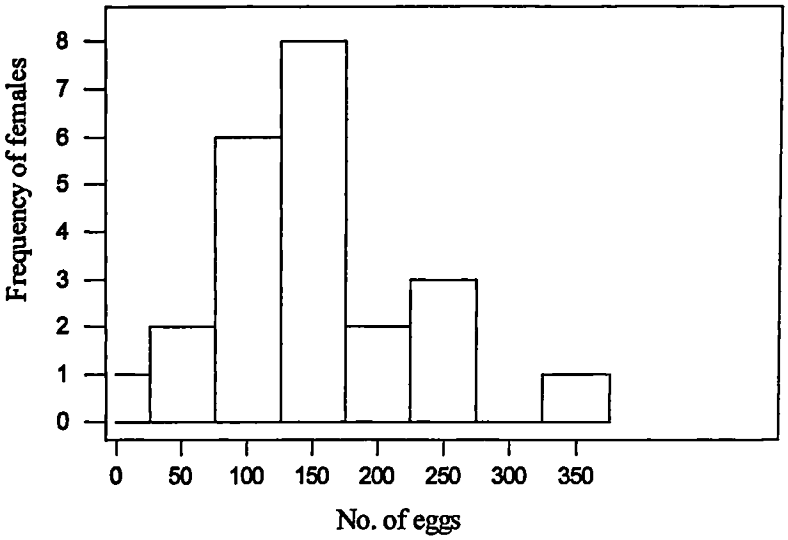


Fig. 6.10 Frequency distribution of number of eggs found in females before oviposition (n=23).

Fig. 6.11 Frequency distribution of number of eggs found in females after oviposition (n=18).

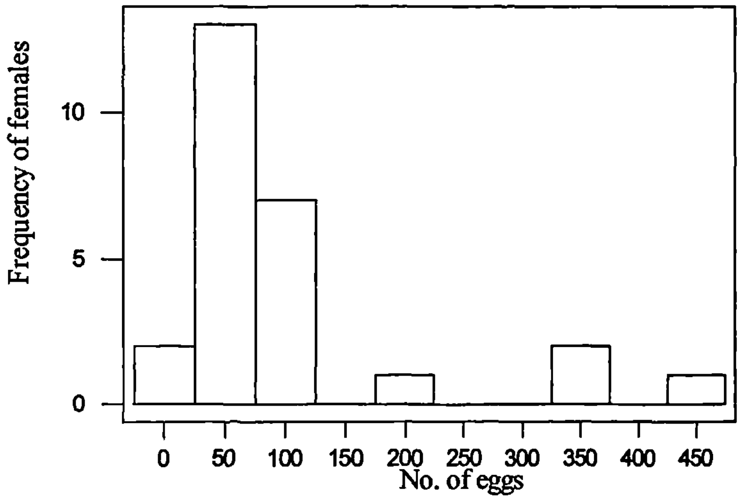


Fig. 6.12 Frequency distribution of number of eggs laid by females during oviposition focals (*n*=27, all focals ended with a natural pair split) derived from plant stem dissections.

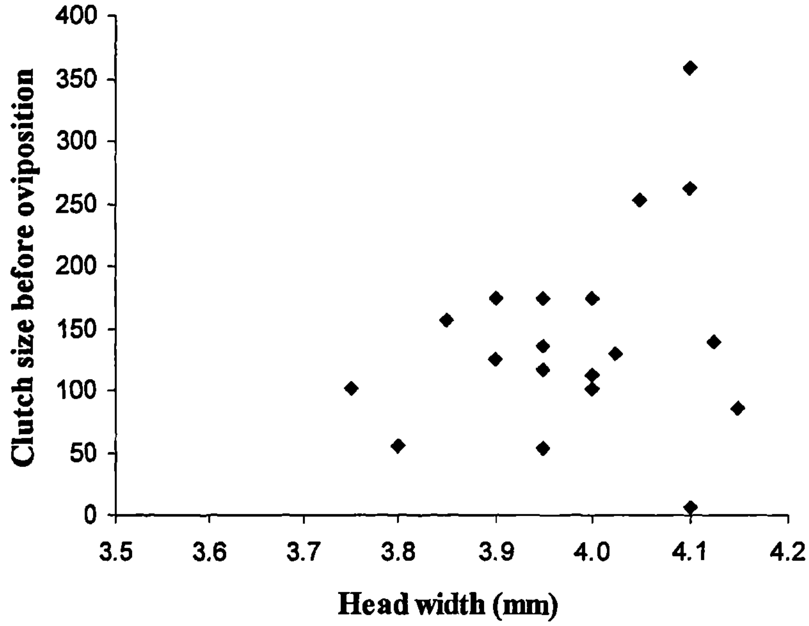


Fig. 6.13 Relationship between clutch size before oviposition and head width (n=20).

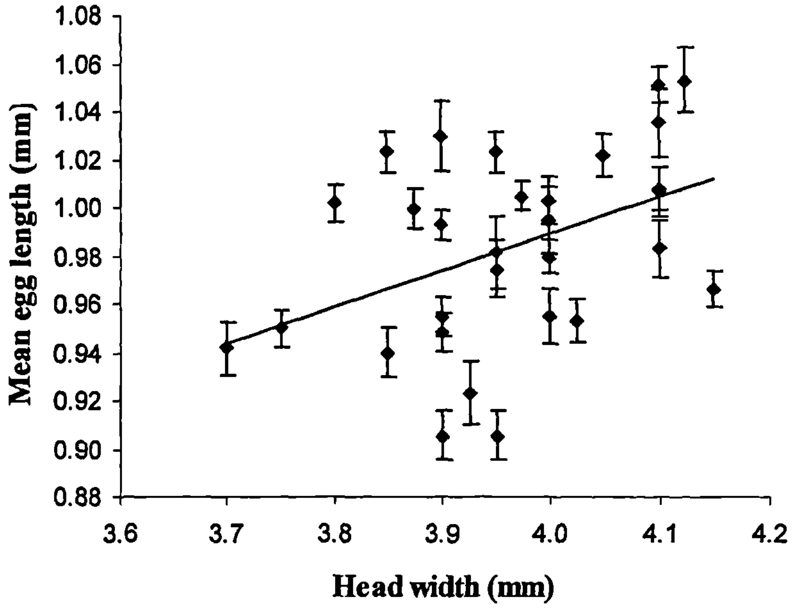


Fig. 6.14 Relationship between mean egg length (± s.e.) and head width (n=32).

Table 6.9 shows the number of females that had different patterns of sperm presence and absence in their sperm storage organs - pre-copula, post-copula and post-oviposition. As expected, all females collected immediately after copulation had sperm in both storage organs. All but one of the fifteen females collected after ovipositon still had sperm in both their spermatheca and bursa indicating that the sperm store is not substantially depleted during one oviposition episode. Consistent with this, most of the females collected before copulation contained sperm in one or both of the storage organs and thus sperm is stored between matings in *C. mercuriale*. The four females containing no sperm before copulation are assumed to have been virgin females.

Fig. 6.15a shows the female reproductive tract of *C. mercuriale*. As in other odonates, the anterior region of the vagina is bounded dorsoventrally by two flat sclerotized plates. In *C. mercuriale*, the outer surface of each plate has a collection of approximately 40 black circular structures - campaniform sensillae that are related to the coordination of sperm ejection during egg laying (Miller 1987). The mean width of this region of the vagina was 393 ± 7μm (ranging from 374 to 426, *n*=8) whilst the mean length was 632 ± 3μm (ranging from 542 to 779). The spermatheca is well defined and joined to the bursa copulatrix via a narrow duct. This spermathecal duct had a mean length of 399 ± 9μm (ranging from 368 to 447, *n*=10) and was 21 ± 1μm wide on average (range 16-24). The spermatheca was ovoid in shape with a mean width of 151 ± 6μm (ranging from 113 to 208, *n*=17) and a mean length of 253 ± 7μm (ranging from 211 to 303). The bursa copulatrix had a mean width of 242 ± 8μm (ranging from 203 to 284, *n*=11) and a mean length of 263 ± 12μm (ranging from 179-311). Thus the volume of the spermatheca is approximately half that of the bursa copulatrix and thus it probably stores a up to a third of the total sperm load. In addition, near the proximal end of the bursa at the side of the vagina, there is a triangular sclerotized plate of unknown function (cf Miller & Miller 1981).

Table 6.9 Frequency of females collected pre-copula, post-copula and post oviposition that showed different patterns of sperm presence (+) or absence (-) in their sperm storage organs.

Bursa	Spermatheca	Pre-copula	Post-copula	Post oviposition
-	-	4	0	0
-	+	4	0	1
+	+	4	4	14
+	-	0	0	0

6.3.1.3 Aedegus morphology

Within the zygoptera four types of penes have been recognised (Waage 1986). Since the penis of *C. mercuriale* cannot be easily classified into one of these types, a detailed description of its form in relation to possible sperm removal function is necessary. The distal segment of the aedegus has an extensible head consisting of a flap of cuticle which folds back along the ventral surface of the penis. This flap (Fig. 6.16a) has two long, recurved horns or cornua, ranging from 478.0 to 561.5 µm in length, and a pair of stout hooks at its base (50µm long). In addition, there is a membranous groove for sperm transfer on the dorsum of the penis head (Fig. 6.16b). Proximally–oriented micro-spination was evident on several areas of the penis. Firstly, long spines were found on the distal end of each cornua that were approximately 4-5 µm (Fig. 6.16c). Shorter spines, around 2-3µm in length, occur along the length of each flagellum and extensively over the ventro-lateral surface of the penis head at the base (Fig. 6.16e). Below the head, on the dorsal surface of the penis shaft, there are dense, overlapping layers of comb-like spines (approx. 4 µm long - MS on Fig. 6.16a, Fig. 6.16d). Sperm masses were found attached to all these sets of spines in male *C. mercuriale* (Fig. 6.16c and Fig. 6.16e clearly indicating their ability to remove sperm form the female sperm storage organs.

The width of the penis head where it attached to the penis shaft was 225µm. It was 100-150 µm (*n*=2) across between the tips of the basal hooks and 100-130µm at the widest distal point before the head bifurcated to form the two cornua. The head was 353µm long from its point of attachment to the penis shaft to the point of bifurcation. The cornua varied in width along their length (*n*=3), ranging from 36-58 µm immediately after bifurcation at the head, from 11-15µm along most of the length of the flagellum, tapering to 3-6µm at the tip.

With regards to which portions of the male's penis have access to the female sperm storage organs during copulation, several inferences can be made. The bursa would accommodate the width of only the head and cornua the shaft being too wide. However the head is longer than the bursa (353 and 263 respectively) and so only a portion of the penis head could enter the bursa. The cornua are narrower over almost their entire length (11-15µm after bifurcation) than the spermathecal duct (15-44µm) and they are somewhat longer than this duct (478-561µm versus 368-447µm) such that they could enter the spermatheca of the female.

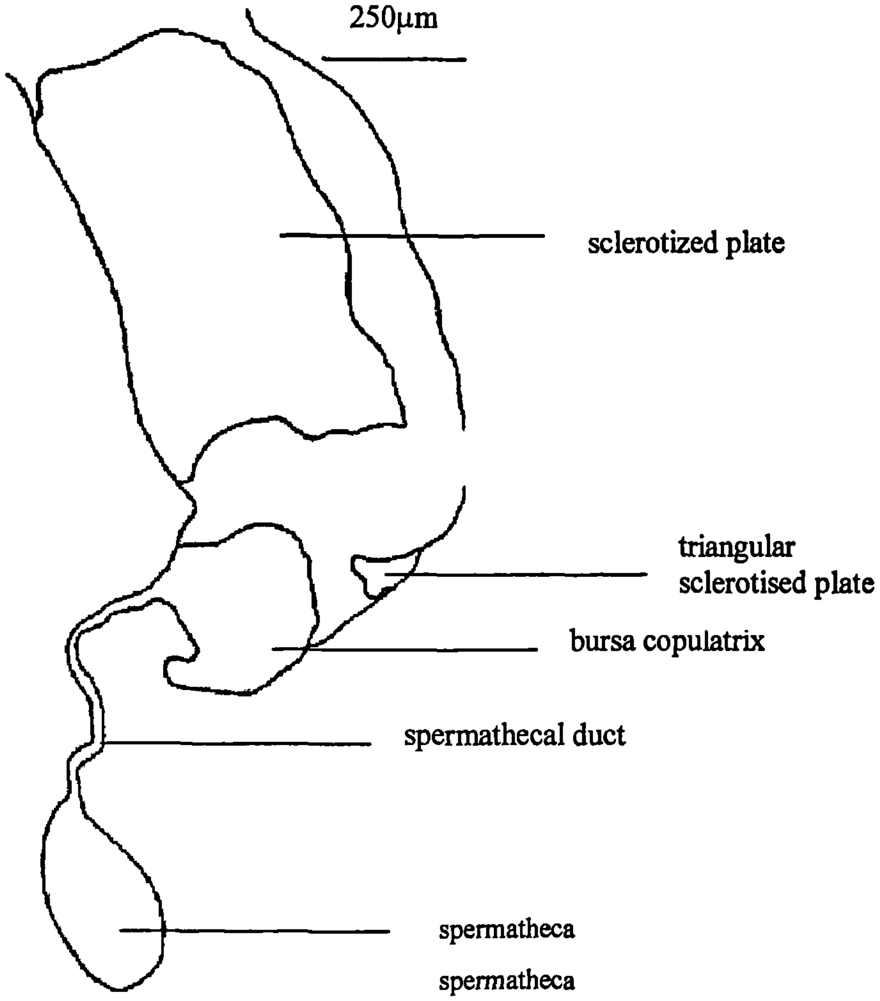


Fig. 6.15 The female reproductive system in *C. mercuriale*; scale bar represents 250μm.

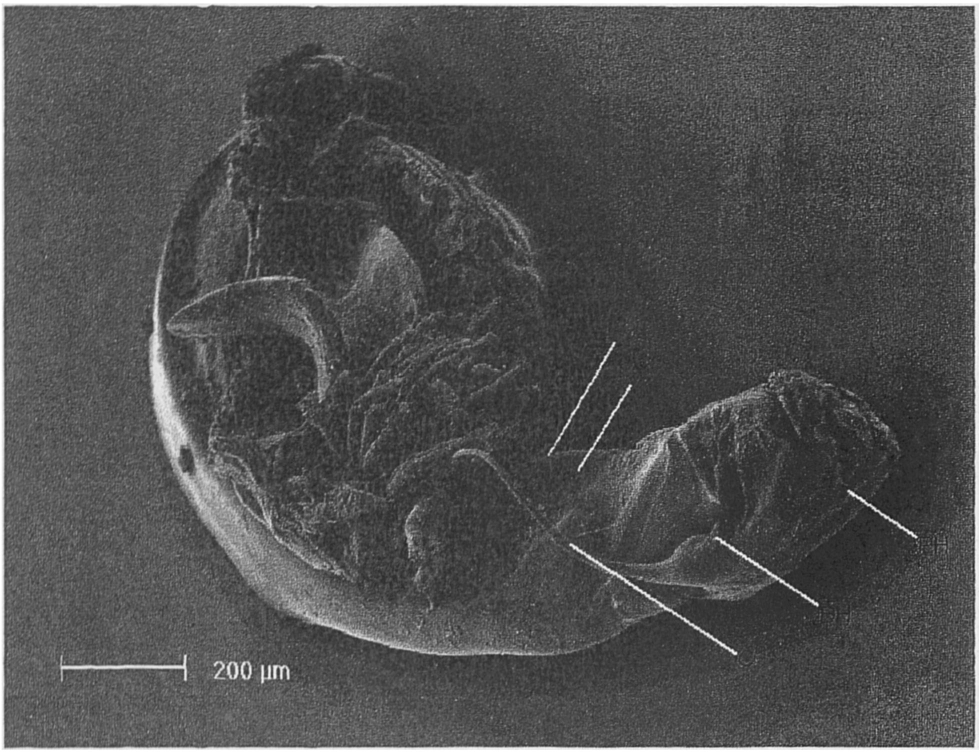


Fig. 6.16a Lateral view of the entire penis of *C. mercuriale* showing the penis shaft (PS) with the region of microspination (MS) and the extensible penis head (PH) with stout basal hooks (BH) and long, recurved cornua (C).

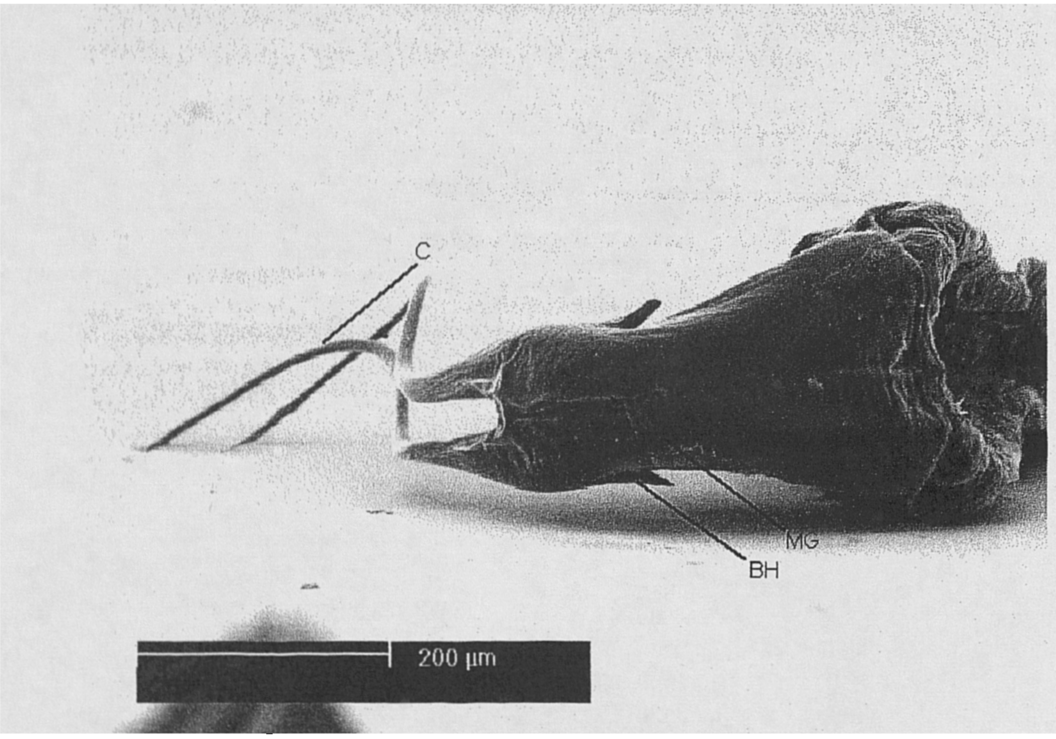


Fig. 6.16b Dorsal view of the penis head (extended) showing the membranous groove(MG), the basal hooks(BH) and cornua(C).

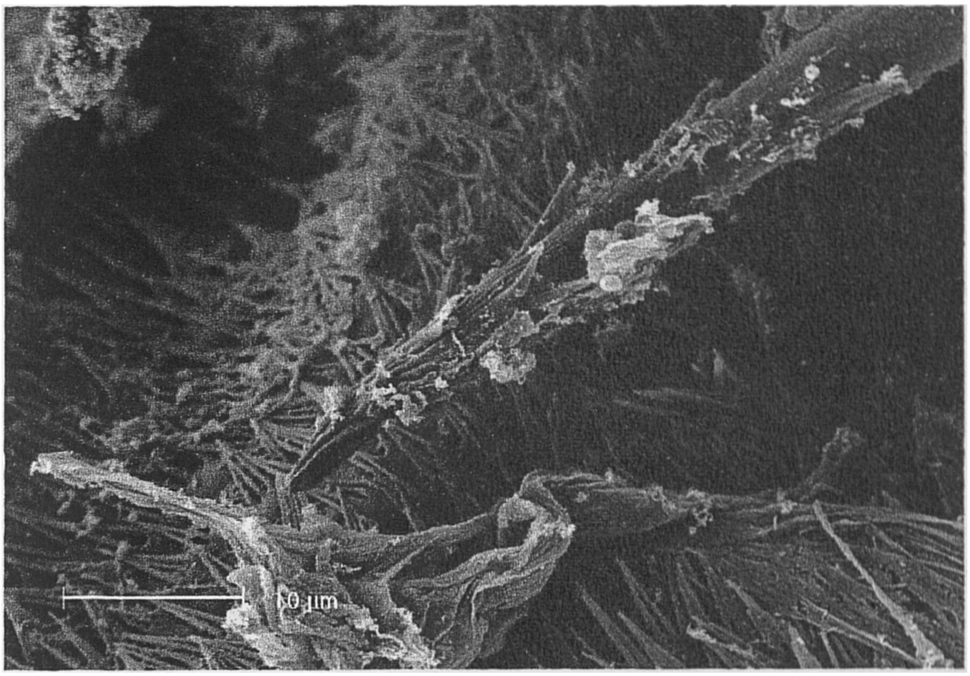


Fig. 6.16c Tip of cornua with proximally-oriented spines, under which sperm masses are trapped. Background shows comb-like spines on dorsal surface of the penis shaft.

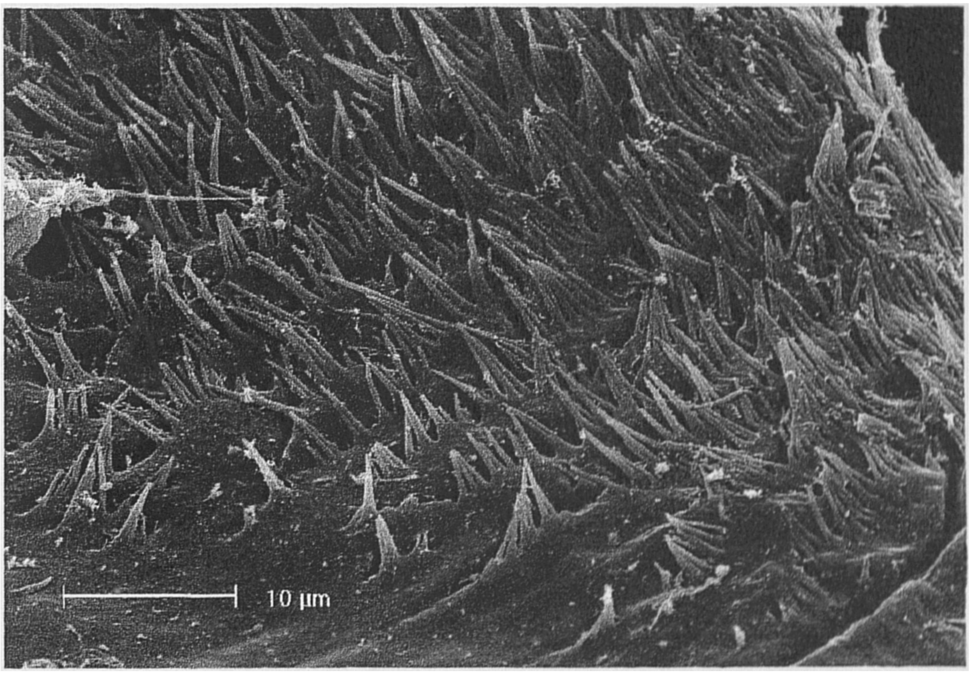


Fig. 6.16d Dense overlapping layers of comb-like microspination on the dorsal surface of the penis shaft.

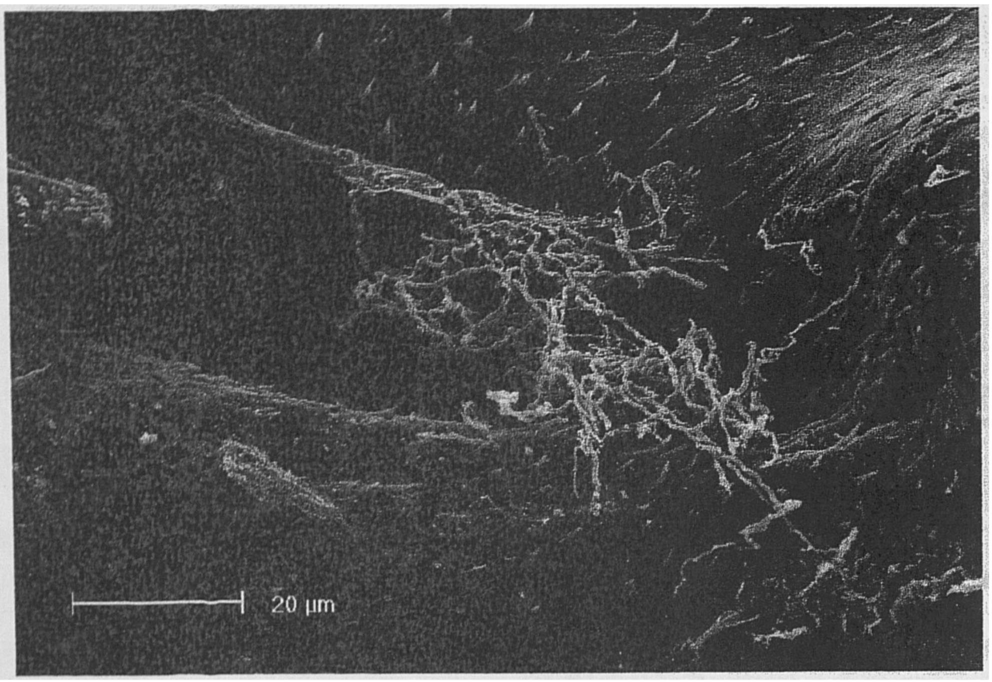


Fig. 6.16e Sperm masses trapped under short spines on the ventral-lateral surface of the penis head.

6.3.2 Variation in mating success

6.3.2.1 Daily variation in mating success

Daily variation in mating success was considerable for males. The proportion of males present at the stream that succeeded in mating varied from between 0-0.49. Average daily mating proportion of males was 0.093 ± 0.019 whilst average daily mating proportion of females was higher at 0.313 ± 0.056. For all days where mating occurred this difference was significant (paired t-test on arcsine transformed data; t=5.07, $p <$ 0.0001, n=22) but may be inflated by the difficulty of detecting females which were not in tandem. In a species with scramble competition, one would expect the proportion of males mating to decrease and the number of males present increases (relative to the number of females). However, since both density of individuals and mating activity vary with environmental conditions such a relationship may be difficult to detect. For days when mating occurred, there was no relationship between the mating proportion of males (arcsince transformed) and the density of males present on a day (F=0.69, p=0.417, R^2=0.03, 21 d.f.). The mating proportion of females showed no relationship with the density of females present on a day (F=0.86, p=0.366, R^2= 0.04, 21 d.f.) but showed a significant increase with the density of males present on a day (F=13.81, $p<$ 0.001, R^2= 0.41, 21 d.f.).

6.3.2.2 Lifetime mating success and mating efficiency

Males

72 matings were recorded involving 116 males, only 2 of which mated twice on the same day. Mean lifetime mating success was 0.62 ± 0.10 (all males) but was 0.83 ± 0.13 when only residents were included. Lifetime mating success deviated significantly from a Poisson distribution when all males were considered (Fig. 6.17, χ^2 = 12.13, p=0.002, 2 d.f., mating success > 2 pooled). This deviation from randomness was due to larger than expected numbers of individuals not mating at all or mating more than twice. Mating success did not deviate significantly from random when only residents were considered (Fig. 6.18, χ^2 = 6.03, p=0.890, 3 d.f., mating success > 3 pooled). This could indicate that observed variation in mating success results from random encounters with females unless phenotypic differences can be found between successful and unsuccessful males (Fincke 1988).

The proportion of males that mated on their first visit to the pond did not differ significantly between those visiting the pond only once (1/30) and residents that visited two or more times (11/86) (χ^2 = 1.72, p = 0.190, 1 d.f.). However the number of males mating on their first visit is low suggesting that marking may effect the probability of mating on the marking occasion. Consistent with this, mating efficiency (i.e. lifetime mating success per hour spent at stream) is lower for individuals that visited once (NR) versus residents (R) (median$_{NR}$ =0, n_{NR}=30; median$_R$ =0.0389, n_R=86; Wilcoxon two sample test W=1160.0, $p <$ 0.0001). Thus to avoid spurious associations between low residency duration and low mating success due to marking, the lifetime mating analysis was carried out firstly including individuals only seen once and secondly excluding such individuals.

Females

I recorded 56 matings by 77 females. Females that mated twice on the same day did so after being separated from the first male (for marking) so these matings were discarded. Mean lifetime mating success was 0.76 ± 0.10 (all females) but was 1.07 ± 0.15 when only residents were included. Mating success did not deviate significantly from a Poisson distribution when all females are considered (Fig. 6.19, χ^2 =0.401, p=0.98, 3 d.f.) or when only residents were considered (Fig. 6.20, χ^2 = 0.000, p=1.00, 3 d.f.). The proportion of females that mated on their first visit to the pond did not differ significantly between those visiting the pond only once (10/32) and residents (20/45) (χ^2 = 1.369, p = 0.242, 1 d.f.). Given that lone females are inconspicuous, females were usually seen in tandem. This led to a high number of individuals mating on their first visit and inflated estimates of mating efficiency (i.e. lifetime mating success per hour spent at stream). However, mating efficiency did not differ between females that visited once versus residents (median$_{NR}$ =0, n_{NR}=32; median$_R$ =0.25, n_R=45; Wilcoxon two sample test W=1113.0, p =0.143). This suggested that individuals only seen once should be included in the lifetime mating success analysis but the analysis was also repeated excluding such individuals.

The distribution of mating success did not differ between males and females for both resident individuals (χ^2=4.532, p=0.339, 4 d.f., with amalgamation of individuals that mated 4 or more times) and all individuals (χ^2=4.834, p=0.305, 4 d.f., with amalgamation of individuals that mated 4 or more times).

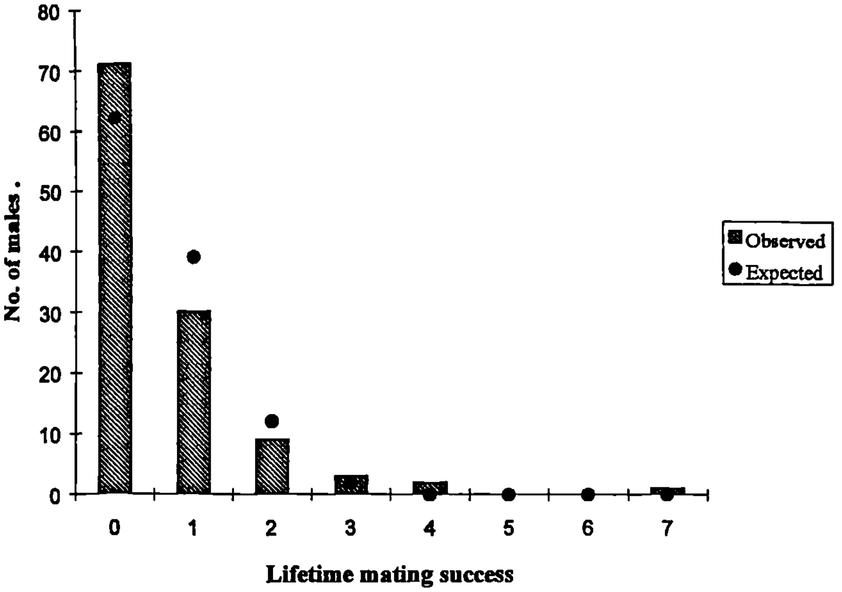


Fig. 6.17 Frequency distribution of lifetime mating success for all males.

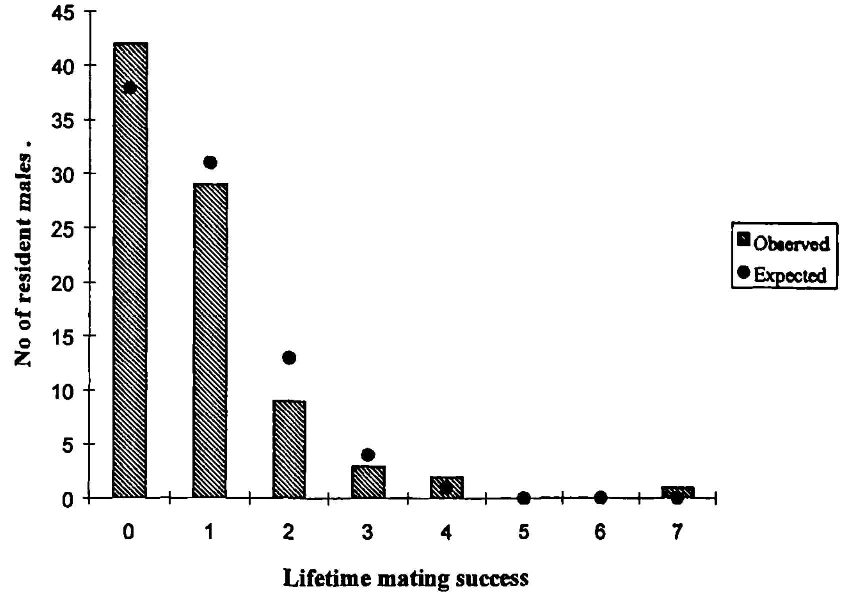


Fig. 6.18 Frequency distribution of lifetime mating success for resident males.

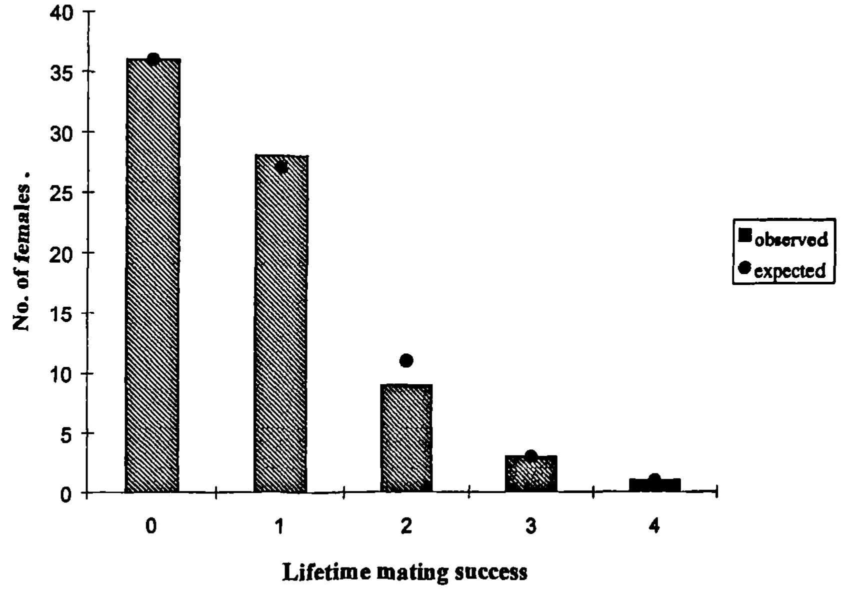


Fig. 6.19 Frequency distribution of lifetime mating success for all females.

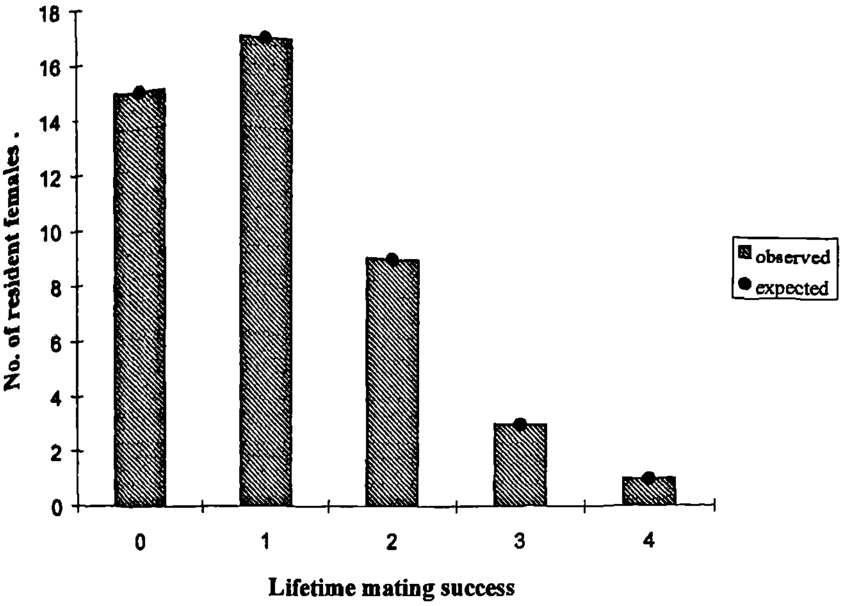


Fig. 6.20 Frequency distribution of lifetime mating success for resident females.

6.3.2.3. Effect of age on lifetime mating success

The effect of age on the probability of mating was examined in males and females under the assumption that the number of matings obtained by any age group should be proportional to the number of individuals of that age in the population (*cf* Fincke, 1982). The observed frequencies of mated individuals in each age group were compared with the frequencies expected under this assumption using chi-squared tests.

Older males were no less successful on a daily basis than younger males (χ^2 = 12.98, p= 0.673, 16 d.f.). Older females are no less successful on a daily basis than younger females (χ^2 = 9.29, p= 0.318, 9 d.f.). Appendices 8 and 9 contain these chi-squared values partitioned by age group for males and females respectively.

6.3.2.4. Effect of body size on lifetime mating success

Mating was not found to be assortative by body size (Pearson's correlation of male size with female size; r_p=-0.051, p=0.76, 36 d.f.). There is a negative relationship between day of entry (square-root transformed) to the mature adult population and body size (left forewing length) for males (all males; F=75.06, p<0.001, R^2=0.530, 71 d.f.; residents; F=72.6, p<0.001, R^2=0.573, 55 d.f.). There is no such negative relationship for females (all females; F=0.03, p=0.869, R^2=0.001, 38 d.f.; resident females; F=1.73, p=0.201, R^2=0.07, 24 d.f.).

There was no difference in body size between residents(R) and non-residents(NR) for males or females (Two sample t-tests males; t=-1.35, p=0.18, 70 d.f., μ_{NR}=16.28 ± 0.26, μ_R=16.62 ± 0.11; females; t=-1.62, p=0.11, 38 d.f., μ_{NR}=18.27 ± 0.15, μ_R=18.56 ± 0.09).

There was no difference in variance in body size between residents and non-residents for males (F=1.65, p=0.179, σ_{NR}= 1.04, σ_R=0.81) or females males (F=1.43, p=0.427, σ_{NR}= 0.57, σ_R=0.48).

To investigate whether stabilising selection operated on body size, F-tests for homogeneity of variance were used to see if mated individuals were significantly less variable in size than unmated individuals. Males that did not mate were less variable in size than mated males (F-test for homogeneity of variance; F=2.08, p=0.038, σ_{mated}= 0.96, n=40, $\sigma_{unmated}$=0.67, n=32). Females that mated were as variable as those that did not mate (F-test for homogeneity of variance; F=1.62, p=0.292, σ_{mated}= 0.47, n=15, $\sigma_{\mathrm{unmated}}$=0.59, n=25). There was no correlation between body size and residency duration (log transformed) for males (all; r_p=0.015, p=0.91; residents; r_p=0.086, p=0.53) or females (all; r_p=0.070, p=0.67; residents; r_p=-0.343, p=0.09).

6.3.2.5. Partitioning of lifetime mating success

Three components of mating success were suggested by (Koenig & Albano 1986) lifespan, proportion of time devoted to reproduction (number of days present at breeding site) and mating efficiency (number of mates obtained/ number of days present at site). Since the subsequent survival analysis (Section 6.3.3) does not allow survival to be estimated for a particular individual, residency duration was used as the lifespan (LSPAN) component here. Time devoted to reproduction is given here as the number of hours present at site (log transformed = HOURS), providing a more accurate measure than the number of days an individual was present at the breeding site. Females were nearly always seen in tandem (artificially inflating estimates of mating efficiency for them as described above) and a high proportion of individuals were not mated and thus had a value of zero for mating efficiency. Thus mating efficiency was not a meaningful variable and could not be included as a component in the lifetime mating success analysis. Thus it was not possible to partition out sexual selection here. In addition, a variable was constructed to represent the proportion of residency duration in which mating was not possible due to unsuitable weather conditions (arcsine transformed =WEATHER). Date of entry to the population (DAY) was also considered.

Stepwise logistic regressions were performed (see methods). These compared mated and unmated individuals to determine which components predict the probability that an individual mates within its lifetime. The analysis was performed for both residents and all individuals for both males and females.

For both resident males (Table 6.10b) and all males (Table 6.10d), HOURS was the first variable to be added to the model and the exponent of the coefficient of HOURS was much higher than 1 (over 50 for both). Thus the number of hours males spent on site had a large, positive effect on the probability of mating for males. For resident males, WEATHER was also added to the model. Thus the probability of mating significantly decreased as the proportion of an individual's lifespan made up of unsuitable weather increased. The exponent for the WEATHER coefficient indicates that the probability of mating approximately halved per unit increase in WEATHER.

For resident females WEATHER then DAY were added to the model (Table 6.10a). The small value of the exponent for the WEATHER coefficient indicates that the negative effect of weather on the probability of mating is much greater for females than males. This finding contrast with the above suggestion that activity of males would be constrained to a greater degree by variation in weather conditions than that of females (Section 6.3.1.1). Although individuals that entered the population earlier had a significantly higher probability of mating, the closeness of the exponent of the DAY coefficient to 1 indicates that the magnitude of this effect is small. When all females were considered (Table 6.10c), the number of hours spent on site seemed to have a large positive effect on the probability of mating, whilst weather had a much smaller negative effect on this probability than when resident females were considered separately.

Table 6.10 Logistic regression analysis of probability of mating for
a Resident females.

	$B \pm s.e.$	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	9.93 ± 3.35		1					
WEATHER	-13.85 ± 5.33	-25.65	1	12.79	0.0003			<0.001
DAY	-0.08 ± 0.04	-21.27	1	4.04	0.045	15	30	0.925
Model χ^2=16.54, p=0.0003, 2 d.f.								

b Resident males.

	$B \pm s.e.$	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	-2.01 ± 0.99		1					
HOURS	3.92 ± 0.97	-58.44	1	22.11	<0.0001	42	44	50.55
WEATHER	-3.07 ± 1.52	-49.52	1	4.27	0.038			0.047
Model χ^2=23.05, p<0.0001, 2 d.f.								

c All females.

	$B \pm s.e.$	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	-2.32 ± 0.76							
HOURS	6.42 ± 1.77	-50.76	1	25.45	<0.0001	35	41	611.89
WEATHER	-2.93 ± 1.30	-42.97	1	9.87	0.0017			0.053
Model χ^2=28.82, p<0.0001, 2 d.f.								

d All males

	$B \pm s.e.$	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	-3.75 ± 0.69							
HOURS	3.98 ± 0.74	-76.513	1	42.57	<0.0001	71	45	53.24
Model χ^2=44.57, p<0.0001, 1 df.								

6.3.3 Analysis of survival and recapture probabilities

6.3.3.1 General model and goodness of fit

None of the tests indicated a significant lack of fit to the CJS model (sum of Test 2 and 3 for the two groups; males: $\chi^2 = 67.25$, 68 d.f.; females: $\chi^2 = 20.62$, 42 d.f.; for both groups, the total value of the goodness-of-fit test was $\chi^2 = 87.87$, $p=0.941$, 100 d.f.). To check for extra-multinomial variation, the average residual variation (σ^2) can be calculated as the expected value of the chi-square goodness-of-fit statistic divided by its degrees of freedom. If the model structure is correct, then under the multinomial assumption $\sigma^2 = 1$. In this analysis, $\sigma^2 = 0.80$ suggesting there is not substantial excess variation and thus it is not necessary to estimate a variance-inflation factor c-hat.

6.3.3.2 Model selection

Table 6.11 shows a selection of models fitted to this dataset, including the best model and others that illustrate the model selection process. The best model of the 16 containing sex and time or their interactions was $\phi_{(.)}\ p_{(s+t)}$.(14th on Table 6.11). The addition of body size as a main effect to model for the recapture rate parameter (i.e. $\phi_{(.)}\ p_{(s+b+t)}$) lowered the AIC by 13.14 and produced a better model than the addition of an interaction term between sex and body size ($\phi_{(.)}\ p_{(s*b+t)}$). The former model ($\phi_{(.)}\ p_{(s+b+t)}$) was also better than one in which body size was added to the survival parameter ($\phi_{(b)}\ p_{(s+b+t)}$). Although recapture rate was found to be time-dependent, models containing rain or temperature variables (bottom of Table 6.11) were not as 'good' as a model with time dependence. Models with time dependence in survival were not selected early in the process of model selection. However, having modelled recapture rate successfully, and given the strong biological expectation that weather would influence survival in adult odonates, weather variables were added to the best model for recapture rate i.e. $\phi_{(.)}\ p_{(s+b+t)}$. The addition of maximum temperature to the model for the survival parameter produced a reduction of 3 in AIC making $\phi_{(maxt)}\ p_{(s+b+t)}$ the best model for this dataset.

6.3.3.3 Recapture probability

Males had a consistently higher recapture probability than females (Fig. 6.22 - $\beta=2.082 \pm 0.310$). The mean recapture probability for males was 0.324 ± 0.027 (ranging from 0 to 0.737) and for females was 0.067 ± 0.008 (ranging from 0 to 0.259). According to the logit function parameters (β) of the model $\phi_{maxt}p_{s+size+t}$, body size has a positive relationship with recapture probability ($\beta=0.632 \pm 0.159$) i.e. larger individuals are more likely to be recaptured than small individuals. This effect is shown despite the fact that large females are less likely to be recaptured than small males. Recapture probabilities seem to vary between occasions. Logit function parameters for these time dependent effects on recapture probability vary between –0.287 and 2.985 for most occasions though parameters for the 43rd and 46th day are –14.849 and –14.560 respectively. Time dependence in recapture probability would not arise due to variation in recapture effort, since equal recapture effort was employed on each recapture occasion. Thus, this time dependence is most likely explained by variation in external weather conditions. If weather variables had been measured at the sampling site rather than at a station some kilometres away, then perhaps their addition to the model for the recapture parameter would have yielded a better model than one including time-dependence.

Table 6.11 Akaike information criteria (AIC_c), Akaike information criterion differences (ΔAIC_c), number of parameters (np) and deviances for a selection of models fitted to the Aylesbeare dataset.

Model	AIC_c	ΔAIC_c	np	Deviance
$\phi_{(maxt)}\, p_{(s+b+t)}$	1608.17	0.00	44	1510.83
$\phi_{(rain)}\, p_{(s+b+t)}$	1610.57	2.40	44	1513.23
$\phi_{(.)}\, p_{(s+b+t)}$	1611.22	3.05	44	1513.88
$\phi_{(b)}\, p_{(s+b+t)}$	1612.74	4.58	45	1512.96
$\phi_{(mint)}\, p_{(s+b+t)}$	1613.54	5.38	45	1513.75
$\phi_{(.)}\, p_{(s*b+t)}$	1613.55	5.38	45	1513.76
$\phi_{(s+b)}\, p_{(s+b+t)}$	1613.57	5.40	46	1511.32
$\phi_{(s)}\, p_{(s+b+t)}$	1613.66	5.50	45	1513.88
$\phi_{(s*b)}\, p_{(s+b+t)}$	1615.71	7.54	47	1510.99
$\phi_{(s*b+t)}\, p_{(s*b+t)}$	1618.72	10.55	66	1464.72
$\phi_{(maxt)}\, p_{(s+t)}$	1621.87	13.70	43	1526.97
$\phi_{(t)}\, p_{(s+b+t)}$	1624.04	15.87	64	1475.45
$\phi_{(.)}\, p_{(s+t)}$	1624.36	16.19	43	1529.46
$\phi_{(b)}\, p_{(s+t)}$	1626.57	18.40	44	1529.23
$\phi_{(s)}\, p_{(s+t)}$	1626.75	18.58	44	1529.41
$\phi_{(.)}\, p_{(s+b+maxt)}$	1648.15	39.98	5	1638.02
$\phi_{(t)}\, p_{(s)}$	1649.04	40.88	20	1607.17
$\phi_{(.)}\, p_{(s+b+mint)}$	1649.36	41.19	5	1639.23
$\phi_{(.)}\, p_{(s+b+rain)}$	1649.52	41.35	5	1639.39
$\phi_{(.)}\, p_{(s+b+meant)}$	1649.67	41.50	5	1639.54

6.3.3.4 Survival probability

According to the 'best' model, $\phi_{maxt}p_{s+size+t}$, mean survival probability was 0.921 ± 0.003 (ranging from 0.834 to 0.952). Paradoxically maximum temperature has a negative relationship with survival probability (β=-0.154 ± 0.081) i.e. the higher the maximum temperature in a time interval the lower the probability of survival over that interval. According to the model with constant survival, $\phi_{(.)}\ p_{(s+b+t)}$, mean survival probability was 0.921 ± 0.008.

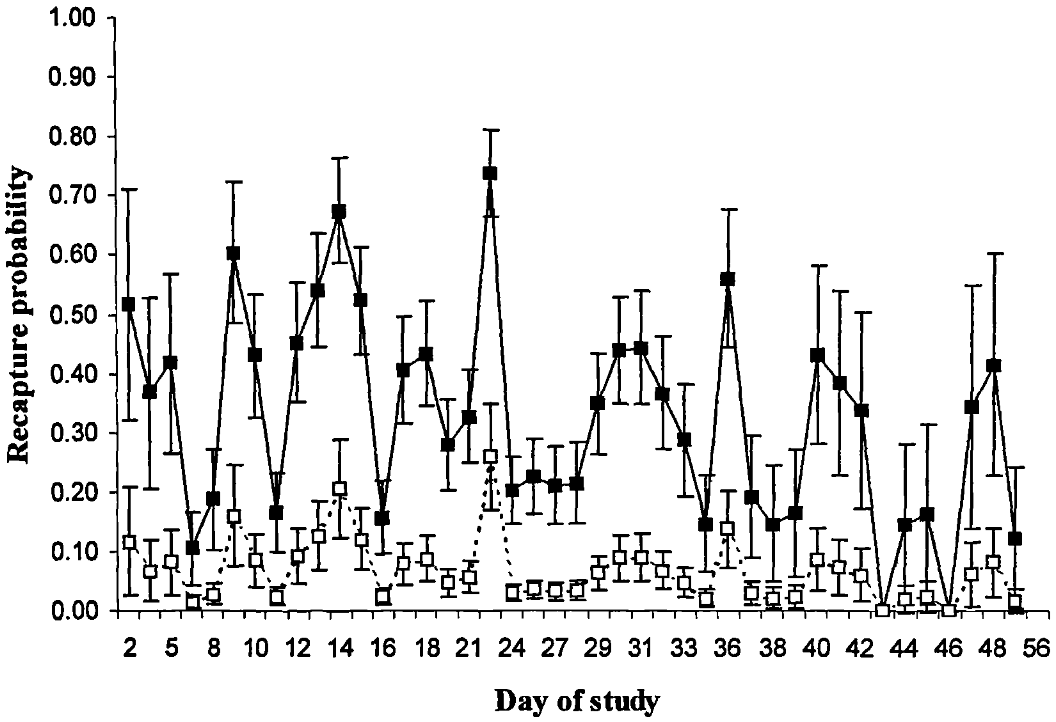


Fig. 6.22 Maximum likelihood estimates (± s.e.) for recapture probabilities of *C. mercuriale* males (black squares and solid lines) and females (white squares and dashed lines) on each day of the study (Day 1=7th June) - calculated from the model $\phi_{maxt}p_{s+size+t}$.

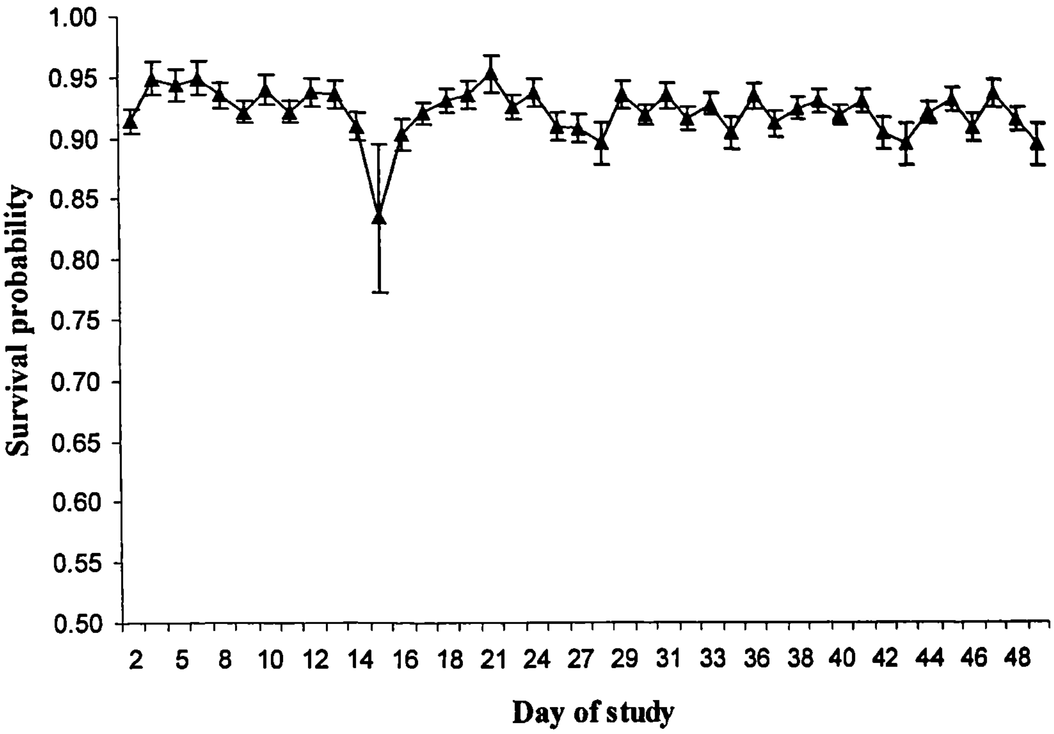


Fig. 6.23 Maximum likelihood estimates (± s.e.) for survival probabilities of *C. mercuriale* on each day of the study (Day 1=7th June) - calculated from the model $\phi_{maxt}p_{s+size+t}$.

6.4 Discussion

Variation in lifetime reproductive success (LRS) can be generated by several, non-exclusive processes; sexual selection, natural selection and/or random processes (Koenig & Albano 1986). An evolutionary response to such selection will only occur if there are phenotypic characters that influence reproductive success and if these phenotypic characters have a genetic contribution (Arnold & Wade 1984b).

Variation in mating success in *C. mercuriale* appears to be governed by a combination of natural selection and random processes such as stochastic variation in weather conditions. Firstly, the distribution of lifetime mating success for both males and females did not differ significantly from a poisson distribution, expected if matings are independent events and occur due to random encounters (*cf* Fincke 1986a). In addition, there was no difference between males and females in the distribution of mating success. A poisson distribution of mating success is normally found for males in non-territorial species (Fincke 1982a; Banks & Thompson 1985b) but not for females. The unmated proportion is low for females but high for males in most odonate populations (e.g.males - 31%; females - 1% in *Enallagma hageni* -\ Fincke, 1982). This arises because of a fundamental difference between the sexes in the relationship between mating success and offspring production, first identified by Bateman (1948).

The number of offspring fathered by a single male increases in proportion with the number of females he mates with. In contrast, a female's fecundity does not increase in proportion with the number of males she mates with. Thus intensity of sexual selection on males to obtain mates and fertilisations is greater. This difference between sexes occurs in odonates because females can store sperm and thus do not need to remate between clutches. Behaviourally, this results in males visiting the breeding site more often, remaining at the breeding site for longer, and being able to cycle between mates more quickly (McVey 1988). This produces a male biased operational sex ratio such that all females present on a day are likely to be mated. Variance in male lifetime reproductive success can also exceed female lifetime reproductive success by chance alone (e.g Fincke 1982b; Banks & Thompson 1985b; Michiels & Dhondt 1991; Cordero & Andres 1999).

In *C. mercuriale*, although male-biased operational sex ratios occurred on most days, there was no difference between males and females in the interval between matings and the mean duration of visits. Weather conditions permitted only short visits of approximately an hour and a half to the breeding site by both sexes. These visits were separated by intervals of several days. In addition, only two out of 116 males and no females mated more than once in a day and thus did not cycle between mates faster than females. In this situation an approximately equal proportion of males and females will have the opportunity to mate on any given day, producing an equal distribution of lifetime mating success between the sexes in *C. mercuriale*. Such an equal distribution between sexes has been attributed in *Ischnura gemina* (Hafernik & Garrison 1986) to serial monogamy (rather than polygyny). In this species, males are non-territorial, spend a long time in copula and mate-guarding. They mate on average once every four days. In *C. mercuriale*, 'serial monogamy' arises, not due to an individual's behavioural strategy, but due to constraints on the time available for reproduction imposed by weather conditions.

Indeed, external weather variables had a significant effect on whether damselflies were active on a particular day and on whether damselflies mated on a particular day. The amount of sunlight and temperature seemed to be the most important variables in producing these effects. Similar effects of weather on activity, especially reproductive activity (e.g. Cordero 1995) are widespread in odonates. Michiels (1989) found that body-surface temperature had a positive exponential effect on flight activity in *Sympetrum danae* (within the range 20-40°C) and also decreased time spent per mate during oviposition and copulation. With regards to other insects, Kingsolver (2000) found considerable variation in flight probabilities of pierid butterflies associated with daily variation in weather conditions.

When lifetime mating success was partitioned, the probability of mating for males of *C. mercuriale* increased with the number of hours a male spent at the breeding site and decreased with the proportion of an individual's lifespan that was made up of unsuitable weather. The probability of mating for females also increased with the number of hours spent at the breeding site, and decreased with the proportion of the lifespan made up of bad weather (considering all females).

Whilst some other authors have found lifespan per se to be important in determining mating or reproductive success (Koenig & Albano 1987; McVey 1988), this study and others have found that the time for which an individual is actually present at the breeding site to be of greater importance (Banks & Thompson 1985b; Banks & Thompson 1987a; Fincke 1988; Marden 1989; Michiels & Dhondt 1991). Time spent at the breeding site in odonates has usually been expressed as the number of sunny days occurring in an individual's lifetime (Corbet 1999). However, the number of sunny days represents the time in an individual's lifetime that were potentially suitable for reproductive activity whilst dividing this time period into hours provides an accurate picture of the time for which the individual was actually active at the breeding site. The fact that even on sunny days not all individuals known to be alive were actually present on site illustrates the necessity of such an accurate measure of an individual's activity. Anholt (1991) pointed out that this component should ideally be expressed at a lower time resolution such as minutes that males were sexually active at the rendezvous. Due to the trade-off between the resolution at which this information could be obtained and the number of individuals that it can be obtained for, the use of hours as a time unit provides the ideal compromise. Time spent at the breeding site has been considered to be a component upon which natural selection would act. For example, the amount of time an individual spent could depend on foraging success. Koenig & Albano (1986) point out that sexual selection could act on this component if time spent at the breeding site depended on the outcome of male-male interactions. Given the lack of male-male interactions observed in *C. mercuriale* and the limiting effect of weather on activity, variance in time spent at the breeding site is probably under natural selection or arises due to random processes.

Maximum temperature was a significant predictor of the probability of mating due to its effect on activity and reproductive activity described above. In addition, the survival analysis showed that external weather conditions, in this case, maximum temperature, seemed to explain a significant amount of variation in the probability of survival in *C. mercuriale*. This is of improtance since survival will partly determine time spent at the breeding site. In contrast to other odonates, a phenotypic variable, body size did not effect survival (Banks & Thompson 1985a; Fincke 1988; Anholt 1991; Michiels & Dhondt 1991). Maximum temperature seemed to have a negative effect on the probability of survival. High temperatures may impose a metabolic cost due to the risk of desiccation or more probably reflects the fact that odonates are more active at high temperatures. More active individuals may run a higher risk of predation (Werner & Anholt 1993) especially if the activity of predators is also increased at high temperatures. They may also deplete their food resources faster than they can obtain them (animals in the field frequently have empty guts suggesting food limitation (Richardson & Baker 1997)). For example, Anholt (1992) attributed the greater mortality suffered by females compared to males during the pre-reproductive period to the fact that the former are more active in foraging to gain mass for reproduction in non-territorial damselflies.

This study is the first in which mating efficiency is measured in relation to the time when males were actually present at the breeding site i.e. the critical period in which female choice, if it exists, can be expressed (Koenig & Albano 1986). However, it was not possible to include mating efficiency as a sexual selection component, in the partitioning analysis. There are biological reasons, already alluded to, as to why this component would not have explained much variation in reproductive success anyway. Firstly, there was little variation in mating efficiency between individuals. This lack of variation arose because, as described, above visits to the breeding site were short, interrupted by long intervals and did not permit cycling between mates. Mated and unmated individuals did not differ phenotypically in *C. mercuriale* i.e. with regards to body size or age. Thus, the negative relationship between emergence date and left forewing length demonstrated for *C. mercuriale* in Chapter 3 (males and females) and here (males only) cannot be attributed to the benefits of gaining mass (and delaying reproduction) to increase mating success. In addition, although lifetime mating success was influenced indirectly by survival in *C. mercuriale* and thus the opportunity for natural selection may arise, survival did not depend on an individual's phenotype. Thus no evolutionary response to selection would be expected in *C. mercuriale*. In fact, relatively little variation in male reproductive success in odonates in general has been attributable to variation in male phenotype (Fincke *et al.* 1997).

Thus *C. mercuriale* is similar to other odonates in two respects. Firstly survivorship (in its contribution to the number of hours present at the breeding site) is an important predictor of reproductive success for males and females (see references above). Secondly, weather is a major constraint on sexual selection where variance in reproductive success is determined by proportion of the lifetime made up of unsuitable conditions (as above) or by the number of sunny days occurring over an adults lifetime (*cf* Thompson, 1990).

However, I postulate that lifetime mating success is particularly strongly influenced by survival and variation in weather conditions in *C. mercuriale,* not only due to the fact that it is a non-territorial, scrambling species but also because it is on the edge of it's range in Britain. Thus climatic conditions here are likely to be less favourable than in core European populations constraining the time spent at the breeding site and, in turn the importance of such components as mating efficiency. Thus, in edge-of-range populations of a species (versus the core populations), random processes and natural selection may be likely to explain more variation in reproductive success than sexual selection components. If sexual selection does occurs in edge-of-range populations, it may be more likely to act on less costly traits such as genital morphology, ejaculate size or sperm morphology rather than mating efficiency which is governed by the activity budget of an individual. Thus, it would be interesting to investigate the components that explain variation in reproductive success in core versus edge-of-range populations in *C. mercuriale* and other odonates.

In another scrambling damselfly, Fincke (1988) found that variation in fertilisations per mating was numerically much less important in determining lifetime reproductive success than the mating components considered here. Thus lifetime mating success constituted a good approximation to lifetime reproductive success. Although, *C. mercuriale* is also a scrambling species, this study provided evidence that variation in fecundity and fertilisations may be important in this species.

Firstly, although there was no significant relationship between body size and clutch size for females, large clutch sizes were only found in the largest individuals indicating that maximum clutch size may be limited by space available in the abdomen (cf Gribbin & Thompson 1990). In addition, larger females produced larger eggs that may be better provisioned for embryonic development, increasing offspring survivorship. This relationship arose in another coenagrionid, because both body size and egg length decreased over the season (Gribbin & Thompson 1990).

Secondly, an examination of the aedegus morphology indicated that males have access to almost all of the female's sperm store. The cornua of the penis was narrower and longer than the spermathecal duct which, in other odonates (Waage 1979; A. Cordoba-Aguilar unpublished cited in Miller 1982; Robinson & Novak 1997), is indicative of a male's ability to remove rival's sperm from both the bursa and the spermatheca of the female. Extensive areas of proximally-oriented microspination were also found on both the extensible head and the sheath of the aedegus which contained masses of sperm. Females were found to store sperm from previous matings and did not show substantial sperm depletion after an oviposition episode. Some females did not lay all their mature egg clutch in one oviposition episode and thus partitioned it between episodes and between males producing a substantial delay between insemination and fertilisation of eggs. This partitioning of a clutch between episodes may also occur in other coenagrionids where a low minimum clutch size is found in females collected before copulation e.g. *Pyrrhosoma nymphula* (68-754 eggs Gribbin & Thompson 1990). The range of egg length (from 0.833 -1.133) is similar to that of *Pyrrhosoma nymphula* (0.96-1.14mm Gribbin & Thompson 1990). Thus all the ecological and behavioural pre-requisites necessary for sperm competiton by sperm displacement are satisfied in *C.*

mercuriale (Waage 1986) and the predominance of mate-guarding throughout oviposition seen in this study suggests it constitutes a substantial selection pressure.

Most previous authors have claimed that males have higher survival than females in both the pre-reproductive (Conrad & Herman 1990; Anholt 1991; Bennett & Mill 1995) and reproductive periods (Banks & Thompson 1985a; Koenig & Albano 1987; Gribbin 1989; Conrad & Herman 1990; Bennett & Mill 1995). But unlike this study, few authors estimated survival and recapture probabilities separately and relied on residency duration (i.e. length of time between first and last recapture), a measure highly dependent on recapture rate, to estimate survival. No difference was found here between males and females in survival probability in *C. mercuriale* or in most damselflies where survival and recapture probabilities have been estimated separately (Anholt 1997; Cordero & Andres 1999). In fact, in the laboratory, where all individuals have the same probability of 'recapture', Cordero (1994) found that females had higher survivorship in three species of coenagrionid. In *Lestes sponsa*, Stoks (2001b) found that mature males had a higher probability of survival than mature females, this difference was not consistent between populations. He concluded that the higher probability of maturation in males produced a male-biased sex ratio in this species. As suspected, males and females differed in recapture probability in *C. mercuriale*. This is probably partly due to the brighter colouration of males but also due to behavioural differences between the sexes (Corbet 1962; Bennett & Mill 1995). More males were present than females on a particular day and they spent longer at the breeding site in their lifetime than females. Whilst no difference was found between males and females in the interval between matings, the mean duration of visits such differences would probably be found in populations where activity is less constrained by external weather conditions and thus increase the sex differences in recapture probability. In fact, males and females did not differ in residency duration such that this variable may have approximated survival well. This is because, in this small population, every individual was seen on every visit to the breeding site. This will not be the case generally since most studies have been carried out on larger odonate populations. Another consequence of the intensity of this study was that the mean residency durations found in this study are much higher than the mean value for zygopterans of 7.6 days (range 3.8-23.3 -Corbet 1999).

In addition, larger individuals were more likely to be recaptured than small individuals. Large individuals maybe less mobile and thus evade recapture less easily than smaller individuals. Marden (1989) found that adding weight to the wings of male damselflies reduced their flight ability (and in turn their mating success). In *Sympetrum danae* on the other hand large size is correlated with high activity in males (Michiels & Dhondt 1991). The effect of size on activity of *C. mercuriale* should be examined to distinguish between these two possibilities. Recapture rate was also found to be time-dependent and since recapture effort was uniform across recapture occasions and weather has been shown to effect damselfly activity, this time-dependence must be due to variation in external weather conditions. The fact that none of the weather variables in the analysis explained this time-dependence probably reflects the fact that conditions at the weather station differ from those in microclimates occupied by *C. mercuriale*.

Values for survival probability for *C. mercuriale* were intermediate in the range found in previous odonate studies for males i.e. from 0.73 for *Ischnura posita* to 0.94 for *Lestes temporalis* (Corbet 1999) and was relatively constant (*cf* Parr 1976; Banks & Thompson 1985a; McVey 1988; Bennett & Mill 1995), ranging only from 0.83 to 0.95 due to weather conditions. Other causes of mortality in the adult stage include predation (McVey 1988) and accumulation of physical damage though these are difficult to record (Corbet 1999). It is probable that the survival through the mature adult stage in this species is higher than through the other stages of its life cycle (Chapter 3 and 5). When investigating the determinants (e.g. climate) of survival (or mortality) at a local scale to predict distribution at larger scales, predictions will be more accurate if local scale investigations are based on the stage of the life cycle which suffers the highest mortality relative to the other stages. For *C. mercuriale* and indeed for most odonates, this is probably the larval stage. For example, Ubukata (1981) investigated mortality from egg to reproductive adult and estimated that only 0.07% of a population of *Cordulia aenea amurensis* reached the mature adult stage. However, this study revealed that in *C. mercuriale*, under poor weather conditions, a huge proportion of the adult stage is spent sheltering in tussocks and copulation also takes place there. This is consistent with the association of adult populations with tussocky vegetation (Chapter 2). Thus shelter-belt vegetation may be a particular requirement for existence of the mature adult stage in edge-of-range populations subject to such weather conditions even if mortality is relatively low in this stage.

Finally, the mark-recapture models used here that separate recapture and survival probabilities have rarely been used on insect populations (but see Kingsolver & Srygley 2000) but have mainly been used to estimate survival in birds and large mammals (Yoccoz *et al.* 1998). Insects pose a unique challenge in this respect for several reasons. Firstly, vertebrate mark-recapture experiments are usually carried out over a timescale of years or months and thus have relatively few encounter occasions whilst adult insect mark-recapture is often carried out on a daily basis yielding tens of encounter occasions. The more recapture occasions there are the more survival and recapture parameters have to be estimated and the larger the effective sample size has to be to avoid a saturated model. Secondly, insect studies commonly involve much larger numbers of individuals that are much less likely to be recaptured due to their relatively small size and high mobility making the data sparse. Another consequence of their size and mobility relative to that of a human observer is that dead or dispersed individuals are unlikely to be recovered as easily as is possible in vertebrates. This means that large insect populations will not be amenable to combined analyses of recoveries and resightings which have allowed unbiased estimates of survival and emigration in vertebrates (Frederiksen & Bregnballe 2000). Finally, any negative effect of the initial marking event is likely to be greater on a small insect than on a vertebrate making it more likely that trap dependency will arise in an insect population, contravening the assumptions of the CJS model. For example, in odonates, estimated mortality due to marking ranges from 20% for *Erythemis simplicicollis* (McVey 1988) to 52% for *Enallagma hageni* (Fincke 1988). Thus the applicability of these models in their current form to insect populations may be restricted.

The reduction by external weather conditions of the mated proportion of the population will influence effective population size which may have implications for population persistence on the edge of ranges. In small populations, genetic problems (e.g. inbreeding depression, loss of evolutionary potential for adaptation to environmental change) may arise through loss of genetic variation due to the joint action of natural selection and genetic drift. The rate of loss due to genetic drift depends on the effective population size (N_e) i.e. the size of the 'genetically idealised' population to which the actual population (N) is equivalent in genetic terms (Begon 1996).

N_e is equal or less than the number of breeding individuals but is usually much less for a variety of reasons (Lande & Barrowclough 1987). In general, N_e is close to N/2 (range N/4 - 3/4N) but a number of factors such as variation in female fecundity can substantially reduce N_e (Nunney 1996). For example, Kelly (2001) found that the fact that mating was non-random and confined to a few breeders in successive generations reduce effective population size to 44% of the actual population size in Serengheti cheetahs. Whilst an unequal distribution of reproductive success has reduced effective population size in some species, in southern Atlantic salmon populations, multiple paternity increased the effective population size (Martinez *et al.* 2000). Some authors have suggested that sexual selection can act to reduce the risk of extinction in small populations because it acts to decrease the fixation probability of deleterious mutations and increases the probability of fixing new beneficial mutations (Whitlock, 2000). In this study, the mated proportion of the population was small and multiple mating did not occur in many females. However, there was little variation in reproductive success. It is unclear how these factors would interact to influence effective population size.

In conclusion, this study has shown that stochastic variation in weather conditions is the constrain activity, survival and mating success in an edge of range population of *C. mercuriale*. This is consistent with the findings of Chapters 2 and 5 that the specificity of this species' habitat requirements arise from the need for a thermally advantageous microclimate.

Chapter 7 Dispersal in *Coenagrion mercuriale*

7.1 Introduction

Dispersal may be defined as an undirected movement (in contrast to migration) away from the habitat of origin (den Boer 1990) and is a life history trait that has profound consequences for populations (Dieckmann *et al.* 1999). When a population occupies a patchy habitat it may form a network of smaller, local populations called a metapopulation (Hanski & Gilpin 1991). Dispersal plays a vital role in both local and metapopulation dynamics (Thomas & Hanski 1997). Firstly, it determines the probability of colonisation of empty habitat. Secondly, dispersal effects the probability of extinction, via processes known as the 'rescue effect' and 'genetic rescue'. The 'rescue effect' refers to the decreased probability of stochastic extinction in small local populations due to a direct positive effect of migrants on the abundance of recipient populations. The latter refers to the replenishment of genetic variation and reduction in inbreeding depression due to an influx of migrants (Ingvarsson & Whitlock 2000; Ingvarsson 2001). Where migrants express heterosis, deleterious recessive alleles can be masked, increased fitness of offspring compared to those produced wholly by resident individuals (Ingvarsson 2000). There is empirical evidence for butterflies that dispersal between local populations influences the persistence of local populations and the rate of colonisation of vacant habitat patches and, in turn, influences metapopulation persistence (Thomas & Hanski 1997 and references therein). Travis & Dytham (1999) have shown the same relationship between population persistence and dispersal rate in model systems.

However, there may be a mismatch between the degree of dispersal favoured under individual selection and that which promotes persistence at the metapopulation level (Dieckmann *et al.* 1999; Thomas 2000). This is because dispersal usually carries a high per capita mortality. Dispersers reach new habitats by chance and the majority of emigrants never locate another patch. For example, it is estimated that between 15-35% of butterflies die between patches (Thomas & Kunin 1999; Hanski *et al.* 2000). Thus the number of emigrants leaving a patch will usually exceed the number of immigrants from other patches (den Boer 1990). Natural selection may favour individuals that remain in the population regardless of the reduction in persistence or frequency of recolonisation events at a metapopulation level. The relative costs and benefits of dispersal will be affected by the size, spacing, quantity, quality and temporal variability of habitat within particular landscapes (Thomas 2000). Increased habitat fragmentation is likely to increase the per capita mortality rate of dispersal such that genes associated with dispersal are likely to be lost from isolated populations (Dieckmann *et al.* 1999) and will lead to non-random extinction of populations and species characterised by different levels of dispersal (Thomas 2000). Thus, for rare species it is pertinent to investigate dispersal ability within and between habitat patches in relation to habitat fragmentation and to evaluate the effect of management regimes on the probability of extinction and colonisation events.

Odonates have inherently patchy habitats (Conrad *et al.* 1999) because they are restricted to water for most of their life cycle – in the egg and larval stages and as breeding adults (Corbet 1980). Despite this, dispersal has been poorly documented in odonates relative to other orders of winged insects (Michiels & Dhondt 1991; Corbet 1999). Odonates are rare among terrestrial arthropods but similar to butterflies in that flight is multifunctional being used both within patches (for location of food, mates and oviposition sites) and between patches for dispersal (Van Dyck & Matthysen 1999). In particular temporary emigration for roosting and maturation is common in female and teneral odonates (Corbet 1980). Thus, they make good subjects for studying the effect of habitat fragmentation on continuous dispersal-related traits and correlations tend to occur between different traits e.g. between within-patch and between-patch dispersal ability (Thomas 2000). For example, *Plebejus argus*, a lepidopteran, has low rates of movement within continuous areas of habitat (mean < 20m), low emigration rates (1.4% exchange) and low colonisation distances < 100m but up to 1km). Thus, it is possible that by studying one or two dispersal traits of a particular species inferences can be made about its other traits drawing on information from other species (i.e. butterflies) for which dispersal is multifunctional.

Most empirical studies on odonate dispersal have focussed on within-patch movements (Garrison & Hafernik 1981; Conrad & Herman 1990; Jenkins 1998; Jenkins 2001) or have considered movements between adjacent waterbodies (Van Noordwijk 1978; Koenig & Albano 1987; Anholt 1990; Thompson 1991; Stettmer 1996). This has lead to the perception that between-patch movement is uncommon in odonates (Fincke 1982; Utzeri *et al.* 1984; Banks & Thompson 1985a; Michiels & Dhondt 1991). However, expansions in distribution, in response to factors such as deforestation, development of agriculture and mining areas and global warming, have been observed in odonates (Sternberg *et al.* 1999) and suggest that some species are capable of movement across unsuitable habitat. *Ischnura pumilio*, described in Chapter 2 as an early successional species, survives in a particular location for 2 to 3 years when climatic conditions are suitable (Corbet *et al.* 1960). The turnover of populations in space and time indicates, albeit indirectly, that between-patch dispersal is occurring in this species. Direct evidence of between-patch dispersal is required for odonates (*cf* Conrad *et al.* 1999).

Here, both within and between-patch dispersal is examined directly in *C. mercuriale*, using data from mark-release recapture techniques in two stronghold populations in Britain (collected by Hopkins & Day 1997). Investigation of between-patch movements is pertinent in this rare species since it occupies two fragmented biotopes in Britain (Chapter 2). Since it is stenotopic, its habitat is particularly patchy within these biotopes and since it occupies early successional stages and shallow, narrow water bodies that are particularly susceptible to drying out (Chapter 2), its habitat is also temporally unstable. In early successional species, temporal instability in habitat means that long term regional persistence is likely to depend on metapopulation dynamics and insects occupying a shifting habitat mosaic (Thomas & Hanski 1997). Long term regional persistence is facilitated when interconnected local populations are asychronous in their dynamics such that when one population goes extinct adjacent populations are sufficiently large to provide migrants to re-found the population (*cf* den Boer 1991; Sutcliffe 1996). Within-patch movements are investigated because, for many early successional species, habitat is managed by rotational cutting or grazing (especially in Europe) and the scale of such management needs to be appropriate to the dispersal ability of the species in question (Chapter 2).

Landscape connectivity is the degree to which the landscape facilitates or impedes the movements of individuals between patches (Taylor *et al.* 1993). As stated above the size, spacing (isolation) quantity and quality of habitat determine the costs and benefits of dispersal (i.e. the extent of per capita mortality of emigration). To quantify the costs and benefits of dispersal in a fragmented landscape, empirical data are required on key parameters of landscape connectivity such as habitat specific movement patterns, rates or capabilities of animals (Pither & Taylor 1998) and movement behaviours in different landscape structures (amount/configuration of suitable habitat Wiens 1997). Although, it was not possible to map habitat and non-habitat explicitly for this species at the time of this study (Chapter 2), the effect of interpatch distances, presence of unsuitable but open habitat, scrub barriers and habitat quality on dispersal are examined to some extent here. These aspects of landscape connectivity can be influenced by management and appropriate regimes that facilitate dispersal should based on such information.

Some phenotypic correlates of dispersal are examined here since, an evolutionary response to changes in landscape will only occur if heritable differences occur between dispersing and resident individuals. Indeed, if dispersers differ from residents (rather than being a random sample) then flight-related traits could evolve towards a less mobile phenotype in the donor population where severe habitat fragmentation results in mortality of *all* emigrants (Van Dyck & Matthysen 1999). In non-territorial odonates, it has been assumed in previous studies that dispersal will be random with respect to phenotype because matings are obtained by scramble competition (Fincke 1982; Banks & Thompson 1985a). In territorial species, dispersal is more likely in females (Conrad & Herman 1990; Bennett & Mill 1995b) or in males that do not hold territories (Conrad & Herman 1990). Thus in odonates, phenotypic correlates of dispersal may reflect phenotypic correlates of other aspects of behaviour that require movement (or non-movement).

Chapter 6 examined phenotypic and time-dependence in survival and recapture rates in a small isolated population. The analysis was repeated here on data for Mynydd Preseli to see if the same variables determine survival in large, open populations where permanent emigration from the study area may lead to underestimation of mortality (Frederiksen & Bregnballe 2000).

Since, recording of this species has only been undertaken relatively recently (Chapter 2) there is only anecdotal evidence for extinction and colonisation events. Here, the spatial configuration of British sites is described in relation to the field observed dispersal ability of *C. mercuriale.* This information, together with that drawn from empirical studies of extinction and colonisation in other insects inhabiting fragmented landscapes, permits speculation on the likely extent of dispersal between populations in Britain. Given this extent of dispersal, further inferences are made about its effect on the persistence of this species (i.e. the processes of extinction and colonisation) in different parts of its British range.

7.2 Methods

Within and between-patch movement are examined here in *C. mercuriale* using the field dataset collected in 1997 by Graham Hopkins and Kieron Day under commission from the Environment Agency, English Nature and the Countryside Council for Wales.

7.2.1 Study sites

The sites used were the Glan-yr-afon Uchaf catchment on Mynydd Preseli in Pembrokeshire (see Chapter 4) and the Crockford Stream system on Beaulieu Heath in the New Forest (see Chapter 3), hereafter referred to as Mynydd Preseli and New Forest respectively. These sites contain two of the largest British populations of *C. mercuriale* and are described in more detail in previous chapters. Here the description is limited to those habitat features that may influence dispersal. Sampling areas were defined in each site in order to facilitate the examination of both within and between-patch movements. Examination of the former was achieved by the designation of 'main' stream patches, divided into subsections and searched daily for individuals. Around these 'main' patches, 'peripheral' patches, separated by unsuitable habitat, were searched regularly for individuals that had moved between patches. The location of sampled and unsampled habitat and areas of scrub is shown for each site in Figs. 7.1 and 7.2). Due to the different configuration of sampled habitat, the two sites provided different opportunities for dispersal and different probabilities of observing it.

In Mynydd Preseli, there was a single main stream patch (560m long) divided in to 19 subsections of between 15 to 50m in length (average 47). There were 14 'peripheral' patches around the main patch separated by distances of between 60 and 800m. On the New Forest site there were two shorter main patches (each 300m in length, divided into 12 x 25m subsections and separated by a 220m stretch of unsuitable stream) and 3 peripheral patches were searched for dipsersing individuals. Thus, the maximum observable within-stream movement was greater in the New Forest than in Mynydd Preseli, whilst the maximum observable between-stream movement was greater in the New Forest (3km versus 1.5km). However, in Mynydd Preseli, more 'peripheral' patches were available in a variety of directions from the main patches and at short to medium distance categories. In the New Forest, suitable patches were arranged linearly on the stream system and, thus, were available in a more limited number of directions from the two main patches. On Mynydd Preseli, most 'peripheral' patches were separated from the 'main' one by a mixture of valley mire and wet heath. In the New Forest, although the stream between patches also consisted of valley mire and wet heath, there were extensive lengths of tall scrub boundaries separating all patches except 1 and 2. Dispersing individuals not travelling along the stream would also cross humid and dry heath.

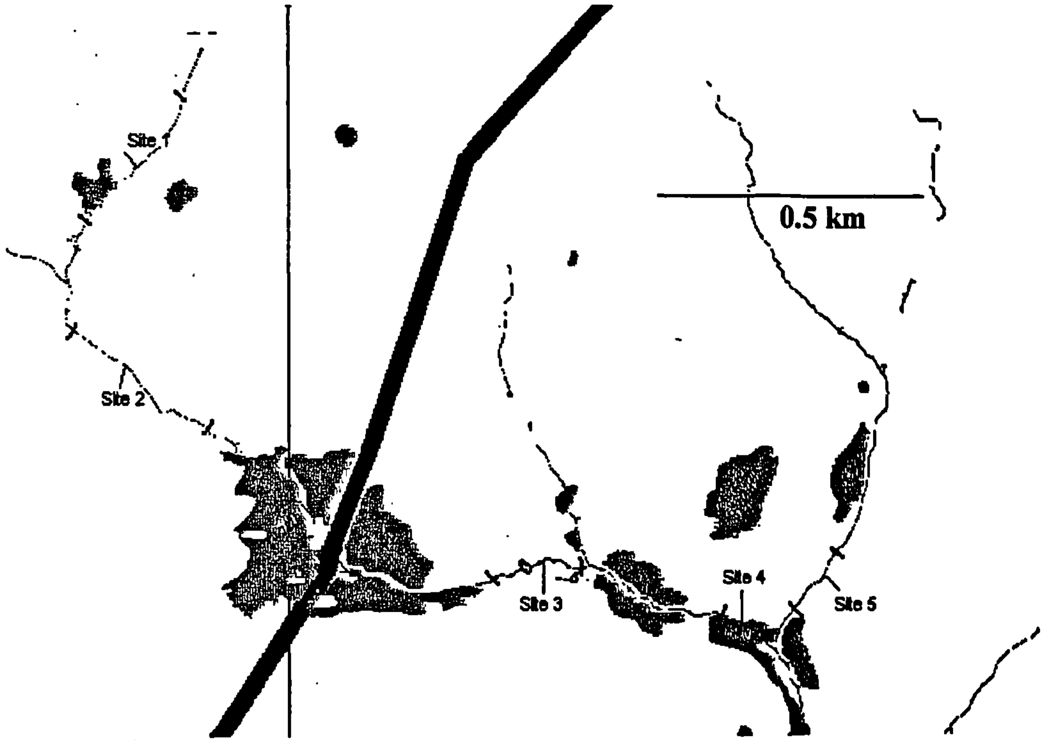


Fig. 7.1 Map of New Forest study area. Extent of lengths of sampled stream (sites 1-5) indicated by short black lines across the stream. Grey shaded areas indicate scrub. Black area shows position of road across site.

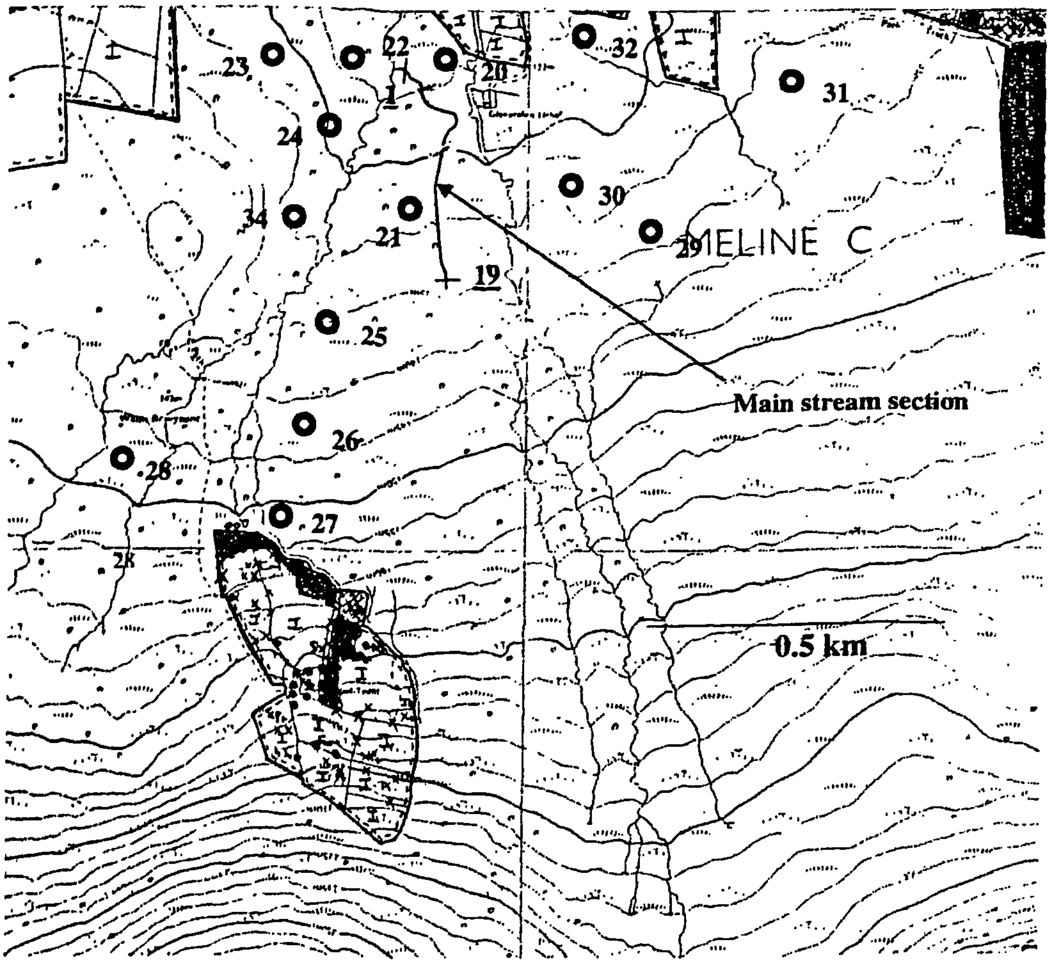


Fig. 7.2 Map of Glan-yr-afon study area, Mynydd Preseli. Limits of main stream section (sections 1-19) are indicated by short lines across stream whilst centres of peripheral patches of mire are indicated by rings (20-34).

7.2.2 Mark-release recapture protocol.

7.2.2.1 New Forest protocol.

Although fieldwork was carried out here between 6th June and 31st July 1997, covering most of the flight season of *C. mercuriale* (Chapter 3), the following standard protocol was adopted between 18th June and 26th July. Each day on which weather permitted activity of damselflies, a four hour mark-recapture exercise was performed in both patches 1 and 2. Each subsection was searched for twenty minutes. Unmarked *C. mercuriale* individuals were each given a unique mark by writing a number on the forewing with an indelible pen and placing a dot of paint on the dorsum of the thorax. Sex, age (teneral or mature adult), left forewing length, and subsection were noted and the individual was released in the middle of the subsection in which it had been found. Releasing all individuals from a central point in the stream system may have created a region of high density that may in turn have affected an individuals' tendency to disperse (Mallet 1986). After marking, the damselflies resumed their normal behaviour rapidly. When individuals were recaptured, their identity, date, subsection and age were noted. Mature adults seen for the first time were scored as being one day old (*cf* Fincke 1982) so that age on subsequent recapture could also be calculated. Since the ages of the adults initially present were not known, individuals marked on the first and second day of the study were discarded from analyses of residency duration, survivorship or age. The study started sufficiently early in the flight season for this correction to be adequate. Sites 3 (620m from site 2, 1060m from site 1), 4 (1090m from site 2, 1470m from site 1), and 5 (1190m from site 2, 1560m from site 1) were searched for marked individuals at less frequent intervals throughout the season.

7.2.2.2 Mynydd Preseli protocol.

Fieldwork was carried out on this site on all days of suitable weather between 10th June and 9th August 1997. A three-hour mark-recapture exercise was performed as described above on the main study stream beginning at 12pm. The order in which the sections were searched was varied randomly. Most peripheral patches were searched every day for individuals though patches further away received less attention.

7.2.3 Estimation of dispersal parameters – differences between sex, size and age groups.

Since individuals were released from the midpoint of a section, the distance between two captures of an individual could be measured. Movements were investigated by calculation of dispersal parameters (modified from Scott 1973). These are defined in Table 7.1 and Fig. 7.3 shows how they are calculated for a hypothetical individual that moved four times in its life. *L*, or net lifetime movement, was calculated to describe where individuals 'ended up' regardless of up and downstream movements and may be important for predicting the likelihood of long distance dispersal within a generation. *X* was calculated to describe the maximum distance moved in one movement. *Y* describes the maximum distance in which an individual was potentially active (e.g. with regards to mating or oviposition) during its mature adult lifetime. These parameters were calculated for all individuals marked in sites 1 and 2 in the New Forest and those marked on the main stream section in Mynydd Preseli. Means of the parameters were calculated, but differences between groups were tested using the two-sample Komolgorov-Smirnov test, which is sensitive to differences in both the shapes and location of two distributions (Sokal & Rohlf 1995). Since only 20.2% of individuals moved more than once, the values of X, Y and L did not differ for 79.8% of individuals.

Table 7.1 Definition of movement parameters.

Name	Definition
L	Net, unidirectional movement of an individual during its lifetime
X	Maximum distance between any consecutive recaptures of an individual
Y	Maximum distance between any site at which an individual is recaptured and its site of marking
d_n	Distance between recapture n and recapture n+1 of an individual
t_n	Time between recapture n and recapture n+1 of an individual
v_n	Velocity between recapture n and recapture n+1 of an individual i.e. d_n/v_n

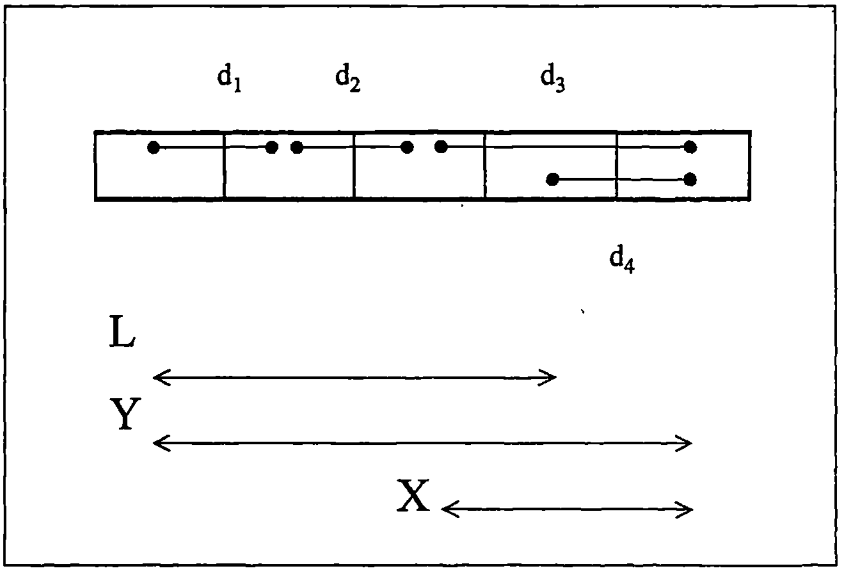


Fig. 7.3 Diagram of four movements between five stream sections with corresponding dispersal parameters.

The relationship between distance dispersed during an interval and a variety of factors were investigated by way of conditional logistic regressions using all movements (1st to 5th) of all males from Mynydd Preseli. The factors of interest were age during movement (taken at the midpoint of the interval), day of season during movement (taken at the midpoint of the interval), length of the interval (in days) and order of movement (e.g. whether it was the first, or fifth movement made by an individual). Since some of these variables are likely to show multicollinearity (e.g. between order of movement and age and between length of the time interval and age for all 1st movements), a stepwise procedure (explained in Section 6.2.2) was used. Three binary variables for dispersal distance were constructed (Table 7.2) and a logistic regression analysis was carried out for each one with age, day of season, length of time interval and order of movement as the independent variables. This analysis included several measurements (i.e. movements) for some individuals and because not all datapoints are independent, it was also repeated analysing first, second and third movements of individuals separately.

Table 7.2 Binary variables created for dispersal distance for conditional logistic regression analysis.

Variable name	Code	Definition
$Distance_0$	0	individuals that moved 0m during the interval
	1	individuals that moved further than 0m during the interval
$Distance_{50}$	0	individuals that moved less than 50m during the interval
	1	individuals that moved 50m or further during the interval
$Distance_{200}$	0	individuals that moved less than 200m during the interval
	1	individuals that moved 200m or further during the interval

7.2.4 Frequency of movements within and between suitable stream patches.

In describing the dispersal potential of endangered species, it is important to distinguish between movements across suitable habitat and those across unsuitable habitat. Thus, movements between two recaptures were divided into three types (for both sites): 1) Non-movement i.e. no movement from where the individual had been captured previously; 2) Within-stream transfer i.e movement to a different part of the same section of stream (within site 1 or within site 2 in the New Forest or within the main stream section in Mynydd Preseli); 3) Between-stream transfer i.e. movement to a different stream section in the New Forest, or from the main stream section to one of the fourteen peripheral patches of suitable habitat in Mynydd Preseli. The frequency of each of these movements was scored and compared between groups using Chi-squared tests. For between-stream transfers, it was noted whether these occurred through scrub boundaries or merely through unsuitable stretches of stream. Sex, body size, lifespan and number of recaptures of transferring and non-transferring individuals were compared.

The effect of the distance between-stream sections on the probability that individuals will transfer between them was analysed as follows. First, for the New Forest site, the numbers of individuals that moved between subsections within-stream patches 1 and 2 were recorded. Since males and females show no difference in their tendency to transfer (see below), the transfers of the two sexes were amalgamated. There were 276 pairwise possible combinations of sub-sections that were divided into 50m distance categories. The presence or absence of transfers was scored for all possible pairwise combinations of subsections (without distinguishing between the two possible directions of the transfers). For each distance category, the proportion of pairs in the category for which transfers took place was calculated. This analysis was repeated in Mynydd Preseli, focussing only on the outward movements (i.e. away from the natal patch) of individuals that were marked initially in the main stream patch and distinguishing between transfers within the main stream patch (361 pairs) and transfers (247 pairs) from the main stream to peripheral sites. This was to investigate whether transfers of a given distance were less likely to occur across unsuitable habitat.

7.2.5 Predicting the probability of dispersal at different distances – fitting dispersal distributions

In both sites, there were stretches of unsuitable stream between the sites that were not sampled, introducing a spatial bias into the observed dispersal distribution. This bias exists because short distance movements will tend to stay within the sampled part of the stream but longer distance movements are more likely fall into the unsampled areas (Stettmer 1996; Rob.Wilson pers.comm.). This is shown in Fig. 7.4, where three different lengths of movement are performed from three different release points along a hypothetical linear stretch of stream. All short movements remain within the sampled area of stream, whilst this is the case for only two of the medium movements and one of the long distance movements. When this phenomenon is considered as movements from a point source in any direction (rather than along a linear habitat feature) the ratio of sampled to unsampled habitat decreases exponentially with distance.

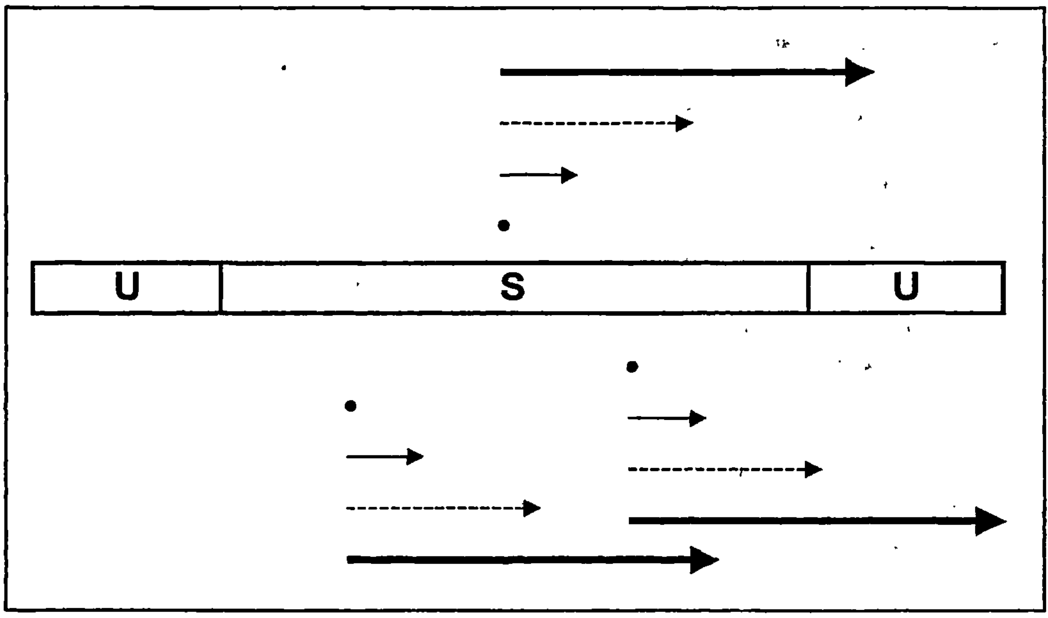


Fig. 7.4 Diagram of short (thin, unbroken arrows), medium (thin, broken arrows) and long distance (thick, unbroken arrows) movements from three release points (black dots) along a sampled (S) and unsampled (U) stretch of stream habitat.

However, in the New Forest, sections of suitable habitat could be well defined and were approximately linear (Fig. 7.1). Thus, the observed dispersal distance could be corrected with the theoretical probability of recapture at each distance interval. This theoretical probability of recapture is equivalent to the ratio of sampled versus unsampled stream at each distance interval. In sites 1 and 2, there were 24 (number of stream sections) x 2 (number of possible directions) = 48 possible displacements from sites 1 and 2. Thus, the theoretical probability of recapture was calculated as the number of possible displacements that ended up in sampled habitat divided by the total number of possible displacements. For example, only 16 of the 48 possible movements of 610m from the 24 subsections in sites 1 and 2 result in an individual remaining in the sampled area. Thus, there is a 33% probability of recapture at 610m. The actual number of movements at each distance interval was divided by the probability of recapture at that interval to obtain a term 'corrected number of movements' which takes into account the potential bias. In Mynydd Preseli, due to the patchy, ill-defined nature of suitable habitat for *C. mercuriale*, only the extent of the main stream section was mapped accurately. Thus, it was not possible to correct for spatial bias formally within this study system.

Many studies have attempted to find regression equations that best describe distributions of dispersal distances in order to predict the likelihood of dispersal in other sites or over longer distances than those observed in the field (e.g. Lewis 1997; Stettmer 1996; Conrad 1999). In this study, a negative exponential function and an inverse power function were fitted to the observed inverse cumulative distribution of distances travelled by individuals dispersing between sections and sub-sections along a linear landscape feature. Data were linearly transformed using either a semi-log plot (negative exponential) or a double log plot(inverse power function) and analysed using regression analysis. Regressions were weighted by the number of individuals recaptured and the best model was that with the highest value of R^2.

7.2.6 Assessing the likelihood of dispersal between populations within actual site configurations found in regions of Britain

The primary aim of this study is to investigate dispersal ability in two large populations of *C. mercuriale*. However it is pertinent to compare field observed colonisation distances and emigrations rates to the distances found between local populations in different regions of Britain. This permits speculation of the likelihood of migration occurring between local populations in different regions given their current configuration.

Information on site location and on habitat requirements of *C. mercuriale* in Britain are not sufficiently detailed to allow the area of potential or actual habitat to be mapped explicitly for Britain at present (Chapter 2). In addition, population sizes have not been estimated accurately. Thus, it is not possible to examine the relative role of habitat area, habitat quality and isolation in determining occupancy in this species (*cf* Hanski *et al.* 1994). The aim of this section is to make qualitative comparison between the dispersal ability of *C. mercuriale* and the distances between its British sites in different regions. For the majority of British sites, population location and extent are indicated by point data in the form of six-figure grid references. Each site is often represented by several such references (independently of population size), most of which may be inaccurate or out of date (Chapter 2 describes this and other limitations). Thus, this analysis uses six-figure grid references from the most recent surveys in each region (1998 & 1999 surveys for Hampshire, 1996-1999 surveys for Pembrokeshire). Since these point data are at a low resolution (100m apart) compared to the size of habitat patches occupied by *C. mercuriale* (Chapter 2), they do not indicate population number or extent in the absence of additional site-based information. For example, if two six-figure grid references are 200m apart they could represent one population or two. Since it is interesting to consider both genetic admixture between two limits within a population and admixture between populations, isolation was described in two ways here. Indices of isolation are normally calculated within spatially explicit configurations of habitat patches represented as polygons (*cf* Hanski *et al.* 1994). Here, an index of isolation was calculated (for the four largest regions listed below) based on 10 nearest grid references within a cluster regardless of population sizes. The distance between each grid reference and the first neighbour further than 250m away was calculated since points within 250m were assumed to be from the same population as the focal grid reference.

Extant British sites fall into several fairly discrete clusters (Chapter 2). There are two extant sites (and populations) in each of the following clusters: Oxford, Devon, Dartmoor, Anglesey, St David's (Pembrokeshire), and the Gower, and six sites in Dorset (with two sub-populations on Povingdon Heath). To describe the likelihood of dispersal in the 'two site' clusters, the distance between the two populations and the distance to the nearest other cluster was measured. For the larger clusters (the rest of Pembrokeshire (Mynydd Preseli), the Itchen and Test Valleys, the New Forest) and Dorset, the extension 'Nearfeat.avx' (Jeness 2001), was used within Arcview to measure the distance between each grid reference and its ten (7 for Dorset) nearest neighbours regardless of population. The isolation index, was calculated for each site in a cluster as the mean of the ten nearest neighbour distances obtained. To express average levels of isolation within a region, the mean of these isolation indices was calculated within each of the four large clusters.

7.2.7 Methods for analysis of survival and recapture probabilities

The procedure used in Section 6.2.3 for survival analysis and for model selection was adopted.

7.3 Results

7.3.1 Probability of recapture, residency duration and survival.

Over 2000 individuals were recaptured in both sites (Table 7.3). The recapture proportion for males was higher than that for females for mature adults in both the New Forest ($\chi^2=26.52$ -Yates correction, $p < 0.001$, 1 d.f.) and Mynydd Preseli ($\chi^2=74.84$ - Yates correction, $p < 0.001$, 1 d.f.) and for teneral adults in Mynydd Preseli ($\chi^2=5.85$ - Yates correction, $p=0.016$, 1 d.f.). Tenerals were less likely to be recaptured than mature adults for both males ($\chi^2=13.08$ -Yates correction, $p < 0.001$, 1 d.f.) and females ($\chi^2=9.32$ -Yates correction, $p= 0.002$, 1 d.f.) in Mynydd Preseli. The small sample of tenerals marked and recaptured in the New Forest prohibited their inclusion in this analysis.

Table 7.3 Number of marked and recaptured individuals and recapture proportion for different age and sex categories – New Forest.

		New Forest			Mynydd Preseli		
Adult stage	Sex*	No. marked	No. recaptured	Recapture %	No. marked	No. recaptured	Recapture %
Mature	M	2350	708	30.1	1474	533	36.1
	F	597	116	19.4	514	80	15.6
Teneral	M	15	5	33.0	66	9	13.6
	F	3	1	33.0	71	1	1.4

*M= male, F = female

7.3.2 Rate of transfer from the natal patch and extent of within and between-patch movements

The frequency of between-patch, within-patch and non-movements are shown in Table 7.4, expressed with regard to both individuals and movements since some individuals were recaptured several times. Males and females did not differ in the proportion of individuals that performed the three types of movement in their lifetime in either the New Forest ($\chi^2=1.59, p =0.452$, 2 d.f.) or in Mynydd Preseli ($\chi^2=2.76, p =0.252$, 2 d.f.). In both sites the majority of individuals moved within a stretch of suitable stream and the proportion of individuals not moving at all was also substantial (20-47%). However, there was a significant difference in the proportion of individuals performing the three types of movements between the two sites (males and females amalgamated - $\chi^2=128.5$, $p < 0.001$, 2 d.f.). A higher proportion of individuals transferred between sites in Mynydd Preseli. The maximum number of times an individual transferred within a patch in its lifetime was 4 in the New Forest and 5 in Mynydd Preseli. The maximum number of times an individual transferred between patches was 1 in the New Forest and 2 in

Mynydd Preseli. In Mynydd Preseli, the large number of between-patch movements allowed individuals that moved between patches (m) to be compared to individuals that did not (nm) with regards to the number of recaptures and residency duration. The number of times that an individual was recaptured did not differ between these two groups in males (χ^2=0.963 p =0.327, 3 d.f.) or females (χ^2=1.03, p =0.309, 1 d.f.). Residency duration was longer in individuals that transferred (t) than in those that did not (r) for males ($\mu_t \pm$ s.e. = 9.79 ± 0.83, n_t=61, $\mu_r \pm$ s.e. =8.35 ± 0.29, n_r=472, Z=1.34, p=0.025) but not females ($\mu_t \pm$ s.e. = 8.57 ± 0.1.37, n_t=14, $\mu_r \pm$ s.e. =7.11 ± 0.64, n_r=66, Z=0.99, p=0.137). The magnitude of this difference in males is not large and probably arises because individuals that move between sites may only be recaptured if they live a relatively long time.

The location and direction of the nine between-patch transfers in the New Forest are shown in Fig. 7.5a. Three of these movements occurred across a scrub barrier and six occurred across unsuitable stream. The location and direction of the between-patch transfers in Mynydd Preseli are shown in Fig. 7.5b. Transfers occurred in several different directions. For males, the majority of transfers involved movement from a peripheral patch to the main stream section (42), 13 were movements from the main stream section to a peripheral patch and only three involved movement between these peripheral patches. For females, 3 transfers were from peripheral patch to stream, 4 between peripheral patches and 6 from stream to patch. Since the scrub on this site consists mainly of low gorse, no movements were observable through scrub barriers of the sort found in the New Forest site. In particular no movements occurred between sites 3, 4 and 5 even though they are relatively close together (Fig.7.5a). Thus, for comparison with the between-patch migration rate of other insect species, the between-patch migration rate is 1.3% for New Forest males and 11.4% for Mynydd Preseli males.

Table 7.4a Frequency and proportion of between-stream movements, within-stream movements and non-movement for males and females – New Forest.

	Males		Females	
Movement type	No. of individuals (%)	No. of movements (%)	No. of individuals (%)	No. of movements (%)
n	676	1066	118	124
Between-patch transfer	9 (1.3)	9 (0.8)	0 (0)	0 (0)
Within-patch transfer	531 (78.6)	686 (64.4)	94 (79.7)	76 (61.3)
Non-movement	137 (20.3)	373 (35.0)	24 (20.3)	48 (38.7)

Table 7.4b Frequency and proportion of between-stream movements, within-stream movements and non-movement for males and females – Mynydd Preseli.

	Males		Females	
Movement type	No. of individuals (%)	No. of movements (%)	No. of individuals (%)	No. of movements (%)
n	533	935	80	96
Between-patch transfer	61 (11.4)	63 (6.7)	14 (17.5)	14 (14.6)
Within-patch transfer	291 (54.6)	434 (46.4)	38 (47.5)	45 (46.9)
Non-movement	181 (34.0)	438 (46.8)	28 (35.0)	37 (38.5)

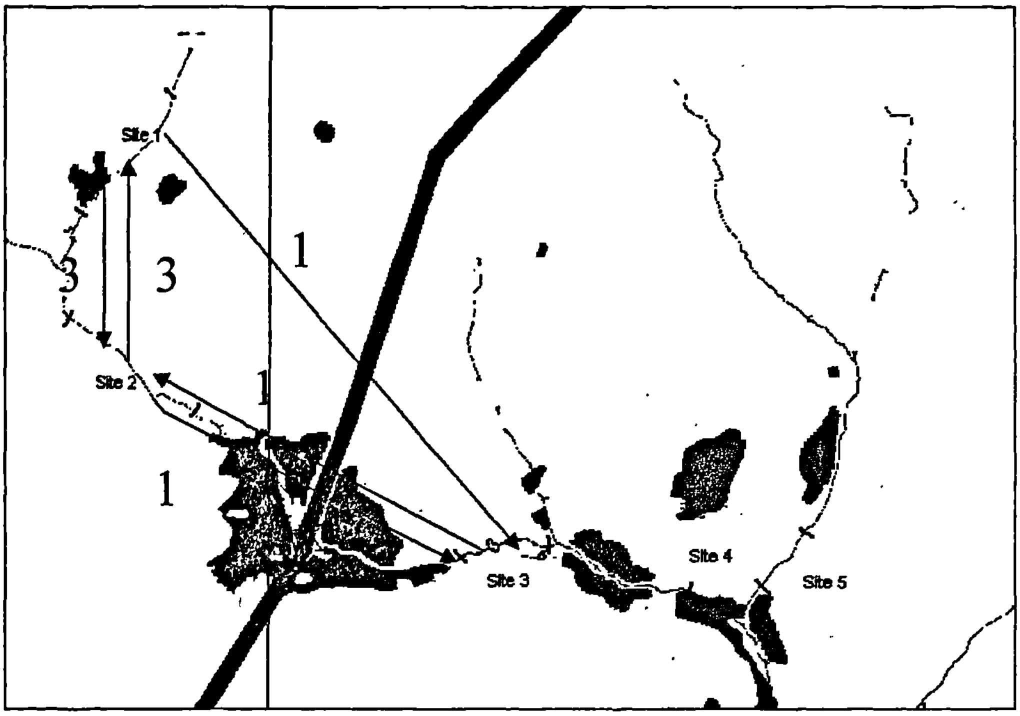


Fig. 7.5a The location and direction of between-patch transfers in the New Forest.

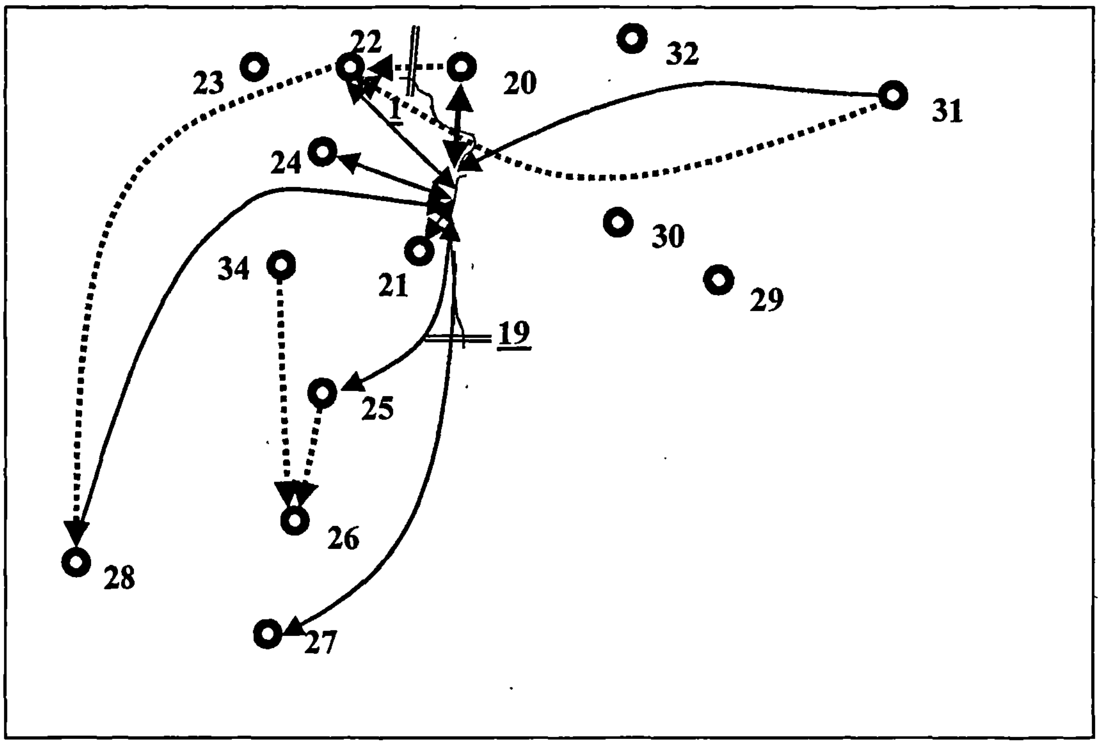


Fig. 7.5b The location and direction of the between-patch transfers in Mynydd Preseli. Solid arrows indicate movements between the main patch and peripheral patches whilst broken arrows indicate movements between peripheral patches. Within-patch movements are not shown here.

The factors affecting the probability of transfers occurring between pairs of sites were examined. Transfers were more likely between pairs of sites that were close together than between sites that were far apart (Fig. 7.6). A negative correlation was found between the mid-point of the distance category and the proportion of pairs in the category between which transfers occurred (New Forest, Transfers between sites 1 and 2 - Spearman's r_s=-0.835, $p < 0.001$, n=16; Mynydd Preseli, transfers to other main stream sections - r_s=-0.865, $p < 0.001$, n=11; transfers to peripheral sites - r_s=-0.748, $p < 0.001$, n=18). There was no difference in the probability of long distance transfers (distance categories between 300-599m) depending on whether the transfers were within the main stream patch or between patches (to peripheral sites) in Mynydd Preseli (χ^2=1.74, p=0.181, 1 d.f.). However, transfers at short (50-149m - χ^2=5.10, p=0.024, 1 d.f.) and medium distances (150-299m - χ^2=10.31, p=0.001, 1 d.f.) were more likely to occur within the main stream patch than between patches. In addition, in Mynydd Preseli, the proportion of individuals that transferred from main sites to peripheral sites was higher than the proportion that transferred from peripheral sites to main sites (χ^2=5.92, p=0.023, 1 d.f.).

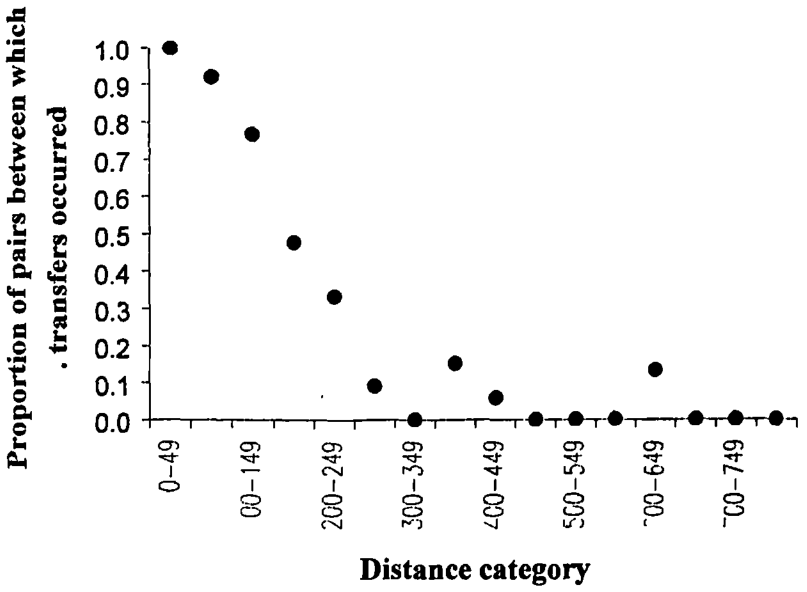


Fig. 7.6a Proportion of pairs between which transfers were observed for each distance category for individuals from sites 1 and 2 – New Forest.

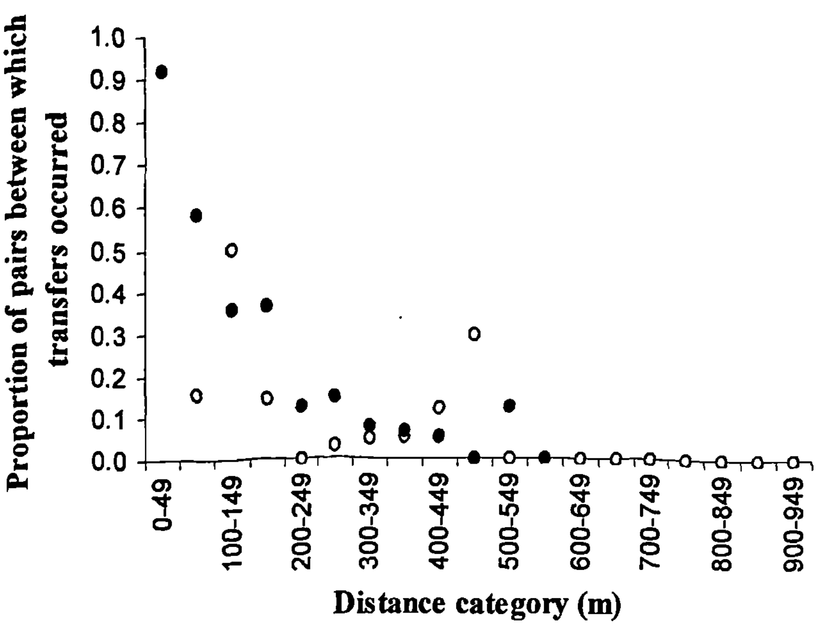


Fig. 7.6b Proportion of pairs of sites between which transfers were observed for each distance category for individuals from the main stream section – Mynydd Preseli. Transfers within the main stream section – closed circles; transfers from the main stream section to peripheral sites – open circles.

7.3.3 The effect of phenotype and time taken for movements on dispersal

To describe the shape of the dispersal distribution, the lifetime movements of individuals are considered regardless of whether movements were between or within-stream transfers. The percentage distributions of dispersal distances for males and females from both sites are shown in Fig. 7.7. In both sites, most recaptured individuals dispersed over short distances but a few moved up to 1km. In the New Forest, 57% of males and 59% of females were recaptured within 25m of their marking site and only 2% of males and 4% of females moved further than 200m. The maximum distance moved was 1060m by a male. The maximum distance a female moved was 275m. In Mynydd Preseli, 43% of males and 39% of females were recaptured within 25m of their site and 9% of males and 14% of females moved further than 200m. The maximum distance moved was 802m for males and 900m for females. All the maximum movements described here occurred over unsuitable habitat. With regards to the time-scale over which large movements occur, the maximum movement achieved in 1 day was 444m (Mynydd Preseli male), and that achieved in 2 days was 610m (New Forest male).

There is no difference between males and females in any of the dispersal parameters for New Forest or Mynydd Preseli (Table 7.5). There was a significant difference between the two sites in the distribution of net lifetime movements (males - Z=2.50, p < 0.001; females – Z=1.25, p =0.045). More dispersal of an intermediate distance occurred in

Mynydd Preseli probably due to the greater availability of habitat at these distances there.

Table 7.5a Medians and Komolgorov-Smirnov Tests comparing dispersal parameters between males and females - New Forest.

	Males		Females			
Parameter	*Median*	μ ±. s.e	Median	μ ± s.e	Z	p
L	25.0	48.13 ± 3.01	25.0	46.24 ± 6.24	0.470	0.639
X	25.0	50.66 ± 2.99	25.0	49.21 ± 6.34	0.959	0.094
Y	25.0	52.22 ± 3.04	25.0	48.39 ± 6.36	0.818	0.202
d_I(m)	25.0	38.23 ± 2.04	25.0	43.81 ± 5.43	-	-
t_I(days)	2.0	3.69 ± 0.11	3.0	4.35 ± 0.34	-	-
v_I (m/day)	8.33	14.87 ± 0.73	6.25	16.31 ± 2.89	-	-

Table 7.5b Medians and Komolgorov-Smirnov Tests comparing dispersal parameters between males and females - Mynydd Preseli

	Males		Females			
Parameter	*Median*	$\mu \pm s.e.$	Median	$\mu \pm s.e.$	Z	p
L	40.0	69.59 ± 4.90	40.0	98.60 ± 18.3	0.948	0.187
X	42.0	72.46 ± 4.88	41.5	100.20 ± 18.20	0.948	0.206
Y	42.0	74.63 ± 4.96	44.0	101.70 ± 18.20	0.958	0.199
t_I(days)	3.67	4.54 ± 0.20	4.0	5.58 ± 0.49	-	-
v_I (m/day)	7.70	18.16 ± 1.43	10.0	21.18 ± 3.89	-	-

In both sites, there is no difference in the body size of individuals that transferred (t – within or between sites) in their lifetime compared to those that remained resident (r) for females (New Forest females – $median_t$=17.85, $median_r$=17.90, Mann Whitney W =1088.5, p=0.67; Mynydd Preseli females - $median_t$=19.38, $median_r$=19.58, W=1517.5, p=0.59) or, in New Forest males ($median_t$=16.20, $median_r$=16.10, W=42852.5, p=0.95). For Mynydd Preseli males, residents were significantly larger than transfers ($median_t$=17.20, $median_r$=17.40, W=46274.0, p=0.0072).

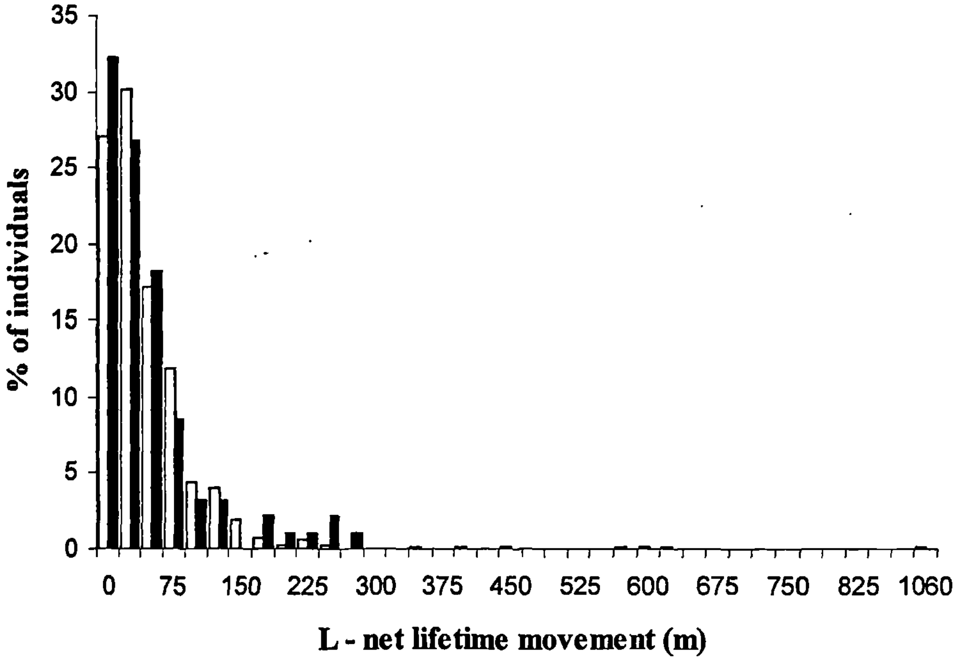


Fig. 7.7a Percentage distribution of net lifetime movements (L) for males (open bars) and females (closed bars) from New Forest.

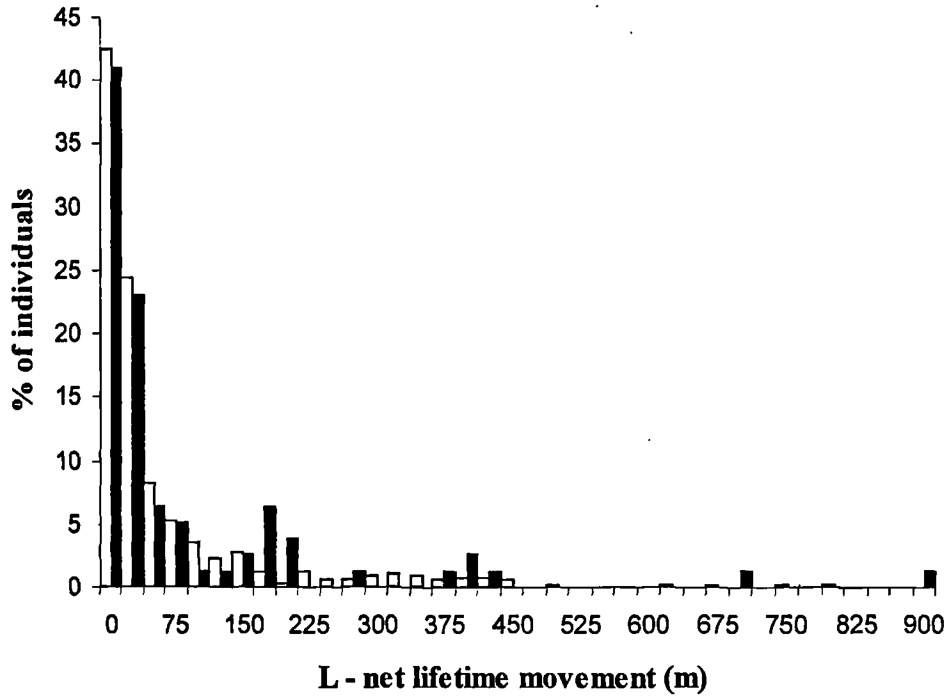


Fig. 7.7b Percentage distribution of net lifetime movements (L) for males (open bars) and females (closed bars) from Mynydd Preseli.

However, there was no correlation between body size and any of the three dispersal parameters for males and females in either the New Forest (males; L – Spearman's rank correlation r_s= -0.033, p=0.41, X - r_s= -0.001, p=0.58, Y - r_s= -0.003, p=0.94; females; L - r_s= -0.119, p=0.26, X - r_s= -0.132, p=0.21, Y - r_s= -0.115, p=0.27) or Mynydd Preseli (males; L – r_s= -0.015, p=0.73, X - r_s= -0.010, p=0.81, Y - r_s= -0.009, p=0.83; females; L - r_s= 0.032, p=0.80, X - r_s= 0.029, p=0.81, Y - r_s= 0.032, p=0.80).

No sex or size bias in dispersal during an individual's lifetime was found. Thus, the relationship between dispersal during an interval between two movements and the following factors was considered for movements 1 to5 of males from both sites (Tables 7.6 and 7.7); age, day of season during movement (mid-point date), length of interval and order of movement (Section 7.2.3). In both sites, the length of the time interval was the only significant variable added to the stepwise logistic regression models to predict the probability of moving more than 0m, the probability of moving at least 50m and the probability of moving at least 200m. Length of time interval had a significant positive effect on the distance moved in an interval in all models. Age, day of season and order of movement were not added to any of the models and thus did not have a significant effect on distance moved in an interval.

The probabilities of moving 0m, at least 50m and at least 200m were modelled separately for movement 1, movement 2 and movement 3 for both sites (yielding 18 stepwise regression models – 3 binary distance variable X 3 movement intervals (1st, 2nd 3rd) X 2 sites). Although in five models no variables were added, and in another three there were insufficient data to fit the model, in 9 models the length of time interval had a significant positive effect on the probability of movement (of 0, 50 or 200m). In one model, the mid point date was added to the model first by the stepwise regression procedure followed by time and had a significant negative effect on the probability of movement suggesting that individuals have a lower probability of movement early in the season. These models are given in full in Appendix 10.

Table 7.6a Logistic regression analysis of probability of moving more than 0m during the interval between two recaptures – Movements 1-5 of Mynydd Preseli males.

	B ± s.e.	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	-0.161 ± 0.119				0.176			0.85
t_1	0.052 ± 0.023	-440.69	1	5.48	0.021	312	355	1.05
Model χ^2=5.48, p=0.019, 1 d.f.								

Table 7.6b Logistic regression analysis of probability of moving more than 50m during the interval between two recaptures – Movements 1-5 of Mynydd Preseli males.

	B ± s.e.	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	-1.831 ± 0.154				< 0.001			0.16
t_1	0.101 ± 0.025	316.59	1	15.63	< 0.001	511	126	1.11
Model χ^2=15.63, $p < 0.001$, 1 d.f.								

Table 7.6c Logistic regression analysis of probability of moving more than 200m during the interval between two recaptures – Movements 1-5 of Mynydd Preseli males.

	B ± s.e.	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	-3.952 ± 0.328				< 0.001			0.02
t_1	0.150 ± 0.040	-105.41	1	11.86	< 0.001	612	25	1.16
Model χ^2=11.86, $p < 0.001$, 1 d.f.								

Table 7.7a Logistic regression analysis of probability of moving more than 0m during the interval between two recaptures – Movements 1-5 of New Forest males.

	B ± s.e.	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	0.092 ± 0.097		1		0.345			1.10
t_1	0.149 ± 0.025	-706.12	1	46.65	<0.001	388	694	1.16
Model χ^2=46.65, $p < 0.001$, 1 d.f.								

Table 7.7b Logistic regression analysis of probability of moving more than 50m during the interval between two recaptures – Movements 1-5 of New Forest males.

	B ± s.e.	Likelihood ratio	d.f.	G	p	n_0	n_1	E^B
Constant	-1.194 ± 0.099		1		<0.001			0.303
t_1	0.140 ± 0.020	-692.35	2	56.57	<0.001	716	366	1.151
Model χ^2=56.67, p <0.001, 1 d.f.								

Table 7.7c Logistic regression analysis of probability of moving more than 200m during the interval between two recaptures – Movements 1-5 of New Forest males.

	B ± s.e.	Likelihood ratio	d.f.	G	p	n_0	n_1	e^B
Constant	-5.352 ± 0.411		1		< 0.001			0.005
t_1	0.222 ± 0.040	-91.58	1	26.57	< 0.001	1064	18	1.249
Model χ^2=26.57, p < 0.001, 1 d.f.								

7.3.4 The effect of a correction for the theoretical probability of recapture on the distribution of dispersal distances

The observed rate of recapture at each distance was corrected for the theoretical probability of recapture at each distance (Section 7.2.4). The effect of this correction on the distribution of distances for all movements between two recaptures (d_rs) is shown in Fig. 7.8. The mean of observed movements was 38.48 ± 2.04m whilst the mean of corrected movements was 57.91 ± 2.74. Whilst the percentage of movements of 0-50m is decreased by this correction, the percentage of movements at all other distance categories is increased. In particular, the percentage of movements of 1km or more increases from 0.09 to 0.25% such that 3 movements not 1 would be expected to move over this distance within a generation. When this correction was performed on the net lifetime movements of individuals that were only recaptured once, it resulted in a substantial increase in the mean net lifetime movement for both males ($\mu_{observed}$ = 41.15m ± 3.43; $\mu_{corrected}$ = 61.77m ± 4.58) and females ($\mu_{observed}$ = 41.18m ± 6.56; $\mu_{corrected}$ = 69.89m ± 8.84).

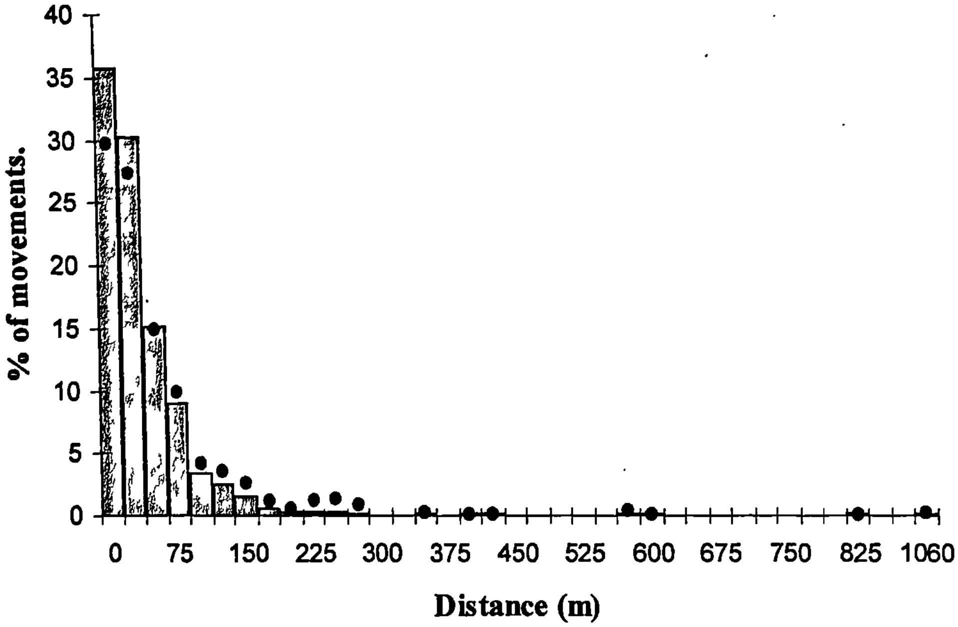


Fig. 7.8 Percentage distribution of movements of different distances for observed data (grey bars) and data corrected for the theoretical probability of recapture (closed circles).

7.3.5 Predicting the probability of dispersal at different distances by fitting dispersal distributions.

The relationship between the probability of dispersal and distance can be described by a negative exponential function where the probability of an individual (I) moving distance, D, is given by:

$$I=e^{-kD}$$

Where k is a species-specific dispersal constant describing the shape of the exponential curve (equivalent to $1/D'$ in Harrison's (1988) equation 4 (cited in Hill *et al.* 1996) where D' represents the average distance moved by individuals between patches). Since Ln I was regressed upon distance, k was the value of the gradient of the regression line.

An inverse power function was also fitted to the data where the probability of an individual (I) moving a certain distance (D km) is given by:

$$I=CD^{-n}$$

where C and n are scaling constants.

Both functions fitted the dispersal data from both sites well (as indicated by the values of R^2 given in Tables 7.8 and 7.9) but the negative exponential function fitted the data from both sites better. However, examination of the semi-log plots of the inverse cumulative proportion of individuals moving certain distances shows that the function fits the data well only over short distances and not at all well over medium to long distance categories (Figs. 7.9-7.10). The weighting procedure, weights distance categories with high numbers of individuals highly. Thus high R^2 values will result due to the large number of individuals in the first distance category regardless of whether the curve fits at longer distances. Therefore, these functions cannot be used to predict long distance movement for any species where most individuals move only short distances. The predicted probabilities of moving 1000m are shown in the last column of Tables 7.8 and 7.9. Comparing these to the observed probability for New Forest males (0.013 from Section 7.3.2) illustrates how these functions underestimate long distance dispersal.

Table 7.8a Regression models for negative exponential - males (M) and females (F) in the New Forest.

Sex	Equation	D' (m)	R^2	F	d.f.	p	P ($L >$ 1000m)
M	$\mathrm{Ln}\, I = -0.0114 \pm 0.0015\, D$	87.7	0.79	60.33	16	<0.001	1.12×10^{-5}
F	$\mathrm{Ln}\, I = -0.0173 \pm 0.0006\, D$	57.8	0.99	902.75	9	<0.001	3.07×10^{-8}

Table 7.8b Regression models for inverse power function males (M) and females (F) in the New Forest.

Sex	Equation	R^2	F	d.f.	p	P ($L >$ 1000m)
M	$\mathrm{Ln}\, I = -0.395 \pm 0.086\, \mathrm{Ln}\, D$	0.57	21.27	17	< 0.001	0.0168
F	$\mathrm{Ln}\, I = -0.376 \pm 0.089\, \mathrm{Ln}\, D$	0.67	17.98	10	0.002	0.0146

Table 7.9a Regression models for negative exponential function males (M) and females (F) in Mynydd Preseli.

Sex	Equation	D'	R^2	F	d.f.	p	P ($L >$ 1000m)
M	$\mathrm{Ln}\, I = -0.0090 \pm 0.0006\, D$	111.7	0.92	245.13	22	<0.001	1.30×10^{-4}
F	$\mathrm{Ln}\, I = -0.0060 \pm 0.0007\, D$	166.9	0.86	77.61	13	<0.001	2.50×10^{-3}

Table 7.9b Regression models for inverse power function males (M) and females (F) in Mynydd Preseli.

Sex	Equation	R^2	F	d.f.	p	P ($L >$ 1000m)
M	$\mathrm{Ln}\, I = -0.447 \pm 0.050\, \mathrm{Ln}\, D$	0.79	81.06	22	<0.001	0.0118
F	$\mathrm{Ln}\, I = -0.345 \pm 0.044\, \mathrm{Ln}\, D$	0.83	61.16	13	<0.001	0.0161

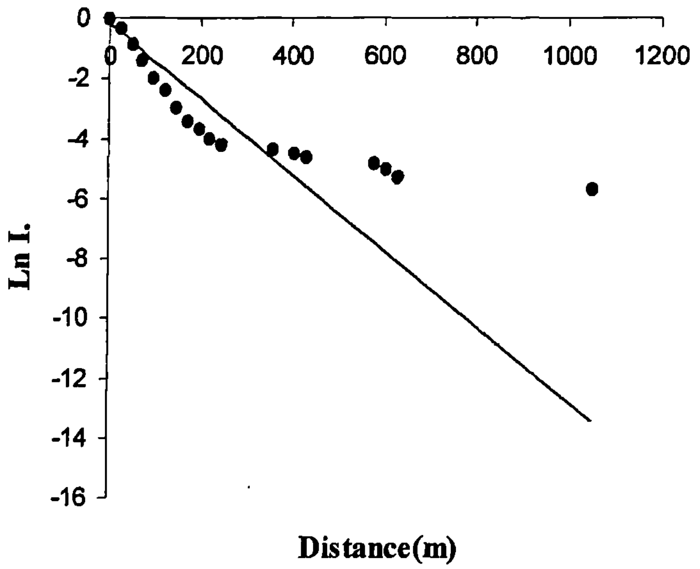


Fig. 7.9a Semi-log plot of the inverse cumulative proportion (I) of individuals moving different distances – New Forest males. The solid line shows the fitted values from the exponential function in Table 7.8a whilst the closed circles are the observed values.

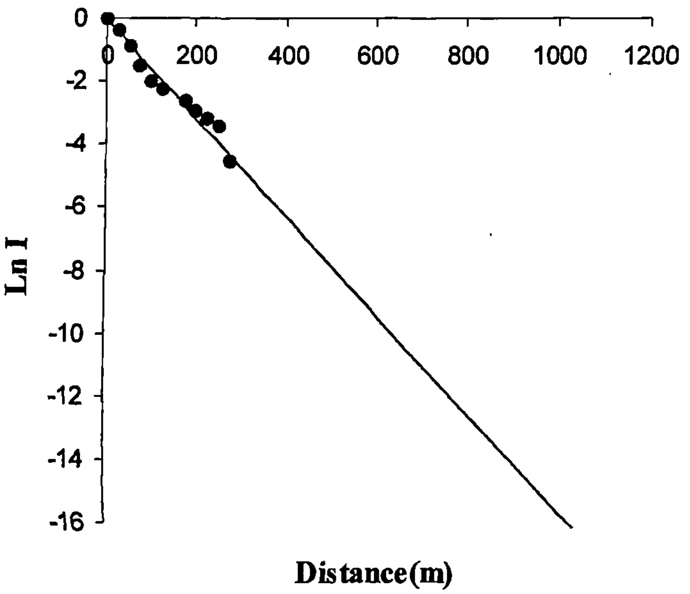


Fig. 7.9b Semi-log plot of the inverse cumulative proportion (I) of individuals moving different distances – New Forest females.

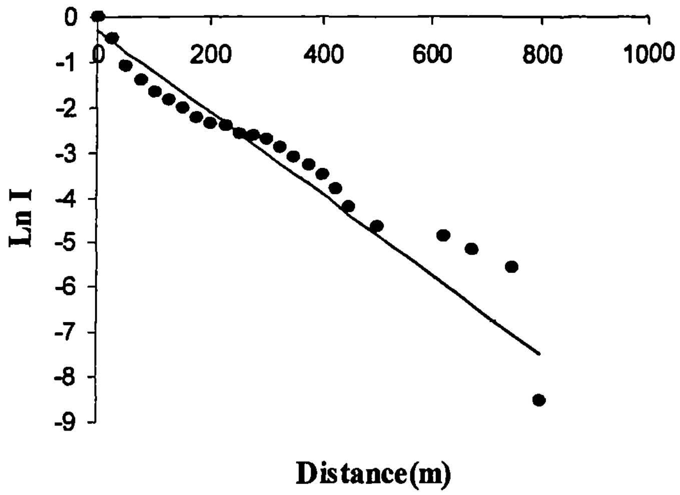


Fig. 7.10a Semi-log plot of the inverse cumulative proportion (I) of individuals moving different distances – Mynydd Preseli males. The solid line shows the fitted values from the exponential function in Table 7.9a whilst the closed circles are the observed values.

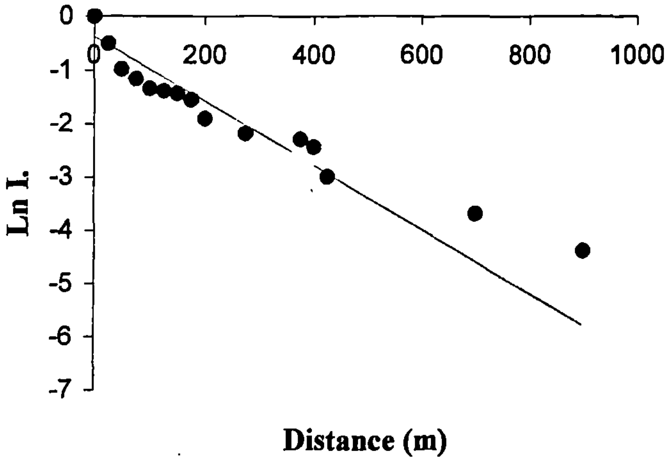


Fig. 7.10b Semi-log plot of the inverse cumulative proportion (I) of individuals moving different distances – Mynydd Preseli females.

7.3.6 Assessing the likelihood of dispersal between populations within actual site configurations found in regions of Britain.

In St David's, Devon, Dartmoor and Gower, the distance separating the two populations in each cluster exceeds the maximum dispersal distance observed for *C. mercuriale,* whilst the distance between populations in the Oxford cluster (and probably also in the Anglesey cluster) does not (Table 7.10). Given that the field observations may underestimate maximum dispersal distance exchange of individuals between populations may occur in Devon, Dartmoor and St David's as well as in Oxford and Anglesey given a sufficient number of generations. Distances between clusters would not permit exchange of individuals between them.

Table 7.10 Distance between populations in 'two site' clusters, and distance to and identity of the nearest neighbouring cluster.

Cluster	No. of sites	Distance between two sites (km)	Distance to nearest cluster (km)	Name of nearest cluster
Oxford	2	0.92	60	New Forest
St David's	2	2.90	25-28	Pembrokeshire
Anglesey	2	*	152	Pembrokeshire
Devon	2	3.87	36-38	Dartmoor
Dartmoor	2	4.10	36-38	Devon
Gower	2	7.10-8.00	42-47	Pembrokeshire

*no data since location of recently discovered colony is unknown.

Percentage frequency distributions of distances between each grid reference point and its nearest neighbour (more than 250m away) are shown for the New Forest (NF), Itchen and Test (IT), and Pembrokeshire (except St Davids - P) clusters in Figs. 7.11-7.13. Given the low number of points for the Dorset cluster, a raw frequency distribution is shown in Fig. 7.14. In the New Forest, 60% of grid references are situated 1km or less away from their nearest neighbour (Fig. 7.11) and 80% are situated 3km or less away. In the Itchen and Test cluster, 85% of grid references are situated 1km or less away from their nearest neighbour and all are situated within 3km of their neighbour (Fig. 7.12). In Pembrokeshire, 90% of grid references are situated 1km or less away with only 5% situated further than 3km away from their nearest neighbour (Fig. 7.13). In Dorset, 3 of the 8 sites are within 1km of their neighbours but all sites are within 3km of their nearest neighbours (Fig.7.14). Thus in these large clusters a high level of exchange between populations is probably possible. Comparison of mean isolation indices across each region (Table 7.11) suggests that grid references in Pembrokeshire are substantially less isolated than in the other three clusters. Many grid references had several other points within 250m of each other as well as having neighbours further away. This reflects the much higher density of grid references in this region. The differences between clusters in both mean isolation index (median$_{NF}$=3.18, median$_{IT}$=1.48, median$_{P}$=0.29, Kruskal-Wallis H=123.12, 2 d.f., $p < 0.001$) and distance to nearest neighbour (median$_{NF}$=0.83, median$_{IT}$=0.40, median$_{P}$=0.32, Kruskal-Wallis H=41.68, 2 d.f., $p < 0.001$) are significant. Thus, a maximum colonisation distance of 1km (as observed in the field) would permit substantial exchange over time between British populations in these larger clusters or sites. If *C. mercuriale* can indeed disperse up to 3km then exchange will be permitted between the majority of populations even within the smaller clusters but only if the intervening habitat is conducive to movement.

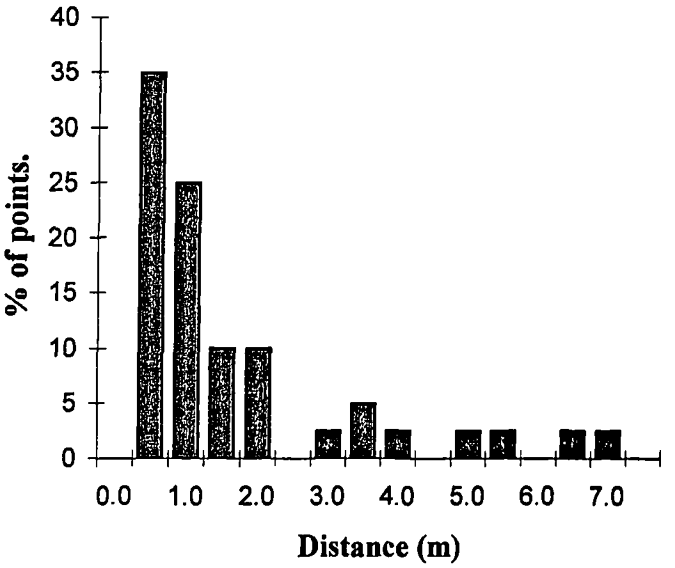


Fig. 7.11 Percentage frequency distribution of distances between each point (grid reference) and its nearest neighbour (> 250m away) for New Forest sites (n=41).

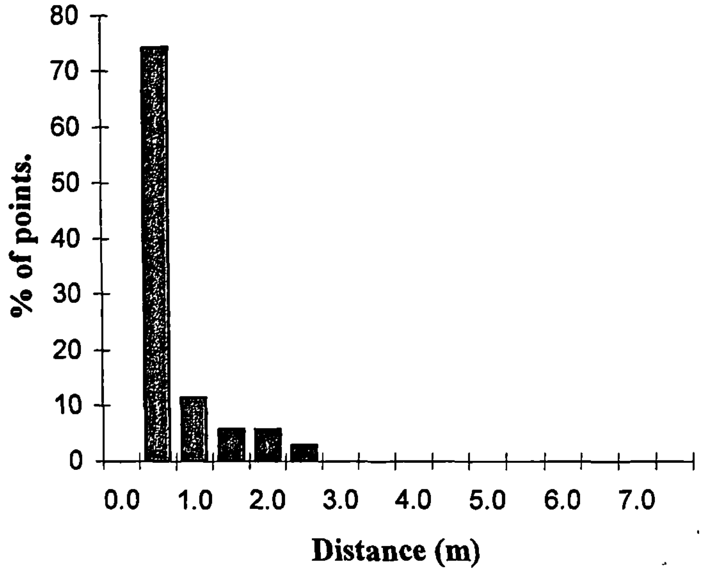


Fig. 7.12 Percentage frequency distribution of distances between each point (grid reference) and its nearest neighbour (< 250m away) for Itchen & Test sites (n=35).

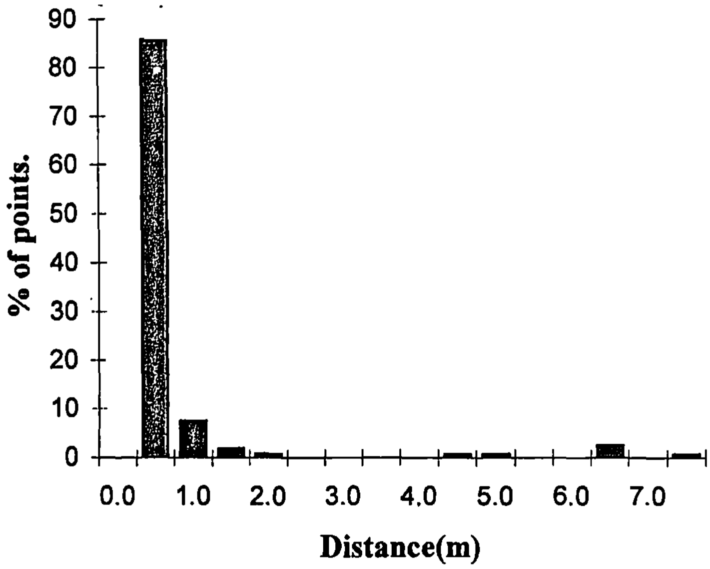


Fig. 7.13 Percentage frequency distribution of distances between each point (grid reference) and its nearest neighbour (< 250m away) for Pembrokeshire sites (n=160).

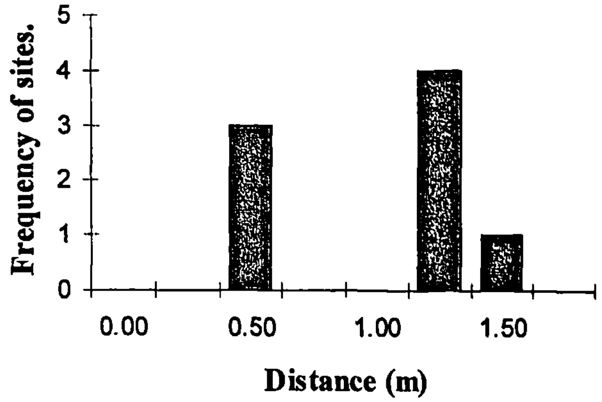


Fig. 7.14 Frequency distribution of distances between each point (grid reference) and its nearest neighbour (< 250m away) for Dorset sites (n=8).

Table 7.11 Number of points, mean (± s.e.) and range of isolation indices within each region for large clusters.

Cluster	μ ± s.e. (km)	No. of points	Range (km)
Dorset	3.97 ± 0.25	7	3.14 – 5.24
New Forest	4.59 ± 0.52	41	1.24 – 13.42
Itchen & Test	2.24 ± 0.44	35	0.39 – 8.80
Pembrokeshire (excluding St David's)	0.52 ± 0.06	160	0.16 – 7.89

7.3.7 Analysis of survival and recapture probabilities

7.3.7.1 General model and goodness of fit

For the New Forest dataset (2266 mature males, 524 mature females, marked in sites 1 or 2) the Goodness-of-fit release tests indicated a significant lack of fit to the C-J-S model (sum of Test 2 and 3 for the two groups; males: $\chi^2 = 240.45$, 169 d.f.; females: $\chi^2 = 53.86$, 65 d.f.; for both groups, the total value of the goodness-of-fit test was $\chi^2 = 294.31$, $p=0.0045$, 234 d.f.). No systematic bias could be detected in the contingency tables for Test 2 and 3 thus the analysis for this dataset was abandoned.

For all individuals from Mynydd Preseli (1110 mature males, 370 mature females) none of the tests indicated a significant lack of fit to the C-J-S model (sum of Test 2 and 3 for the two groups; males: $\chi^2 = 107.65$, 106 d.f.; females: $\chi^2 = 17.82$, 37 d.f.; for both groups, the total value of the goodness-of-fit test was $\chi^2 = 125.47$, $p=0.851$, 143 d.f.). To check for extra-multinomial variation, the average residual variation (σ^2) can be calculated as the expected value of the chi-square goodness-of-fit statistic divided by its degrees of freedom. If the model structure is correct, then under the multinomial assumption $\sigma^2 =1$. In this analysis, $\sigma^2 = 0.877$ suggesting there is not substantial excess variation and thus it is not necessary to estimate a variance-inflation factor c-hat.

7.3.7.2 Model selection

Table 7.12 shows a selection of models fitted to this dataset, including the best model and others that illustrate the model selection process. The best model of the 16 containing sex and time or their interactions was $\phi_{(t)}\ p_{(s+t)}$.(2nd on Table 7.12). The addition of an interaction between body size and sex (including the main effects of both) to the model for the recapture rate parameter (i.e. $\phi_{(t)}\ p_{(t+s*b)}$) lowered the AIC by 1.39 such that both models provided a similar fit to the data. Both models were better than any models with the addition of a main effect of body size to models of either recapture or survival. Although both recapture rate and survival rate were found to be time-dependent, models containing rain or temperature variables were not as 'good' as a model with time dependence.

7.3.7.3 Recapture probability

Males had a consistently higher recapture probability than females (Fig. 7.15a - $\beta=1.772 \pm 0.309$). The mean recapture probability for males was 0.223 ± 0.021 (ranging from 0.015 to 0.435) and for females was 0.042 ± 0.011 (ranging from 0.002 to 0.311). According to the logit function parameters (β) of the model $\phi_{(t)}\ p_{(t+s*b)}$, body size has a positive relationship with recapture probability ($\beta=0.339 \pm 0.184$) i.e. larger individuals are more likely to be recaptured than small individuals. This effect is shown despite the fact that large females are less likely to be recaptured than small males. Recapture probabilities seem to vary substantially between occasions. Logit function parameters for these time dependent effects on recapture probability vary between –2.030 and 1.260 for most occasions though parameters for the 2nd, 22nd, 24th and 28th day are around –14.

Table 7.12 Akaike information criteria (AIC_c), Akaike information criterion differences (ΔAIC_c), number of parameters (*np*) and deviances for the models fitted to the Mynydd Preseli dataset.

Model	AIC_c	ΔAIC_c	*np*	Deviance
$\phi_{(t)}\ \rho_{(t+s*b)}$	5080.00	0.00	48	4981.81
$\phi_{(t)}\ \rho_{(s+t)}$	5081.39	1.39	47	4985.29
$\phi_{(t)}\ \rho_{(t+s+b)}$	5083.05	3.05	48	4984.86
$\phi_{(t+b)}\ \rho_{(t+s*b)}$	5083.80	3.80	51	4979.33
$\phi_{(rain)}\ \rho_{(t+s*b)}$	5084.05	4.06	32	5019.08
$\phi_{(t+b)}\ \rho_{(s+t)}$	5084.41	4.41	49	4984.13
$\phi_{(t+b)}\ \rho_{(t+s+b)}$	5084.71	4.71	50	4982.34
$\phi_{(.)}\ \rho_{(s+t)}$	5084.96	4.97	29	5026.16
$\phi_{(s+t)}\ \rho_{(s+t)}$	5085.50	5.50	49	4985.22
$\phi_{(.)}\ \rho_{(t+s*b)}$	5085.78	5.78	31	5022.86
$\phi_{(b)}\ \rho_{(s+t)}$	5086.77	6.77	30	5025.91
$\phi_{(maxt)}\ \rho_{(t+s*b)}$	5086.78	6.78	32	5021.80
$\phi_{(s)}\ \rho_{(s+t)}$	5086.79	6.79	30	5025.93
$\phi_{(.)}\ \rho_{(t+s+b)}$	5086.81	6.81	30	5025.95
$\phi_{(meant)}\ \rho_{(t+s*b)}$	5087.09	7.09	32	5022.11
$\phi_{(b)}\ \rho_{(t+s*b)}$	5087.23	7.23	32	5022.25
$\phi_{(b)}\ \rho_{(t+s+b)}$	5088.10	8.10	31	5025.18
$\phi_{(s*t)}\ \rho_{(s+t)}$	5098.67	18.67	60	4975.25
$\phi_{(t)}\ \rho_{(s*t)}$	5103.55	23.55	64	4971.65
$\phi_{(s+t)}\ \rho_{(s*t)}$	5105.30	25.31	65	4971.28
$\phi_{(.)}\ \rho_{(s*t)}$	5105.56	25.56	45	5013.64
$\phi_{(s)}\ \rho_{(s*t)}$	5106.86	26.87	46	5012.86
$\phi_{(s*t)}\ \rho_{(s*t)}$	5107.91	27.91	71	4961.10
$\phi_{(s+t)}\ \rho_{(t)}$	5132.69	52.70	49	5032.41
$\phi_{(s)}\ \rho_{(t)}$	5140.65	60.66	29	5081.85
$\phi_{(s*t)}\ \rho_{(t)}$	5145.02	65.02	62	5017.36
$\phi_{(.)}\ \rho_{(t)}$	5173.94	93.94	28	5117.19
$\phi_{(t)}\ \rho_{(rain+s*b)}$	5472.17	392.18	24	5423.62
$\phi_{(t)}\ \rho_{(meant+s*b)}$	5472.18	392.18	22	5427.71
$\phi_{(t)}\ \rho_{(meant+s)}$	5473.66	393.66	20	5433.27
$\phi_{(t)}\ \rho_{(rain+s)}$	5483.01	403.02	21	5440.59
$\phi_{(t)}\ \rho_{(maxt+s*b)}$	5488.21	408.21	22	5443.74
$\phi_{(t)}\ \rho_{(maxt+s)}$	5489.05	409.05	20	5448.66
$\phi_{(.)}\rho_{(.)}$	5694.11	614.11	2	5690.10

Time dependence in recapture probability would not arise due to variation in recapture effort, since equal recapture effort was employed on each recapture occasion. Thus, this time dependence is most likely explained by variation in external weather conditions. Weather variables do not constitute significant predictors of recapture probability, probably because mark-recapture exercises were not carried out in the full range of weather conditions but only when damselflies were active.

7.3.7.4 Survival probability

According to the 'best' model, $\phi_{(t)}\ \rho_{(t+s*b)}$, mean survival probability was 0.882 ± 0.029 (ranging from 0.495 to 1). Survival probabilities varied substantially between occasions. Logit function parameters for these time dependent effects on survival probability varied between –5.60 and –13.87.

For comparison, residency duration was calculated as the interval between first and last recapture. There was a significant difference between males and females in residency duration in both sites when all individuals were included in the analysis (Mynydd Preseli - $\mu_m \pm$ s.e.= 3.71 ± 0.14, n_m= 1474, range$_m$=1-38; $\mu_f \pm$ s.e.=1.99 ± 0.14, n_f= 514, range$_f$ =1-25; Komolgorov Smirnov Z=4.02, p<0.001; New Forest - $\mu_m \pm$ s.e.= 3.02 ± 0.09, n_m= 2068, range$_m$=1-34; $\mu_f \pm$ s.e.=2.09 ± 0.13, n_f= 597, range$_f$ =1-28; Komolgorov Smirnov Z=5.64, p<0.001). There was no sex difference in residency duration when only those individuals that were recaptured at least once were included in the analysis (Mynydd Preseli - $\mu_m \pm$ s.e.= 8.56 ± 0.28, n_m= 530; $\mu_f \pm$ s.e.=7.36 ± 0.58, n_f= 80, Komolgorov Smirnov Z=0.77, p=0.376; New Forest - $\mu_m \pm$ s.e.= 8.37 ± 0.16, n_m= 1154; $\mu_f \pm$ s.e.=7.55 ± 0.47, n_f= 149; Komolgorov Smirnov Z=1.20, p=0.052).

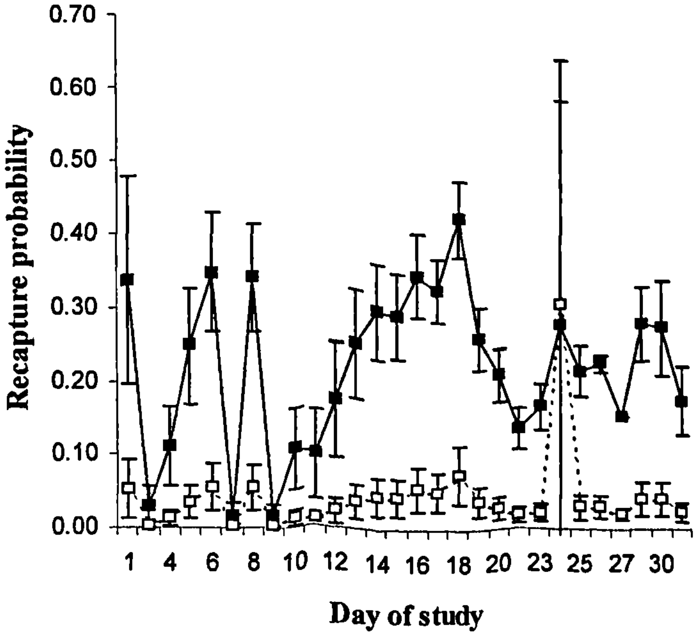


Fig. 7.15a Maximum likelihood estimates (± s.e.) for recapture probabilities of *C. mercuriale* males (black squares and solid lines) and females (white squares and dashed lines) on each day of the study (Day 1=10th June) - calculated from the model $\phi(t)$ $p(t+s*b)$.

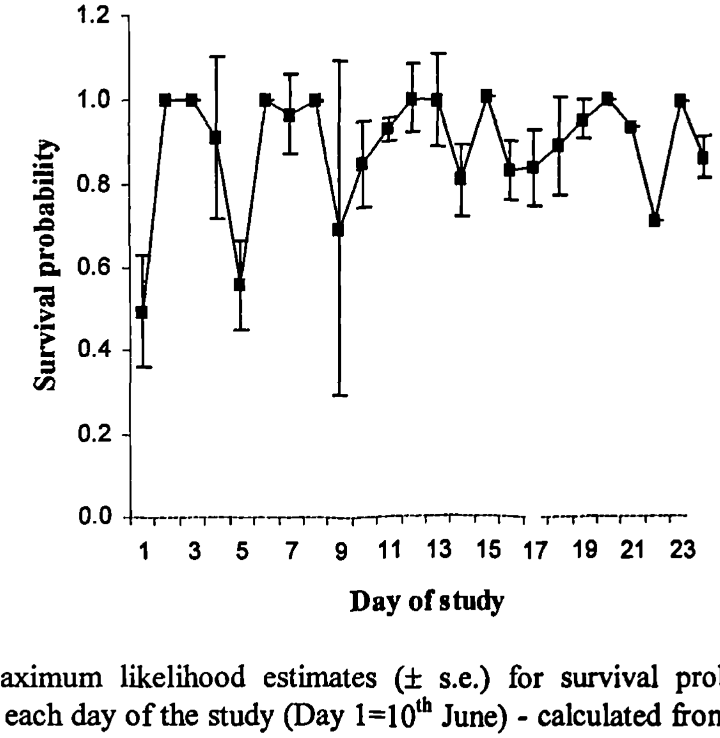


Fig. 7.15b Maximum likelihood estimates (± s.e.) for survival probabilities of *C. mercuriale* on each day of the study (Day 1=10th June) - calculated from the model $\phi(t)$ $p(t+s*b)$.

7.4 Discussion

Here the mobility of mature adult *C. mercuriale* (with regards to the extent of within and between-patch movements, the probability of emigration and maximum colonisation distances) are discussed with reference to mobility in other populations of this species, other odonates and other insects. The likelihood of between-patch movements in relation to aspects of landscape connectivity (different habitat types and interpatch distances) is described. The likelihood of dispersal between populations in the present configuration of British Southern Damselfly sites is examined together with prediction of the consequences for the population persistence (i.e. extinction and colonisation) of *C. mercuriale* in its fragmented landscape. Phenotypic correlates of dispersal are also discussed and areas for further work are highlighted.

7.4.1 Mobility of *C. mercuriale* compared to other British and European studies.

The mobility of *C. mercuriale* in the two British sites studied here was greater in several respects than that observed in previous studies. Hunger & Roske (2001) found that 96% of individuals in a population in southwestern Germany remained within 25m of the site in which they were marked. In this study, the proportion was much lower (20-47%) and the majority of individuals (46-80%) moved within the natal patch. The maximum within-patch and between-patch movements were greater in this study, being 610m and 1060m respectively versus 170m and 300m respectively by Hunger & Roske (2001). In Britain, although within-patch movements of up to 500m (away from the breeding stream) have been observed (Hold 1997; Hopkins & Day 1997; Jenkins 1998), Jenkins (2001) found a low rate of movement (1/1223 individuals) between two adjacent streams (75-150m apart) in the New Forest. If the scale over which dispersal is measured is smaller than that at which organisms move then dispersal distances are underestimated (W. Koenig cited in Dieckmann *et al.* 1999). The disparity in observed mobility between this study and previous ones probably arises due to the larger sample size and larger distances between and within sampled patches. For example, the maximum distance between sampled patches in the German population was approximately 600m (Hunger & Roske 2001). In addition this current study covered much of the flight period of *C. mercuriale* in each site, giving an adequate description of per generation migration rate, whereas previous studies have been restricted to a relatively small portion of the flight period. Other sources of variation in emigration rate across populations are discussed later.

7.4.2 Mobility of *C. mercuriale* compared to that of other odonates

Since *C. mercuriale* fly weakly and close to the vegetation in comparison to other blue damselflies (Winsland 1997a), previous authors have suggested that this species has poorer dispersal ability. However, between-patch migration rate of 11.4% in *C. mercuriale* in Mynydd Preseli was comparable to that of other similarly sized odonates such as *Ischnura elegans* (11%), *Enallagma cyathigerum* (11%) and *Coenagrion puella* (16%) derived in a pond system with similar interpatch distances (Conrad *et al.* 1999). In fact, den Boer (1990) hypothesised that weak fliers may be better dispersers than strong fliers since they are less able to resist wind movement if dispersal is passive.

Comparing the relationship between the probability of dispersal and distance in *C. mercuriale* to that for odonates in the pond system used by Conrad *et al.* (1999), the decline in probability of dispersal with distance seemed to be steeper in this species. Since *C. mercuriale* is one of the smallest damselflies, this is consistent with the finding that larger species have a higher mean probability of dispersal (Conrad *et al.* 1999).

7.4.3 Time required for dispersal relative to lifespan of *C. mercuriale.*

It is significant that *C. mercuriale* was capable of moving considerable distances between patches in periods of time (1-2 days) that constituted a small fraction of the mean mature adult lifespan of individuals (7-8 days). Indeed, a small fraction of individuals in Mynydd Preseli performed two such movements within their lifetime. Whilst *C. mercuriale* was found to move around 0.5 km in 1 or 2 days, larger zygopterans such as *Calopteryx splendens* and *C. virgo* (Stettmer 1996) can move around 1km in the same time period. Due to sparse recapture data for particular individuals, the time interval between recaptures did not explicitly reflect the time taken for a movement. However, despite this, the time interval rather than point in season or age was a significant predictor of the probability of moving more than 0, 50 or 200m. Since both male and female odonates reproduce throughout their mature adult lifespans and, given the relatively short time required for dispersal, individuals should be able to reproduce during and after dispersal and thus may make a genetic contribution to patches other than the natal patch during their lifespan. Thus, odonate systems are likely to fulfil the assumptions required for the application of Wright's models of effective neighbourhood sizes (Wright 1946 cited in Watt *et al.* 1977), which estimate how many surrounding conspecifics an individual could possibly mate with.

7.4.4 Effects of some aspects of landscape connectivity on dispersal in *C. mercuriale.*

With regards to landscape connectivity, this study provides some evidence that the probability of dispersal in *C. mercuriale* may depend on aspects of landscape structure such as the distance between patches and the type of intervening habitat. There was a significant correlation between the probability of dispersal and distance between pairs of sites for both within and between-patch movements. Similarly, Conrad *et al.* (1999) found that the greatest number of dispersal events occurred between the two ponds that were closest together in his study system. Thus, it is expected that for *C. mercuriale*, as with many species of butterflies (Thomas & Hanski 1997), isolation will negatively affect patch occupancy (with regards to both colonisation of empty habitat and population persistence). Indeed, Roske (1995) found that, in the Upper Rhein region, a high proportion of population extinctions occurred in regions that were isolated from other populations and suggested that reintroduction may be unsuccessful in such areas. Generally rare butterflies in Britain are those that are restricted to large, non-isolated habitat patches, whilst small and isolated patches remain vacant (Thomas *et al.* 1992)

Once a more detailed habitat definition has been obtained for *C. mercuriale* in Britain (Chapter 2), spatially explicit modelling to predict habitat occupancy in relation to habitat area (and quality) and isolation should be carried out.

The habitat between locations seemed to influence dispersal at short to medium distances since, in Mynydd Preseli, movements within the stream were more likely than between-patch movements at a given distance category. This suggests that the valley mire habitat between patches constituted a greater barrier to dispersal than continuous stream habitat. Habitat specific movement rates have been found in other odonates. Pither (1998) found that *Calopteryx maculata* moved more rapidly (from breeding streams) through neutral, pasture habitat than through forest habitat which was used for foraging. In a sympatric species, *Calopteryx aequabilis*, that forages in forest habitat less consistently, no difference was found in movement rate between habitats. Indeed, *Calopteryx maculata* move over a larger area in fragmented landscapes where pasture separates forest and stream resources patches than in unfragmented landscapes where no such separation occurs (Taylor & Merriam 1995). Jonsen (2000), by way of simulation models based on these empirical data for both species, showed that these medium scale movement behaviours could be used to predict broader scale patterns in these species' distribution in heterogeneous landscapes. In addition, the occurrence of a small number of between-patch movements across tall scrub boundaries in the New Forest study system suggests that dispersal is possible across scrub boundaries, if infrequent (Jenkins 1998). Emigration rate should be examined experimentally in a range of patches or streams differing in their proportion of boundary covered by scrub or tall vegetation. Such an approach revealed that emigration in the Glanville fritillary (*Melitaea cinxia*) increases with the proportion of the patch boundary bordered by open fields (Kuusaari *et al.* 1996). Interestingly, Hansson (1991), in a review of dispersal traits across a wide range of plant and animal species, found that specialists (with regarsd to resource or habitat use) tend to be more affected by boundaries (in terms of a reduction in the likelihood of dispersal) than generalists. It would be interesting to compare the effect of boundaries on dispersal in a range of odonates across the stenotopic-eurytopic spectrum. More specifically, further work is required on habitat specific movement rates and on resource use in *C. mercuriale* to determine what type of management will facilitate movement between resource patches in both heathland and chalkstream populations of this species.

Unfortunately, landscape structure with regards to the configuration of sampled and unsampled habitat also influences the detectability of dispersal (Solbreck, 1980). It has already been discussed above how differences in the maximum interpatch distance resulted in an underestimation of the dispersal ability of *C. mercuriale* in previous studies. In addition, when the New Forest data were corrected for the theoretical probability of recapture at each distance, the probability of movements of more than 1 kilometre increased from 0.09% to 0.25% of movements and the mean movement increased from 39 to 58m. Stettmer (1996) similarly found that such a correction increased estimates of mean movement in two calopterygid species from 135 – 189m.

Thus it is difficult to ascertain whether differences in landscape connectivity (differences in the amount of scrub, type of habitat between patches) or in the configuration of sampled and unsampled habitat are responsible for the differences in the rate of dispersal observed between the two sites in this study. In the New Forest a much lower proportion of individuals moved between sites than in Mynydd Preseli. The availability of numerous patches close to the natal patch and in a range of directions seemed to favour between-patch movement in Mynydd Preseli. Within some species, more extensive dispersal has been found in patches linked by linear landscape features or corridors of suitable habitat (see Mann 1995 for a review) probably because per capita mortality of dispersers is reduced. This may occur by chance when corridors of suitable habitat link patches. In addition, even when patches are linked by unsuitable habitat, dispersal mortality may be reduced because individuals are better able to use linear features to predict the location of suitable patches of habitat. However, simulations in some model systems suggest that dispersal rates of individuals within corridors are much lower than those of individuals in mainland patches (Travis & Dytham 1999), especially if the corridors are long and thin (e.g. streams). More empirical data are needed on relative dispersal rates in landscapes with corridors (of suitable and unsuitable habitat) versus those without and on how individuals perceive habitat patches using proximate cues. It may be that species such as *C. mercuriale* that inhabit unlinked patches of mire on some sites and patches linked by streams on other sites may provide suitable model systems for such investigation. In addition, these phenomena may lead to cross species differences in dispersal ability, say between pond-dwelling odonates (that inhabiting scattered patch arrangements) versus stream dwelling odonates (that inhabit linear patch arrangements).

Aspects of landscape connectivity not considered here that may have a significant effect on dispersal include habitat quality and stability. In calopterygids, Stettmer (1996) found that individuals were less likely to disperse in favourable habitat. Mechanisms that reduce dispersal will be favoured by natural selection particularly when habitat quality is stable. For example, among lake-dwelling *Enallagma* species, McPeek (1989) found that larvae of three of the species required the presence of fish for survival whilst two did not. The four species living in constant favourable conditions, of either fish-containing or fishless lakes had limited dispersal due to a tendency to remain at the natal lake (individuals could not directly detect fish-containing versus fish-less conditions). In contrast, in *Enallagma ebrium,* a species living in winterkill lakes that cycle between the fishless and the fish-containing condition (that permits larval survival), a substantial number of individuals dispersed away from the natal lake. There is anecdotal evidence for dispersal within a habitat patch by *C. mercuriale* due to temporal changes in vegetation or water availability (Chapter 2). It would be interesting to investigate whether this species' tendency for between-patch dispersal depends on the temporal stability of the habitat.

7.4.5 Likelihood of colonisation of empty habitat and expected degree of dispersal between populations

Pollard (1993) defined butterfly mobility on the basis of a range of dispersal traits including movement within the natal patch, emigration rate from the natal patch, and maximum colonisation distances. *Coenagrion mercuriale* is similar to butterflies at the sedentary end of this spectrum such as *Plebejus argus,* (Thomas & Hanski 1997) in that it has low rate of movement within continuous areas of habitat (average > 25m), low emigration rates (1.3-11.4%) and low colonisation distances (approximately 1km). Thus for *C. mercuriale*, within and between-patch dispersal traits are correlated as expected in species in which flight is multifunctional (but also found in some orthopterans (Kindvall

1999). It is necessary to consider whether these dispersal traits are sufficient for colonisation events to occur.

Extinctions and colonisations are rare events in most species and are thus hard to directly observe (Imms & Yoccoz 1997; but see Nieminen *et al.* 2001 for an example). In some species, long term distributional records have been analysed to examine the factors affecting extinction and colonisation. However, since British *C. mercuriale* populations have been newly recorded in the last two decades and recorder effort has varied between regions and time periods (Chapter 2) there is only anecdotal evidence for colonisation and extinction in this species.

However, a mismatch has been found between field estimates of long distance dispersal and indirect evidence from colonisation events in several butterflies (Hill *et al.* 1996; Lewis *et al.* 1997; Guttierez *et al.* 1999). For example, *Hesperia comma* disperses up to a maximum of 1km but colonisation events have been observed at 8.6 km from source populations (Thomas & Hanski 1997). Even, in *Plebejus argus*, a more sedentary species, colonisation has occurred over distances exceeding the maximum dispersal distance and there is detectable genetic differentiation between populations (Lewis *et al.* 1997). Thus in *C. mercuriale* too, actual colonisation distances are probably greater than field observed maximum dispersal distances. The observation of the same maximum dispersal distance in a study covering only a small proportion of the flight period in 1998 (Thompson & Purse 1999) and the finding of individuals up to 3km away from closest known reproductive habitat in Germany (by Jentzsch & Norgall (1988) cited in Hunger & Roske 2001) supports this suggestion. In additon colonisation events may have occurred at two British sites, Horsebush Bottom (Jenkins 2001) and Roundhill (pers. obs. 1998) which were 0.5km and 2.7km respectively away from source populations.

Functions were fitted here to dispersal distributions to try to predict long distance movement beyond the range observed in the field. Exponential decay functions have been used to estimate migration rates between patches in spatially explicit models of butterflies (e.g. Hanski *et al.* 1994). As for other odonates (Stettmer 1996; Conrad *et al.* 1999), a negative exponential function was found to best fit the relationship between probability of dispersal and distance in *C. mercuriale.* However, the fit obtained was a statistical artefact and this function vastly underestimated the probability of long distance dispersal even within the field observed range of dispersal distances (*cf* Stettmer 1996). Similar problems will arise when fitting dispersal functions to data for any organism where a large number of individuals are recaptured at short distances from their natal patch.

Thus site configurations were examined in Britain to qualitatively describe the likelihood of colonisation events. Within large clusters (such as the New Forest, Itchen and Test valleys, and Pembrokeshire) there is a high probability that sites that became empty would be rapidly recolonised and dispersal events would be frequent. In small isolated clusters (such as St David's, Devon, Dartmoor and Gower) dispersal and colonisation events would occur rarely (and only if the maximum dispersal distance is indeed further than that observed in the field). In addition, due to the greater distances between sites, the per capita mortality of dispersers will be greater in populations within smaller clusters. As emphasised in Section 7.1, long term population persistence does not only depend on one-off colonisation events. Several dispersal events may be required to 'rescue' populations from stochastic or genetic extinction. For example, wide variation in population numbers and bottlenecks increase extinction risk due to inbreeding depression in small populations unless alleviated by very high population numbers (Dunham *et al.* 1999) which may only be provided by dispersal. Thus small isolated clusters of populations of *C. mercuriale* may be at risk from extinction due to the rarity of dispersal events.

The rate of dispersal has been examined here in two large stronghold populations of *C. mercuriale* that are relatively well connected to other areas of suitable habitat. There is some evidence from butterflies that dispersal rates can vary within a species due to landscape connectivity (discussed above) but also with density of individuals. For example, *Erynnis tages* is reasonably mobile with maximum dispersal distances of 660m and 24% of individuals moving more than 100m. However, since most source population sizes were small (less than 200m at peak) then the number of potential colonists in the system was small and colonisation was limited (especially in isolated sites) and local extinctions were frequent (Guttierez *et al.* 1999). In contrast, due to its larger population sizes, *Plebejus argus* produced a substantial number of colonists despite low probabilities of migration per individual (Lewis *et al.* 1997). In *C. mercuriale*, population sizes are generally smaller within the small clusters listed above such that the frequency of dispersal events may be even lower in these clusters due to a low absolute number of migrants. In some species, higher dispersal rates have been found in small populations (Hill *et al.* 1996; Sutcliffe *et al.* 1997; Kindvall 1999). Whilst this may act to increase dispersal rates in small patches in small clusters, the per capita mortality of dispersal may deplete the natal population to a great extent and lead to extinction. Thus it seems that *C. mercuriale* populations in small clusters will be particularly prone to extinction. Indeed, in butterfly systems, Thomas (1997) stated that a metapopulation rarely persists for very long at less than 10 populations but usually does so for extended periods at more than 20 local populations.

In addition, rate of dispersal from a patch may depend on the interaction between habitat quality and habitat selection behaviour. For example, in a stream-dwelling ephemeropteran, *Baetis bicaudatus*, the availability of rocky substrates protruding above the water surface determined the rate of local oviposition rates. When such substrates were unavailable, females were forced to disperse from their natal patch further upstream (Peckarsky *et al.* 2000). It would be interesting to investigate the relationship between availability of oviposition habitat (such as that described in Chapter 5) and rates of dispersal in populations of *C. mercuriale.*

Cowley (2001) has found that sedentary species of butterfly occur at higher densities than intermediate or highly dispersive species and thus infers that such species will have lower minimum habitat area requirements. For example, *Plebejus argus* can occupy smaller habitat patches than the more dispersive *Hesperia comma* (Thomas & Hanski 1997). However, before concluding that *C. mercuriale* will have small minimum habitat area requirements, being as sedentary as *Plebejus argus*, it is necessary to consider how odonates differ from butterflies in their use of resources. Most stages of a butterfly's life cycle and adult activity are restricted to one or two resource types i.e. one or a few plants or one or two types of vegetation structure. In contrast, odonates require a range of resource types (*cf* Conrad *et al.* 1999) including vegetation areas around the stream for roosting and foraging areas, perching and breeding areas, oviposition substrates and larval habitat. Thus odonates in general may have much larger minimum area requirements than butterflies and may be less able to survive in small, isolated patches of habitat. In addition, when habitat consists of transient or successional vegetation, as for *C. mercuriale*, much larger minimum habitat areas may be required (Thomas & Hanski 1997). Overgrowth of vegetation constitutes the main cause of population decline and extinction in this species (Chapter 2).

Buchwald (1989) suggested that *C. mercuriale* shows more conservative dispersal behaviour on the edge of its range in Germany and cited the constancy of small populations in isolated areas of limestone marsh of alpine range. There are no empirical data on mobility in populations across the range of *C. mercuriale.* However survival, general activity and breeding activity are negatively affected by adverse weather conditions on the British range edges of this species (Chapter 6). Given the multifunctionality of flight, dispersal will probably be similarly negatively affected by adverse weather conditions at this northern range edge. For example, Watt (1977) found that some *Colias* species fly into the air only when the temperature is suitable for continuing activity. This not only influenced general activity but also affected rates of movement in relation to weather and microclimate.

7.4.6 Dispersal mortality, and survival and recapture rates in populations with permanent emigration

Estimates of survival probability in the Mynydd Preseli study site (0.88 on average) were similar to those obtained on Aylesbeare Common (Chapter 6 - 0.92 on average), a small isolated population. Again, no sex bias in survival was found, males were much more likely to be recaptured than females, and large individuals were more likely to be recaptured than small ones. Again, survival and recapture probabilities were both time-dependent and thus probably weather dependent though again the addition of specific weather variables did not provide better models than time dependence. Thus despite the downward bias in survival estimates due to permanent emigration (Frederiksen & Bregnballe 2000) from the study area in Mynydd Preseli, similar variables were found to influence survival and recapture probabilities. However, since per capita mortality rate of dispersal is the important demographic process in local patch dynamics, it is important to try to estimate this in further investigations in *C. mercuriale.* Frederiksen (2000) used combined resighting and recovery data to produce unbiased estimates of survival and emigration. Despite recent success in recovery of roosting individuals of *C. mercuriale* using ultraviolet marking methods and night-time recovery (Hunger & Roske 2001), it is unlikely that sufficient recovery data will be obtained in the field for this, or indeed any, insect species (Chapter 6).

An alternative approach uses maximum likelihood methods with capture histories from multisite mark recapture studies to produce separate estimates of mortality within a patch and mortality during dispersal based on the assumption that only the latter is affected by isolation from the source patch (Hanski *et al.* 2000). Since these models require data from 10 or more discrete populations and are spatially explicit (with respect to both patch area and isolation), they were inappropriate for the data discussed in this chapter. It is recommended that future mark-recapture studies of *C. mercuriale* be designed with the application of these models in mind.

Given the drawbacks of field estimates of dispersal highlighted in this discussion, the use of population specific molecular markers would be essential in determining the actual level of dispersal between populations of *C. mercuriale* (*cf* Waser & Strobeck 1998).

7.4.7 Phenotypic correlates of dispersal

There was no sex bias in dispersal with regards to distance moved within patches or probability of emigration between patches in *C. mercuriale* (*cf* Stettmer 1996; Conrad *et al.* 1999), as expected for a non-territorial, scrambling species. Sex biases in within-patch dispersal have only been observed in species where males hold territories and thus the relative benefits of remaining in the natal patch versus dispersal differ for males and females or for resident versus introduced males (Henderson & Herman 1984). For example, Waage (1980) found that females were less site specific and ranged further in each day than male *Calopteryx maculata* presumably because females are comparing the oviposition sites in territories held by males. In a non-territorial scrambling species, mate location is probably less likely to be the proximate cause for dispersal than foraging or inbreeding avoidance. It has also been assumed that mature females, spending less time at the breeding site (visiting the breeding site less frequently and for shorter periods) will be more likely to be passively dispersed between patches. However, this assumption that dispersal is more likely in individuals that spend more time roosting remains untested.

In contrast to Michiels & Dhondt (1991) who found an increase in dispersive activities late in life in *Sympetrum danae*, no age bias in dispersal has been found in mature adult *C. mercuriale*. The recapture rate of tenerals was too low to assess dispersal during the maturation phase in *C. mercuriale*. It has been assumed that the teneral adult stage is the main dispersive stage in odonates (Parr 1976; Henderson & Herman 1984; Utzeri *et al.* 1984), although Conrad *et al.* (1999) found no difference in dispersal between teneral and mature adults in 11 pond-dwelling odonates. This assumption is made again because teneral individuals spend time away from the breeding site to roost during maturation (see above) and partly due to the observation of a 'maiden flight' (Corbet 1980) in tenerals. Although dispersal is thought not to occur in larval odonates, recent work using harmonic radar to tag and monitor movements of stream-dwelling caddis flies has deduced that dispersal in the larval stage of some aquatic insects is more extensive than previously thought.

A size bias in dispersal would be expected if dispersal was density dependent because small larvae that had been subjected to poor conditions (or high densities) may have more to gain from dispersal. (Crowley *et al.* 1987). This expectation is not supported by empirical studies on odonates. Anholt (1991) subjected larvae to a wide range of competitive regimes, returned them to the natal pond and allowed them to disperse. He found that dispersing individuals were heavier than non-dispersing ones. Thompson (1991) found no difference of any kind between dispersers and non-dispersers in *Coenagrion puella.* A size bias in dispersal was not found consistently here in *C. mercuriale.*

Since few phenotypic characteristics of dispersers versus non-dispersers were measured here, it is not possible to conclude that dispersing individuals constitute a random sample of the natal population in *C. mercuriale*. Neither is it possible to speculate on the trajectory of evolution of dispersal related traits in this species. However, it would be interesting to investigate whether differences in flight morphology exist between *C. mercuriale* populations that differ in their degree of isolation and habitat area and indeed whether these differences are heritable (*cf* Thomas *et al.* 1998). For example, Taylor & Merriam (1995) found that increased wing lengths, wing widths and thoracic weights of *Calopteryx maculata* in fragmented versus non-fragmented populations. Whilst this study found that fragmentation selected for a more mobile phenotype studies on butterflies (discussed in Van Dyck & Matthysen 1999) have suggested that less mobile phenotypes are found in isolated habitats.

7.4.8 Management to facilitate dispersal in *C. mercuriale*

Detailed management recommendations for *C. mercuriale* are given in Chapter 8. However, there are specific recommendations that arise from this study of dispersal. Firstly, the likelihood of colonisation events should be maximised by active management of empty habitat within 1-3km of other populations particularly within large clusters of sites. Empty patches should be managed in as many different directions and distances from the source populations as possible. Scrub boundaries should be removed (with the retention of some shelter) between populations to promote frequent exchange of individuals and also between resource patches (e.g. roosting and breeding areas) within a patch. Where possible, habitat between populations and resource patches within sites should be encouraged to develop as valley mire or wet heath since these may be more conducive to stepping-stone dispersal than grassland or dry heath found between many sites (Chapter 2). Such stepping-stone movements have allowed some butterfly species to colonise sites at greater distances than their maximum single dispersal distances (Thomas *et al.* 1992; Lewis *et al.* 1997). Control of vegetation growth and water levels on all sites will maximise the area of suitable habitat and maintain the temporal stability of the habitat. Population abundance will increase and in turn act as a buffer against extinction through stochastic events or inbreeding depression, and increase the absolute number of potential dispersers within a system.

An early version of the species action plan for *C. mercuriale* (HMSO 1994) discusses the possibility of re-introduction of *C. mercuriale* to empty habitat patches in Britain and sites suggested subsequently include those near to small clusters e.g. Venn Ottery Common, near the Devon cluster. Oates (1990) found that for butterflies, such re-introductions rarely succeed in the long term especially in single or small groups of habitat patches. Introduced populations may have to exceed some threshold before establishment is likely or may require frequent dispersal events for persistence. Thus in most cases largest and highest quality and least isolated patches should be targeted

(Thomas & Hanski 1997). It is thus recommended that management effort be directed towards maximising the likelihood of natural colonisation events instead (as above). Persistence of extant small populations in smaller clusters could potentially be enhanced by the artificial introduction of individuals from other populations although more direct evidence of the 'rescue effect' (due to an increase in abundance) and 'genetic rescue' may be required before this action can be justified.

Chapter 8 Discussion

This chapter discusses some of the main findings of this thesis, outlines appropriate monitoring of the species and its habitat and recommends management regimes for *Coenagrion mercuriale* in Britain.

8.1 Ecology of *C. mercuriale.*

Coenagrion mercuriale was found to be worthy of individual species protection since it fulfilled several of the criteria used to assess rarity (Gaston 1994; Rabinowitz *et al.* 1986; Schoener 1987). Chapter 2 revealed that *C. mercuriale* is restricted in its national and global distribution probably by climatic variables including temperature. It has a discontinuous distribution within its biotopes and has declined more than 30% in its British distribution in 15 years (at the 1km grid square resolution). *Coenagrion mercuriale* is a stenotopic odonate (sensu Steytler & Samways 1995) being highly sensitive to a number of habitat factors such as sunlight, shade, water flow and aquatic and bankside vegetation structure. Thus this species is not only restricted to two fragmented biotopes but the specificity of its habitat requirements restricts its distribution within the biotope at a coarse scale, and within a watercourse at a smaller scale.

Many of the habitat features used by the species at this broad scale seemed to reflect a requirement for a thermally advantageous microclimate e.g. use of shallow, sun-exposed, permanently flowing waterbodies. This requirement restricts *C. mercuriale* to an early successional stage of its biotopes and, in turn, its habitat is temporally unstable. Many of the thermally advantageous habitat features used by populations at a broad scale, were also selected by individuals at a small scale - during emergence and oviposition (Chapter 5). For example, both *C. mercuriale* populations and ovipositing adults were associated with areas of dark peat or silt that absorb radiant heat and thus warm quickly in sunlight. Soft-stemmed, submerged and semi-emergent herbs were favoured for oviposition whilst tall emergents with rigid upright stems were favoured for emergence. Whilst these plant species probably acted as direct cues as to their suitability for either of these two processes, there is some evidence at a broad scale (Chapter 2) that adults were associated with perennial herbs that indirectly indicated the permanence of the water flow and high minimum winter temperatures.

Chapters 3 and 4 revealed that British edge-of-range populations of *C. mercuriale* differ from core populations in aspects of development. In Britain, *C. mercuriale* is semi-voltine with no splitting of a year group into cohorts whereas in some core populations, larvae can complete their development in one year (Thelen 1992). The growth period of the larvae was restricted to between April and October whilst further south in its distribution this period would presumably be longer. No diapause was found in the egg stage and there was no evidence that entry in to the final three instars depended on a series of rising temperature thresholds. A facultative diapause in the penultimate instar may synchronise emergence in this species.

The flight period is shorter in Britain than in mainland Europe and there was evidence that the process of emergence depended on temperature since, after controlling for season, sunlight had a significant effect on daily emergence. In addition, there is evidence that larval *C. mercuriale* can postpone emergence following metamorphosis until conditions are favourable.

Climatic variables influenced *C. mercuriale* in other ways affecting survival, whether individuals were present at the breeding site and whether they engaged in reproductive activity given that they were present (Chapter 6). Adverse weather conditions shortened the opportunity for activity to such an extent that males could not cycle between mates faster than females and individuals did not vary in mating efficiency. Thus mating success of both males and females depended on the number of hours spent at the breeding site and the proportion of an individual's lifespan made up of bad weather. It is postulated that sexual selection may have less influence on reproductive success or may act on less costly traits in edge-of-range populations of thermophilic species. In such populations the proportion of mated individuals may also be low reducing the effective population size. Empirical data on mate location and predator escape behaviour and flight-related morphology are required within the framework of habitat fragmentation (Van Dyck & Matthysen 1999) and in the context of distance from range edges. In addition, *C. mercuriale* individuals spent the majority of their time in vegetation surrounding the breeding stream due to adverse weather conditions, highlighting the importance of shelter belt vegetation as a resource in edge-of-range populations.

Whilst some other insects that exploit temporally or spatially unstable habitats have been found to be highly mobile (e.g. *Ischnura pumilio* - Fox 1994), *C. mercuriale* was found to be relatively sedentary in field experiments (Chapter 7). Field experiments often underestimate colonisation distances. Thus it was deduced that the field observed dispersal rate was probably sufficient for colonisation events and exchange of individuals to occur frequently between populations in large site clusters in Britain (Mynydd preseli, New Forest, Itchen and Test Valleys). In addition dispersal seemed highly dependent on aspects of landscape structure (rather than phenotype) such that higher rates of dispersal could be facilitated with appropriate management (see Section 8.3).

Mortality was investigated at several stages in the life cycle of *C. mercuriale*. At the egg stage, mortality during the hatch period was found to average 14% (but was highly variable - Chapter 5) whilst at emergence it was found to be low (around 5% - Chapter 3). Low recapture rates after the adult pre-reproductive period may suggest mortality may be substantial during this period whilst, in the mature adult stage, it was consistently low (Chapter 6 and 7). Given that the larval stage makes up 95% of the lifespan of a semi-voltine species, the highest percentage mortality probably occurs in this stage. Although all larval instars have been observed to use submergent herbaceous vegetation both in Britain (Chapter 4) and Germany (Thelen 1992), examination of other habitat features used by this stage (and by the egg stage) is essential, Given that *C. mercuriale* occupies small streams that are heterogeneous in vegetation and physical structure and is highly sensitive to a number of habitat features, empirical field investigation of larval habitat use will be difficult and should be combined with controlled choice tests in the laboratory. Following such investigation, each of the broad scale habitat preferences (Chapter 2) should all be explicitly attributable to small scale habitat use by the different life stages of *C. mercuriale*. In addition, it would then be possible to map habitat (or resource) patches for this species and investigate the effects of habitat area and isolation on patch occupancy within a grid system. Distinctions between habitat and non-habitat, often used in metapopulation models (Thomas & Hanski 1997), will be hard to apply to odonates given the range of resources used, and to *C. mercuriale* given that it is stenotopic. Thus habitat quality (and, in turn, stability) should eventually be included in models of patch occupancy (and persistence). Thomas (1999) recommends the combination of habitat area and distance into a single weighted distance function (neighbourhood) but some measure of patch quality in a grid square (compared to some optimum habitat quality) could also be incorporated. The effect of aspects of landscape connectivity on a range of behaviours including dispersal could then be investigated.

8.2 Monitoring of *C. mercuriale*.

The UK Biodiversity Action Plan for *C. mercuriale* (HMSO 1995) has three actions explicitly related to monitoring and management. These are 'encourage sympathetic management of sites' - Action 5.2.2; 'ensure hydrology remains favourable'- Action 5.2.3; and 'Monitor sites, seeking to identify threats'- Action 5.5.2. The achievement of the first two management actions is discussed in the next section. Here, strategies for monitoring of *C. mercuriale* are considered. Surveillance is a continued programme of surveys designed to provide a time series of observations whilst monitoring is intermittent surveillance, carried out to establish whether a pre-defined standard is being met (Hellawell 1991; JNCC 2000).

When sites are designated as SSSIs, as part of the Natura 2000 series of sites (SPAs, SACs) or as Ramsar sites (wetlands designated under the Ramsar Convention), species or habitats of conservation importance on the site are identified as interest features for that site. These features will have one or more attributes that define favourable condition on a site and should be monitored. For example, for a species this may be populations size or structure, habitat requirements or distribution (JNCC 2000). The Common Standards Monitoring model defines broad upper and lower thresholds for these attributes that define favourable condition. Action is triggered when the site falls outside the lower threshold with respect to a particular attribute. This thesis not only provides some information on how best to observe population size or structure of *C. mercuriale*, it also provides information on the habitat attributes required by the species.

8.2.1 Counting *C. mercuriale* on monitoring visits.

Firstly, it is necessary to consider which life stage of *C. mercuriale* to count. Although, habitat use by larvae will more accurately reflect the requirements of the majority of the life cycle (Section 8.1) and larval sampling can be carried out at any time of year, larvae are extremely difficult to sample quantitatively and time-consuming to identify in comparison to adults. Exuviae of *C. mercuriale* are also very difficult to find given the tussocky vegetation structure on most streams. In contrast, the mature adult stage is easy to sample and identify (*cf* butterflies - Pollard, 1991) and also reflects the output of individuals after mortality (mediated by habitat condition) sustained in the egg, larval and pre-reproductive adult stages. Since exuviae and larvae are hard to find and identify, it will be difficult to 'confirm breeding' at a site (as defined for odonates by Smallshire (2000)). However, only on sites with very small concentrations of adults (e.g. peak count < 10) is there a large probability that all individuals could be transient. Confirmation of breeding is only required for these sites.

It was shown in Chapter 3 that the peak emergence at Upper Crockford occurred in mid-July. There is considerable regional and yearly variation in the length and peak of emergence (due to the interaction of season and weather variables) with peak emergence in other regions occurring between the end of June and the end of July (Jenkins 1995; Kerry 1994). Thus to maximise the count of individuals, a monitoring visit should be carried out between early July and mid-July unless surveillance for that region strongly indicate that peak emergence lies outside this period. In Chapter 6, it was revealed that both general and reproductive activity peak at 12am and that the presence of *C. mercuriale* on a day is highly dependent on weather conditions (sunlight and temperature). It is thus recommended that visits be carried out between 11am and 1pm on sunny days with no or little cloud cover, no strong winds (less than Force 3 or 4 on the Beaufort scale), when the temperature exceeds 17°C. It should be borne in mind that, depending on weather conditions, between 25-75% of individuals alive will be present at the breeding stream (Fig. 6.6) such that any count is likely to be an underestimate of the number of individuals alive. In addition, in Chapter 2, absolute population numbers was related to transect counts for Aylesbeare Common, Devon and Upper Crockford, New Forest and indicated that annual population sizes could be underestimated up to ten fold by maximum daily counts. However, these examples should not prompt undue optimism for persistence of populations with maximum counts of less than a few 10's of individuals. To set upper and lower limits for a count as a species attribute for monitoring on a site, consideration should be given to the maximum count of individuals normally supported on a site (or part of a site).

Monitoring of butterflies (Pollard 1991; Pollard & Yates 1993) and other odonates (Brooks 1993) has previously employed a method known as a 'Pollard walk' (Pollard 1977) where a fixed transect is walked through the site, sometimes within a fixed amount of time, and individuals observed within 5m of the fieldworker are counted. For *C. mercuriale*, standardising counts by fixing the time taken for counts may be inappropriate given that the amount of habitat available is likely to vary widely between sites and the habitat is often very difficult to move through (pers. obs.). It is recommended that fixed transects (of a known distance) be walked along waterbodies (or mire where streams are more diffuse) and include areas of both low and high concentrations of individuals. Where streams are less than 5m wide one transect up the stream should be walked but where the stream or mire is up to 10 or 20m wide (e.g. Upper Crockford, New Forest), two or more transects should be walked on different parts of the site - each with separate thresholds for counts of individuals. The time taken to walk transects should be recorded in order to make sure that similar amounts of time are taken on each visit. The order of magnitude of time per unit distance which have been successful on transects is between 20-30 minutes per 50m of stream.

In Britain, the majority of the adult lifespan of *C. mercuriale* may be spent roosting, feeding or sheltering in surrounding vegetation (Chapter 6). Despite this, it is not appropriate to monitor adults during this activity since they are much harder to count in such habitat. The timing of counts within the season and day (given above) should, in any case, ensure the concentration of individuals at the watercourses such that separate transects in shelter-belt vegetation are unnecessary.

Chapter 2 described the limitations of point data in the form of grid references for biological recording. Monitoring visits could simply record that a particular threshold count has been passed at a particular grid reference. When further resources are available for monitoring, it is recommended that counts and habitat attributes on transects are recorded within cells on a grid (at a minimum resolution of 10 by 10m). This grid should overlay a map that at least contains polygons that represent the area covered by the watercourse and the area utilised on previous monitoring visits by *C. mercuriale*. This will facilitate detection of change in counts in response to alteration in particular habitat attributes on the grid and allow comparison in densities of *C. mercuriale* across sites.

8.2.2 Habitat attributes that indicate favourable habitat condition for *C. mercuriale* in Britain.

In Chapter 2, the main threats to the condition of habitat for *C. mercuriale* in Britain were found to be overgrowth of bankside vegetation (27 sites) or channel vegetation (7 sites) and reduction in water availability (22 sites) due mainly to canalisation, artificial drainage, siltation, headward erosion and scrub or tree growth. Four sites were perceived to be threatened by nutrient run-off from agricultural land. Thus, those habitat attributes that relate to vegetation structure and physical features of watercourses are likely to constitute key attributes for *C. mercuriale*. It is also important to focus observational effort on those features (from Table 2.16) which can actually be influenced by management (i.e. not factors such as altitude, temperature, slope, geology) and those that can be perceived easily by fieldworkers.

In light of these considerations, Tables 8.1 and 8.2 present key and subsidiary habitat attributes that generally indicate favourable condition of sites for *C. mercuriale* in heathland and chalkstream biotopes respectively. Given the regional variation shown in some of these attributes (e.g. plant species presence – Chapter 2), a set of attributes, based on the one provided here, should be drawn up for each site on which *C. mercuriale* is an interest feature. The upper and lower limits of attributes suggested in Tables 8.1-8.2. are similarly general. The number of attributes that indicate favourable condition for *C. mercuriale* may be greater than that for other rare species in Britain and thus this species may be more costly to monitor. Since, *C. mercuriale* uses a wide range of resource types (as do other odonates - Chapter 1) and is highly stenotopic, it is difficult to provide a shorter list of attributes that adequately describe favourable habitat

Table 8.1 Key and subsidiary habitat attributes (with suggested upper and lower limits) that indicate favourable condition for *C. mercuriale* on heathland sites in Britain.

Key habitat attributes	*Definition of upper and lower limits for favourable condition*
1. Open, unshaded, shallow lengths of watercourse/mire with permanent discernible flow (approximately 10 cm/s)	Upper limit of extent on site: 100% of watercourse/mire Lower limit of extent on site: % of watercourse/mire covered by such habitat in last survey or at least 50% of watercourse/mire
2. Stream lengths with cover of submerged and semi-emergent, herbaceous macrophytes including some cover of *Hypericum elodes, Potamogeton polygonifolius.*, or *Ranunculus* sp., with some *Carex* sp., or *Juncus* sp.,	Lower and upper limit of cover: 20-80% Upper limit of extent on site: 100% of watercourse/mire Lower limit of extent on site: % of watercourse/mire covered by such habitat in last survey or at least 50% of watercourse/mire
3. Areas of adjacent bankside vegetation with medium height of tussocks and/or medium height of emergents in stream	Lower and upper limit of height 0.2-0.6 m Upper limit of extent on site: 100% of bankside, 50% of ditch Lower limit of extent on site: % of watercourse or bankside covered by such habitat in last survey or at least 30% of bankside Lower and upper limit of scrub/or trees shading watercourse: 0-40% cover
4. Dystrophic to mesotrophic conditions indicated by a lack of areas of watercourse with encroachment of algae (except brown flocculent algae), bacterial film or invasive tall emergents such as *Juncus effusus, J. acutiflorus, J. subnodulosus* and *Phragmites* sp.	Upper limit of extent on site: 25% of watercourse Lower limit of extent on site: 0% of watercourse See above for upper and lower limits of tall emergents
5. Some cover of peat or other organic substrate in watercourse or mire	Upper limit of extent on site: 100% of watercourse/mire Lower limit of extent on site: % of watercourse/mire covered by such habitat in last survey or at least 50% of watercourse/mire
Subsidiary habitat attributes	*Definition of upper and lower limits for favourable condition*
6. Small areas of tall scrub or trees within 20m of watercourse or mire but not on intervening habitat between two areas of population	See above for upper and low limits of scrub on watercourse

Table 8.2 Key and subsidiary habitat attributes (with suggested upper and lower limits) that indicate favourable condition for *C. mercuriale* on chalkstream sites in Britain.

Key habitat attributes	*Definition of upper and lower limits for favourable condition*
1. Open, unshaded, lengths of ditch with slow flow or with moderate flow in central channel and shallow slow-flowing areas at ditch edges	Upper limit of extent on site: 100% of ditch/stream Lower limit of extent on site: % of ditch/stream covered by such habitat in last survey or at least 50% of ditch/stream
2. Ditch edges with broad fringe of herbaceous semi-emergent and submerged macrophytes including some cover of *Glyceria maxima, Mentha aquatica, Rorripa-nasturtium aquatica, Ranunculus* sp. *Veronica* sp.	Lower and upper limit of cover: 20-80% for both emergent and submergent portion Upper limit of extent on site: 100% of ditch/stream Lower limit of extent on site: % of ditch/stream covered by such habitat in last survey or at least 50% of ditch/stream
3. Areas of adjacent bankside vegetation with medium height of tussocks and/or medium height of emergents in ditch/stream	Lower and upper limit of height 0.2-0.6 m Upper limit of extent on site: 100% of bankside, 50% of ditch Lower limit of extent on site: % of ditch or bankside covered by such habitat in last survey or at least 30% of bankside Lower and upper limit of scrub or trees shading ditch: 0-40% cover
4. Mesotrophic conditions indicated by a lack of areas of watercourse with encroachment of algae (except brown flocculent algae), bacterial film or invasive tall emergents such as *Phalaris arundinacea, Solidago canadensis, Filipendia ulmaria* and *Rubus* sp.	Upper limit of extent on site: 25% of watercourse Lower limit of extent on site: 0% of watercourse See above for upper and lower limits of tall emergents
5. Some cover of peat or other organic substrate in ditch/stream	Upper limit of extent on site: 100% of ditch/stream Lower limit of extent on site: % of ditch/stream covered by such habitat in last survey or at least 50% of ditch/stream
Subsidiary habitat attributes	*Definition of upper and lower limits for favourable condition*
6. Small areas of tall scrub or trees within 20m of ditch/stream but not on intervening habitat between two areas of population	See above for upper and low limits of scrub on watercourse

condition. Similarly, monitoring for any stenotopic species in Britain may be more costly. The permanence of the water flow may be a key attribute that is particularly difficult to observe given intermittent monitoring visits, since the area covered by watercourses can contract considerably over summer (Chapter 5). In this regard, small sites especially may warrant more regular surveillance. Large sites on which a range of management regimes are being employed may also be worthy of regular surveillance to provide further information on population responses to these regimes.

8.3 Management recommendations for *C. mercuriale.*

This section describes management practices that are recommended for maintenance of favourable condition of habitat for *C. mercuriale* in Britain. General strategies for employment of each management practice are given with elaboration of separate strategies for heathland and chalkstream biotopes or for different regions as necessary. A number of the proximate habitat features (section 2.4.) and habitat attributes (section 8.2) for *C. mercuriale* are influenced by each management practice and they are not referred to explicitly here. When implementing management practices, it will be necessary to bear the habitat features and attributes in mind more specifically to ensure that favourable condition is achieved.

8.3.1. Grazing

The use of moderate grazing regimes should reduce establishment of scrub and invasive emergents on most sites. As discussed in Chapter 2, the type of grazing animal used influences the structure of the resulting sward (Bacon 1990; Kirby 1992). Grazing by heavier animals such as cattle or horses is recommended to produce poaching of watercourse margins and diversity of tussock structure favoured by *C. mercuriale*. Cattle, in particular, will graze further into boggy areas than other animals (Bacon 1990). An open structure is maintained on sites in Mynydd Preseli and the Gower by sheep grazing such that a change of grazing stock would be counter-productive.

When deciding which stock to use, an awareness is also required of the sward compositions produced by different grazing animals in different biotopes. As stated in Chapter 2, cattle grazing on wet lawns reduces *Molinia* dominance but maintains cover of *Juncus acutiflorus* (Sanderson, 1998). On Aylesbeare Common in Devon, burning of *Molinia* had to be carried out prior to grazing before animals would feed on *Schoenus nigricans* since cattle prefer the former species over the latter (Kerry, 1994). In addition, on this site, where animals are forced to feed only on sedges and rushes on watercourses, it was necessary to supplement their diet with high protein block. The number of animals required to achieve moderate grazing pressure will depend on how accessible the watercourse is to such animals. Obviously watercourses should not be fenced off from grazing animals, perceived as a threat on several sites by Stevens & Thurner (1999), and fences could be employed to concentrate stock on areas of watercourse containing *C. mercuriale* (e.g. Aylesbeare common -Kerry 1999). Where access is limited by the height of the stream banks above the water surface, reprofiling is recommended unless the banks are providing shelter for adults.

The time of year for which stock should be grazed will depend on the accessibility of the site, the biotope and the number and type of animals used. On most sites cattle seem to be grazed for some period between April and October, whilst horses and stock on unenclosed commons (reagrdless of type) are grazed all year round. After instigation or alteration of changes in grazing regime, more frequent monitoring visits may be required to check that favourable condition is being maintained.

8.3.2 Vegetation clearance

8.3.2.1.Clearance of bankside vegetation and scrub

Bankside plant species which commonly shade or choke watercourses occupied by *C. mercuriale* include *Myrica gale, Juncus* sp., *Molinia caerulea, Schoenus nigricans* and *Sparganium erectum* (Chapter 2). Whilst some of these plant species will be prevented from attaining excessive cover or height by grazing, some clearance of vegetation may be required to supplement this practice. On heathland sites, hand clearance of *Myrica gale* may be required since is unpalatable to stock (particularly cattle) . Where hand clearance of scrub, trees or tree stumps is necessary, it is recommended that, to preserve a degree of shelter, this practice is employed only on areas of wet heath, valley mire or areas within 5 of a ditch edge on chalkstream sites. In some sites, where trees or scrub pose a risk to water availability (section 2.3.4), due to excessive growth and transpiration, removal is recommended.

On chalkstream ditches, some mowing or cutting of bankside herbs and rushes may be beneficial within short stream sections and on a rotational basis. On meadow streams and ditches in south-west Germany, adult abundance at the watercourse was compared adjacent to cut and uncut sections of bankside. Cut sections were not used for the first few weeks after mowing but, after longer periods, these sections contained the largest populations of *C. mercuriale* (Roske 1995). Surveillance should be carried out to investigate the effect of cutting in British Chalkstream sites before this management practice is employed more broadly.

8.3.2.2 Clearance of channel vegetation

Wholesale removal of the channel vegetation by mechanical means is not recommended as is has been found to adversely affect populations of many aquatic macroinvertebrates (Dawson *et al.* 1991) and populations of *C. mercuriale* in particular (Winsland 1994). Mechanical excavation of the channel on meadow brooks and ditches in south-west Germany produced dramatic reductions in population of *C. mercuriale* in the first year after clearance. Signs of population recovery to previous levels were evident by the third year (Roske 1995). This recovery was most likely due to spread of populations from uncleared ditches into the newly excavated ditch and not due to recovery of the population of the ditch itself. Thus channel clearance should not be carried out on small, isolated ditches.

Intermittent selective cutting by hand is recommended for heathland sites. Larger watercourses on chalkstream ditch systems may tolerate selective mechanical cutting. Strange (1999) recommends cutting aquatic vegetation in the central area of a ditch whilst retaining a broad fringe of emergent vegetation. Cutting should be performed yearly, on a rotational basis on short, adjacent (i.e. not isolated) stream sections. Consecutive cuts should not be carried out in the same section within a 3 to 5 year period. Spoil from clearance of vegetation or silt in any site should be deposited on only one bank or area of the site (D. Winsland pers.comm; Strange, 1999) to prevent encroachment of *Myrica gale.*

8.3.3. Burning

Burning has been employed in winter on 13 (once illegally) of the heathland sites considered in Chapter 2. Controlled burning has long been used to enhance the quality or grazing on heathland (Tubbs 1974). An example of the use of burning on a *C. mercuriale* site in conjunction with grazing has already been described in section 8.3.1. In addition, some expansion of population was observed on Hartland Moor following burning in 1999 (DSDSG 2000). However, on three sites, burnt gorse overhanging runnels was perceived to be a threat to *C. mercuriale* habitat and was associated with a lack of aquatic vegetation (Stevens & Thurner 1999). Cordrey (1997) states that burning may damage *Sphagnum* and pollute watercourses. Many heathland sites occupied by *C. mercuriale* are small and burning carries the threat of loss of both aquatic vegetation and shelter-belt vegetation on a substantial portion of a site. It is also detrimental to other components of the fauna such as vertebrates (Webb 1990). Thus, it should only be employed in small patches on large sites, when there is strong evidence that burning has produced a positive effect in the past and when other methods of maintaining open heathland have proved unsuccessful. Whenever burning is carried out, burnt vegetation should be removed from the site to minimise pollution.

8.3.4. Watercourse alteration

To maintain water availability on water meadow ditch systems, drop board weirs can be used to maintain high water levels in spring and summer and to create shallow surface flooding in winter. These are more effective than semi-permanent wooden weirs on sites with cattle since poaching around the ends of the boards prevents control of water flow. On one heathland site, the use of weirs has been advocated, to recreate a system of small runnels (e.g. Afon Brynberian - Skidmore, 1996). However the shallowness of most heathland streams may preclude the use of such structures. On heathland sites that receive a man-made water supply, it is imperative that the supply be maintained or enhanced (e.g. Povingdon, Dorset). It is recommended that the canalisation, drainage, abstraction and dredging of watercourses and peat cutting near watercourses are avoided.

Given that loss of larval population results from dredging and digging operations, watercourse restructuring in areas of extant population should be undertaken with caution, especially on small watercourses occupied on heathland. As described in Chapter 2, new runnels and ponds excavated on a few heathland sites have produced population expansions (Kerry 1994). It is recommended that such action is only carried out in areas presently unused by the species (but adjacent to utilised areas) or on a small proportion of the watercourse on large sites.

On large water meadow ditch systems, construction of shallow berms (0.6-0.9m wide) in the bank profile will produce areas of shallow watercourse that can be colonised by semi-emergent and emergent herbs (Strange 1999). As well as providing structural components of the vegetation required by *C. mercuriale*, the growth of such vegetation will slow water flow and may help prevent headward erosion and siltation. Berms can be created by infilling ditches to the required width, held in place by wooden faggots held in place with stakes (Strange 1999).

8.3.5 Water quality

Nutrient run-off from farmland should be minimised (through bans on use of artificial fertilisers) in catchments of watercourses containing *C. mercuriale* populations. This will prevent eutrophication and in turn, encroachment of tall emergents, algae or bacterial films into watercourses. Sheep dip should not be dumped in catchments of watercourses. Care should be taken that wormers (such as Ivomectin) and other drugs that are likely to be excreted by grazing animals are not generally toxic to invertebrates (Strange 1999). Where watercourses are fed by clay pit outflow, levels of suspended solids should be maintained below 25 mg/litre (M. Drake pers.comm.).

8.3.6 Adjacent land use

On meadow ditch systems where improved grassland is adjacent to watercourses, the latter may remain ungrazed since stock will prefer the nutrient enriched grass (Evans 1989). In meadow brooks and ditches in Germany, due to the preferences for adjacent land use described in section 2.3.5, the maintenance of a protection strip, a minimum of 10m wide of extensive grassland around watercourses has been recommended (Buchwald *et al.* 1989). Where possible, agricultural land adjacent to sites in Britain should also be used extensively. If the conversion of the entire adjacent field to extensive use is inappropriate, the maintenance of a protective strip of at least 20m, on either site of the watercourse, is recommended.

8.3.7 Dispersal and re-introduction

Management recommendations to facilitate dispersal between sites are described in detail in section 7.4.8. Generally, the management practices described above should be employed, to maintain empty sites within 1-3 km of extant populations in favourable condition. They should also be employed in as much of the intervening habitat as possible. Given the low success rate for other taxa (Oates & Warren 1990), re-introduction to empty habitat is not considered a priority for this species.

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Appendices

Appendix 1. Sample Site Questionnaire

Sites database

Region | Dartmoor | Devon | Gower | Anglesey | Pembroke | New Forest | Test&Itchen | Oxford |

| Heathland | Chalkstream |

Site name ________________ **Site no.** ________

Grid references ________________

Documents

1st date **last date**

Ownership | Private | Crownland | Common | NT |

Conservation status | SSSI | SPA | cSAC | Ramsar | NT |

STREAM CHARACTERISTICS

slope aspect ______

Stream type runnel ______ flushes ______ ditch ______ other ______

Length of stream ________________

Width of stream ________________

Substrate

	high	low
peat		
sand		
gravel		

water source

spring	
ground water	
clay pit outflow	
carrier	

importance of shade

Source of shade

Willow		Myrica		Sparganium	
Birch		Molinia		Gorse	
Trees		Carex		Bracken	
Juncus		Pine			

Flow rate | Fast | Medium | Slow | Sluggish | Static |

cm

water depth ________________

peat depth ________________

MANAGEMENT

GRAZING

Type of animal

Cattle		Sheep	
Horse			
Pony			
Deer			

Intensity

Light	
Medium	
Heavy	

No of animals per hectare ________________

Is whole of area accessible? ________________

Evidence of poaching?

Timing of grazing | Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec |

BURNING

Yes or no ________

Frequency

Last burn | Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec |

SCRUB CLEARANCE

Clearance of

Willow		Myrica	
Birch			
Molinia			

Frequency

Timing of clearance | Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec |

FLOW DIVERSION ________________

Describe ________________

ADDITIONAL MANAGEMENT INFO ________________

GENERAL HABITAT DESCRIPTION

nutrient status

oligotrophic	
mesotrophic	
eutrophic	

HABITAT TYPE

Phase 1	stream	surround	NVC	stream	surround
Dry Heath			M21a		
Humid Heath			M25		
Wet Heath			M29		
Wet Lawn			M14		
Valley Mire			M13		
Gorse			M15		
Bracken			M16		
Carr			H4		
Scots pine			H3		
Acid Grassland			H8		
Improved Grassland			H10		
Unimproved Grassland			others		
Humic acid grassland					
Parched Acid Grassland					
Broadleaved Wood					
Water meadow					
other					

Evidence for base richness

pH ________ calcium ________

Conductivity ________ nitrate ________

Maximum count ________

Total	Pairs	Males	Females

adults assoc w
larvae assoc w

conditions ______________
____
____

Perceived threats -	high	medium	low
scrub			
insuffic grazing			
drainage			
canalisation			
dessication			
burning/clearance			
pollution			
nutrient run-off			
silt in water			

	high	medium	low
headward erosion			
peat slumping			
freezing			
drying up			

GEOLOGY ______________________________ ALTITUDE __________
______________________________ __________

VEGETATION

	stream	bankside
height of vegetation		
% cover of submergent veg		
% cover of emergent veg		
algae?		

density of vegetation						
stream	sparse	open	adundant	choked		
bankside	sparse	open	adundant	choked		

Plant species	stream main com	stream present	bankside main com	bankside present	assoc w pres of adults
Acrocladium caspidalum					
Agrostis					
Agrostis curtisii					
Agrostis setacea					
Alismo plantago aquatica					
Anagallis tenellum					
Apium nodiflorum					
Berula erecta					
Betula					
birch					
bracken					
Calluna vulgaris					
carex sp					
carex flacca					
carex nigra					
carex echinata					
carex dioica					

Plant species	stream main com	stream present	bankside main com	bankside present	assoc w pres of adults
carex panicea					
Cirsium palustre					
Cirsium dissectum					
D praetermissa					
Dactylorhiza maculata/fuschii					
Drosera					
Drosera rotundifolia					
Drosera intermedia					
Eleocharis palustris					
Eleocharis multicaulis					
Elodea canadensis					
Equisetum fluviatale					
Erica tetralix					
Erica cinerea					
Eriophorum angustifolium					
Eriophorum					
Hydrocotyle vulgaris					
Hypericum elodes					
Hypnum cypressiforme					
Glyceria maxima					
Juncus					
Juncus acutiflorus					
Juncus articulatus					
Juncus bufonius					
Juncus bulbosus					
Juncus acutiflorus					
Juncus articulatus					
Liverwort					
Mentha aquatica					
Molinia caerulea					
Myrica gale					
Narthecium ossifragium					
Pedicularis sylvatica					
Pillwort					
Pinguicula lusitanica					
Phalaris arundinacea					
Polygala serpyllifolia					
Potamogeton polygonifolius					
Potentilla erecta					
Ranunculus flamminula					

Appendix. 2. Values of water chemical parameters from 1998 surveys.

(‘high’ is given when the value for a chemical parameter exceeds twice the maximum value in the calibration curve, ‘-‘ is given when no data were available or when negative in value).

Site name	Survey date	Habitat	Region	Grid reference	pH	Conductivity	Soluble Reactive Phosphate	Total Soluble Phosphate	Soluble unreactive phosphate	Total Phosphate	Particulate phospate	Nitrate	Ammonia
Cors Erddreiniog (Nant Isaf) - site of population 1983-1991	May-98	H	Ang	23/478822	8.1	600	0.000	0.015	0.015	0.000	-	high	0.000
Cors Erddreiniog (Nant Isaf) - flushes, site of population 1992 onwards	May-98	H	Ang	23/478823	7.8	690	0.015	0.000	-	0.000	-	0.359	high
Cors Erddreiniog (Nant Isaf)	May-98	H	Ang	23/478824	8.4	540	0.021	0.028	0.007	0.000	-	high	0.107
Cors Erddreiniog (Nant Isaf)	May-98	H	Ang	23/478825	8.4	700	0.005	0.000	-	0.000	-	high	0.210
Tor View Moor - Source*	May-98	H	Dar	20/689919	7.5	110	0.011	0.000	-	0.006	-	high	0.000
Tor View Moor	May-98	H	Dar	20/690918	7.8	110	0.004	0.000	-	0.000	-	0.650	0.057
Colaton Raleigh - Source*	Apr-98	H	Dev	30/048867	7.8	80	0.010	0.000	-	-	-	0.064	0.044
Colaton Raleigh	Apr-98	H	Dev	30/050868	7.2	120	0.006	0.000	-	-	-	0.000	0.000
Colaton Raleigh	Apr-98	H	Dev	30/050868	7.4	90	0.007	0.000	-	-	-	0.000	0.000
Aylesbeare Common - Source*	Apr-98	H	Dev	30/054907	7.1	241	0.003	0.000	-	-	-	high	0.025
Aylesbeare Common	Apr-98	H	Dev	30/055906	7.2	234	0.000	0.000	0.000	-	-	high	0.000
Aylesbeare Common	Apr-98	H	Dev	30/055907	7.1	60	0.000	0.000	0.000	-	-	high	0.000
Venn Ottery	Apr-98	H	Dev	30/062920	7.0	239	0.000	0.000	0.000	-	-	high	high
Venn Ottery - Source*	Apr-98	H	Dev	30/063915	7.0	302	0.010	0.000	-	-	-	high	0.182
Hense Moor	Apr-98	H	Dev	31/174075	7.4	90	0.000	0.000	0.000	-	-	0.000	0.000
Povingdon - Upper Outflow Mire	May-98	H	Dor	30/891827	8.3	410	0.013	0.006	-	0.033	-	0.339	0.118
Povingdon - Lower Outflow Mire	May-98	H	Dor	30/891831	8.3	420	0.007	0.000	-	0.014	-	0.553	0.484
Povingdon - Orchard Cottage Mire	May-98	H	Dor	30/892832	7.9	390	0.012	0.037	0.026	0.034	-	0.000	0.377
Povingdon - Orchard Cottage Mire	May-98	H	Dor	30/894833	7.5	400	0.012	0.023	0.011	0.031	0.007	0.000	0.474
Creech Heath	May-98	H	Dor	30/927835	7.1	160	0.014	0.009	-	0.059	-	0.024	0.336
Blue Pool (Norden Heath)	May-98	H	Dor	30/940830	7.9	280	0.006	0.013	0.007	0.000	-	0.258	0.253
Hartland Moor	May-98	H	Dor	30/943842	7.4	270	0.010	0.028	0.018	0.033	0.005	0.735	0.243
Corfe Common West	May-98	H	Dor	30/956814	7.3	240	0.017	0.041	0.024	0.062	0.021	0.000	0.341
Corfe Common East	May-98	H	Dor	30/967811	7.4	230	0.011	0.002	-	0.000	-	high	0.259

Appendix 2. continued.

Site name	Survey date	Habitat	Region	Grid reference	pH	Conductivity	Soluble Reactive Phosphate	Total Soluble Phosphate	Soluble unreactive phosphate	Total Phosphate	Particulate phospate	Nitrate	Ammonia
Rhossili Down	May-98	H	Gow	21/425899	5.6	180	0.065	0.053	-	0.052		0.000	0.549
Rhossili Down	May-98	H	Gow	21/427901	5.6	190	0.122	0.011	-	0.117	-	0.000	0.061
Cefn Bryn	May-98	H	Gow	21/499908	7.9	270	0.037	0.009	-	0.019	-	0.075	0.085
Cefn Bryn	May-98	H	Gow	21/505908	8.6	340	0.008	0.023	0.015	0.034	0.011	0.000	0.068
Upper Crockford	Apr-98	H	Nfor	40/346997	-	-	0.028	0.043	0.015	-	-	0.304	0.121
Upper Crockford - Source*	Apr-98	H	Nfor	40/348998	-	-	0.012	0.000	-	-	-	0.578	0.133
FrogMoor, Norley Wood	Apr-98	H	Nfor	40/351978	-	-	0.026	0.039	0.013	-	-	0.399	0.057
Lower Crockford	Apr-98	H	Nfor	40/355989	-	-	0.020	0.015	-	-	-	0.173	0.121
Upper Peaked Hill - Source*	Apr-98	H	Nfor	40/358998	-	-	0.012	0.048	0.035	-	-	1.084	0.180
Upper Peaked Hill	Apr-98	H	Nfor	40/360995	-	-	0.009	0.000	-	-	-	0.405	0.097
Lower Peaked Hill	Apr-98	H	Nfor	40/361990	-	-	0.015	0.003	-	-	-	0.357	0.026
Bagshot Moor	Apr-98	H	Nfor	40/369999	-	-	0.015	0.048	0.033	-	-	0.405	0.103
Kings Sombourne	Apr-98	C	I&T	41/347315	-	-	0.072	0.113	0.041	-	-	high	0.131
Hatchet Pond	Apr-98	H	Nfor	41/360013	-	-	0.015	0.070	0.055	-	-	0.435	0.098
Itchen Valley Country Park	Apr-98	C	I&T	41/455160	-	-	0.306	high	0.132	-	-	1.245	0.161
Itchen Valley Country Park	Apr-98	C	I&T	41/460169	-	-	0.320	high	0.249	-	-	high	0.150
Itchen Valley Country Park (Ditch 12)	Apr-98	C	I&T	41/461168	-	-	0.317	high	high	-	-	high	0.039
Mariners Meadow, Twyford	Apr-98	C	I&T	41/475240	-	-	0.049	0.127	0.078	-	-	high	0.031
Widden Bottom	May-98	H	Nfor	40/289993	7.9	350	0.042	0.077	0.035	high	0.400	0.000	high
GreenMoor North	May-98	H	Nfor	40/335995	7.6	160	0.033	0.037	0.004	0.080	0.043	0.000	0.310
GreenMoor South	May-98	H	Nfor	40/338989	7.1	120	0.000	0.000	0.000	0.036	0.036	0.420	0.142
Millersford West	May-98	H	Nfor	41/184164	7.4	130	0.009	0.000	-	0.031	-	0.000	0.000
Millersford East	May-98	H	Nfor	41/187168	7.2	140	0.014	0.001	-	0.037	-	0.000	0.035
Gypsie Hollies	May-98	H	Nfor	41/194127	7.0	80	0.012	0.017	0.006	0.040	0.022	0.000	0.197
Common Moor	May-98	H	Nfor	41/205045	7.2	150	0.010	0.000	-	0.007	-	0.000	0.000
Mill Lawn	May-98	H	Nfor	41/228034	7.1	240	0.014	0.025	0.011	0.070	0.045	0.012	high
Holmsley Station	May-98	H	Nfor	41/232009	7.6	90	0.019	0.017	-	0.001	-	0.000	0.000

Appendix 2. continued.

Site name	Survey date	Habitat	Region	Grid reference	pH	Conductivity	Soluble Reactive Phosphate	Total Soluble Phosphate	Soluble unreactive phosphate	Total Phosphate	Particulate phospate	Nitrate	Ammonia
Rooks Bridge	May-98	H	Nfor	41/233037	7.2	220	0.008	0.020	0.012	0.000	-	0.714	0.089
Burley Lawn	May-98	H	Nfor	41/234036	7.1	210	0.007	0.009	0.002	0.070	0.060	0.000	0.216
Rooks Bridge	May-98	H	Nfor	41/235036	7.3	240	0.005	0.000	-	0.021	-	0.783	0.047
Rock Hills	May-98	H	Nfor	41/240030	6.3	70	0.005	0.001	-	0.016	-	0.000	0.431
Stagbrake Bog	May-98	H	Nfor	41/246031	7.7	140	0.010	0.014	0.004	0.017	0.003	0.000	0.035
Duckhole Bog	May-98	H	Nfor	41/253024	7.0	80	0.000	0.000	0.000	0.005	0.005	0.000	0.327
Duckhole Bog	May-98	H	Nfor	41/258030	7.0	80	0.005	0.000	-	0.047	-	0.000	0.216
Oberwater	May-98	H	Nfor	41/260034	6.0	160	0.000	0.026	0.026	0.009	-	0.000	0.202
Three Beech Bottom	May-98	H	Nfor	41/292002	6.9	150	0.139	0.111	-	0.146	-	0.000	0.373
Setley Plain	May-98	H	Nfor	41/296003	7.1	300	0.007	0.000	-	0.000	-	0.529	0.035
Round Hill	May-98	H	Nfor	41/329020	7.6	190	0.009	0.000	-	0.006	-	0.000	0.000
Applemore	May-98	H	Nfor	41/394071	8.1	530	0.012	0.000	-	0.014	-	high	0.123
Dry Sandford Pit	May-98	H	Oxf	41/461999	7.8	680	0.163	0.124	-	0.244	-	high	0.000
Cothill Fen	May-98	H	Oxf	41/467996	7.2	1030	0.000	0.024	0.024	0.014	-	0.000	0.000
St David's Head	May-98	H	Pem	12/729281	7.9	430	0.002	0.000	-	0.042	-	0.015	0.085
St David's Head	May-98	H	Pem	12/729282	7.6	450	0.028	0.000	-	0.000	-	high	0.112
Clegyr Boia	May-98	H	Pem	12/741253	7.8	580	0.000	0.025	0.025	0.024	-	high	0.000
Clegyr Boia	May-98	H	Pem	12/742253	7.8	590	0.052	0.014	-	0.022	-	high	0.000
Pont Clegyr	May-98	H	Pem	12/769252	7.3	450	0.067	0.028	-	0.074	-	high	0.509
Pont Clegyr	May-98	H	Pem	12/769253	7.6	460	0.021	0.031	0.009	0.043	0.012	high	0.402
Letterston	May-98	H	Pem	12/930288	7.4	160	0.012	0.043	0.031	0.044	0.001	high	high
Waun Fawr	May-98	H	Pem	22/016303	7.6	100	0.026	0.000	-	0.011	-	high	0.004
Waun Fawr	May-98	H	Pem	22/017304	6.7	100	0.078	0.207	0.129	0.063	-	0.030	0.243
Waun Fawr - Source*	May-98	H	Pem	22/017305	6.7	-	0.003	0.026	0.024	0.019	-	1.533	0.144
Carnillingi Common	May-98	H	Pem	22/046375	6.7	70	0.000	0.029	0.029	0.023	-	0.000	0.000

Appendix 2. continued.

Site name	Survey date	Habitat	Region	Grid reference	pH	Conductivity	Soluble Reactive Phosphate	Total Soluble Phosphate	Soluble unreactive phosphate	Total Phosphate	Particulate phospate	Nitrate	Ammonia
Pendrisil	May-98	H	Pem	22/068342	6.7	110	0.002	0.000	-	0.308	-	high	0.152
Ffon Dyrysieniog	May-98	H	Pem	22/101341	7.1	60	0.021	0.010	-	0.000	-	0.000	0.007
Brynberian	May-98	H	Pem	22/108338	6.5	40	0.002	0.000	-	0.000	-	0.000	0.360
Brynberian	May-98	H	Pem	22/109338	6.9	40	0.010	0.000	-	0.029	-	0.314	0.269
Brynberian	May-98	H	Pem	22/115343	7.1	60	0.015	0.000	-	0.021	-	0.000	0.108
Glan-yr-afon Uchaf - Source*	May-98	H	Pem	22/118345	7.1	70	0.000	0.023	0.023	0.016	-	0.000	0.121
Glan-yr-afon Uchaf	May-98	H	Pem	22/118346	7.1	70	0.016	0.013	-	0.023	-	0.000	0.256
Cwm Garw	May-98	H	Pem	22/119309	6.9	55	0.151	0.044	-	0.021	-	0.138	0.004
Cwm Garw	May-98	H	Pem	22/119312	6.7	60	0.000	0.028	0.028	0.032	0.003	0.133	0.000
Tewgyll Fachs	May-98	H	Pem	22/139305	6.7	60	0.000	0.013	0.013	0.015	0.002	0.000	0.000
Tewgyll Fachs	May-98	H	Pem	22/141305	6.9	75	0.000	0.017	0.017	0.018	0.001	0.000	0.000
South Waun Isaf (ungrazed)	May-98	H	Pem	22/142295	6.3	75	0.000	0.030	0.030	0.021	-	1.252	0.000
North Waun Isaf (grazed)	May-98	H	Pem	22/143303	6.6	110	0.000	0.012	0.012	0.010	-	0.000	0.025
West Cleddau	May-98	H	Pem	22/156317	6.6	80	0.000	0.005	0.005	0.024	0.019	0.000	0.286
West Cleddau	May-98	H	Pem	22/159322	6.8	85	0.000	0.014	0.014	0.013	0.000	0.000	high

Appendix 3 Sex ratio of *C. mercuriale* and *C. tenellum* in each cage.

	C. mercuriale				*C. tenellum*			
Cage no.	Males	Females	Ratio M:F	N	Males	Females	Ratio M:F	N
1	31	19	1.63	50	1	1	1.00	2
2	32	28	1.14	60	4	2	2.00	6
3	11	5	2.20	16	36	22	1.64	58
4	25	16	1.56	41	1	2	0.50	3
5	15	8	1.88	23	1	2	0.50	3
6	53	35	1.51	88	7	9	0.78	16
7	15	7	2.14	22	4	4	1.00	8
8	3	2	1.50	5	15	13	1.15	28
9	23	24	0.99	47	0	4	0.00	4
10	9	15	0.60	24	4	11	0.36	15
15	10	5	2.00	15	12	8	1.50	20
16	15	12	1.25	27	1	3	0.33	4
17	17	12	1.41	25	7	13	0.53	20
18	1	2	0.50	3	17	13	1.31	30
19	14	21	0.67	35	9	7	1.29	16
Total	274	211	-	481	119	114	-	233

Appendix 4 The proportion of marked individuals recaptured 0-6 times for all sex and age categories.

	Adults				Tenerals			
No. of recaptures	Male	%	Female	%	Male	%	Female	%
0	1591	68.61	318	84.80	276	94.20	211	97.24
1	496	21.43	45	12.00	15	5.12	5	2.30
2	149	6.51	9	2.40	2	0.68	1	0.46
3	65	2.93	3	0.80	0	0	0	0
4	14	0.78	0	0	0	0	0	0
5	3	0.34	0	0	0	0	0	0
6	1	0.30	0	0	0	0	0	0
Total marked	2319		375		293		217	

Appendix 5 Interval between first and second recapture and state of maturity of recaptured teneral adults.

ID No.	Interval (days)	Mature?	ID No.	Interval (days)	Mature?
496W	1	No	365W	13	Yes
331W	2	No	118W	14	Yes
467W	2	No	53W	17	Yes
487W	2	No	130W	23	Yes
293W	2	No	402W	27	Yes
58W	3	No	174W	32	Yes
64W	3	No	167W	35	Yes
272W	3	No			
442W	3	No			
239W	4	No			
400W	4	No			
800W	4	Yes			
22W	5	Yes			
260W	8	Yes			
413	12	Yes			

Appendix 6 Monthly X-Y instar separation plots for larvae of *C. mercuriale* (Figs 9a-9t)

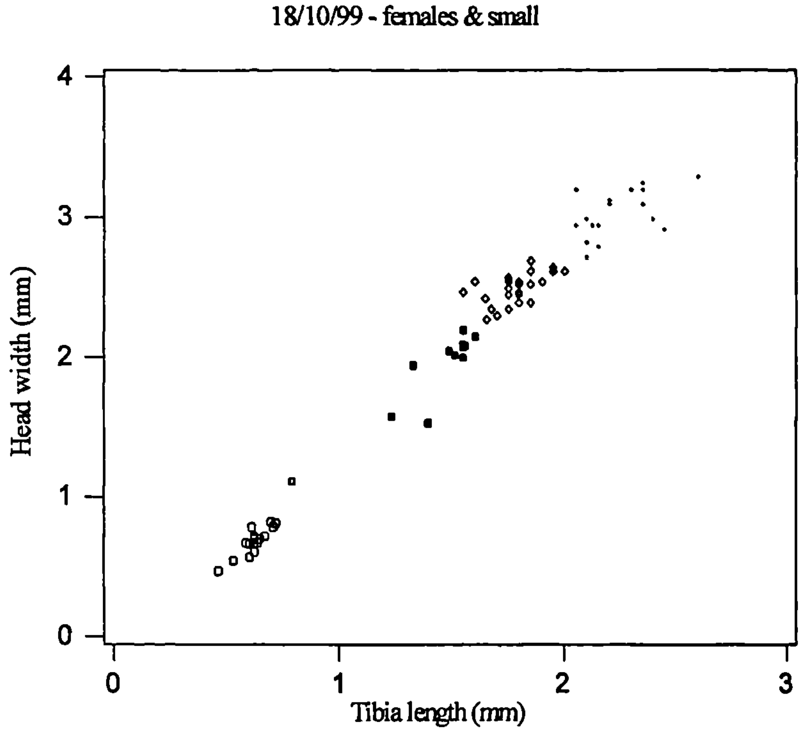


Fig. 9a

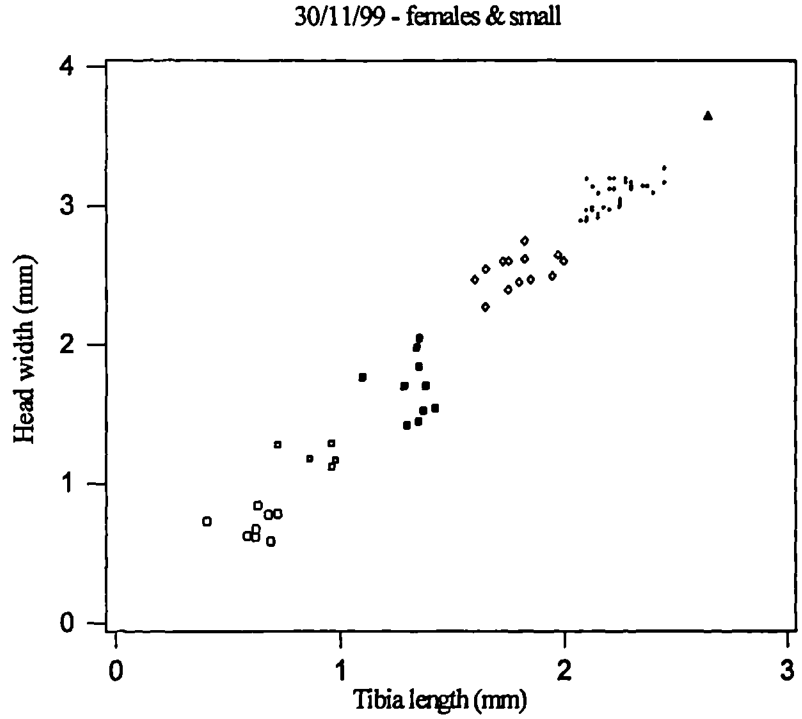


Fig. 9b

12/01/00 - females & small

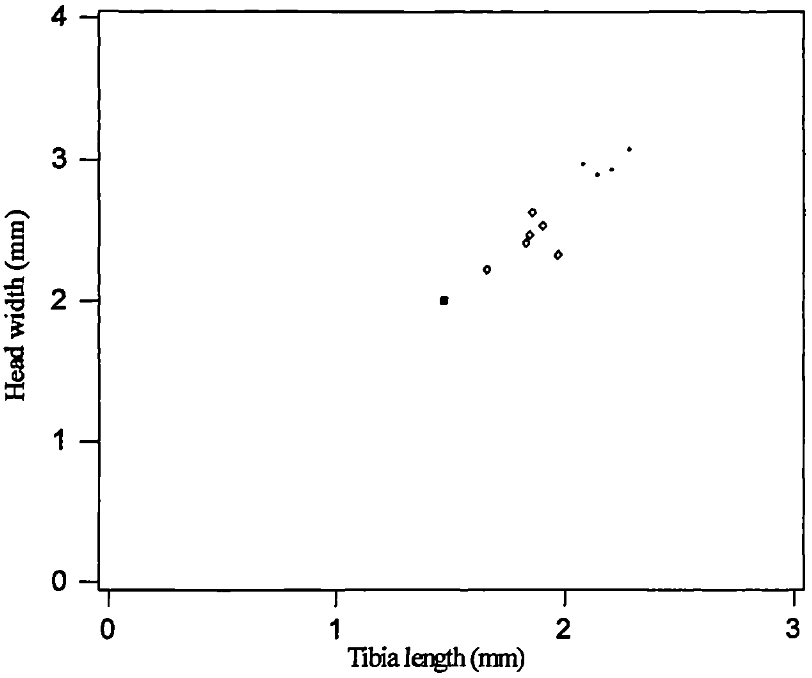


Fig. 9c

23/02/00 - females & small

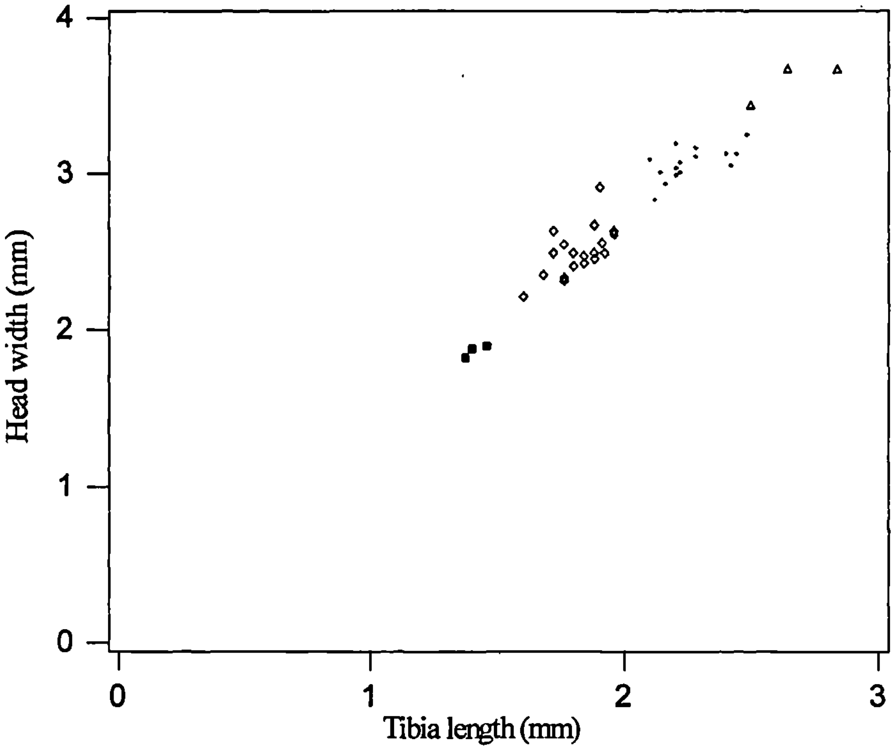


Fig. 9d

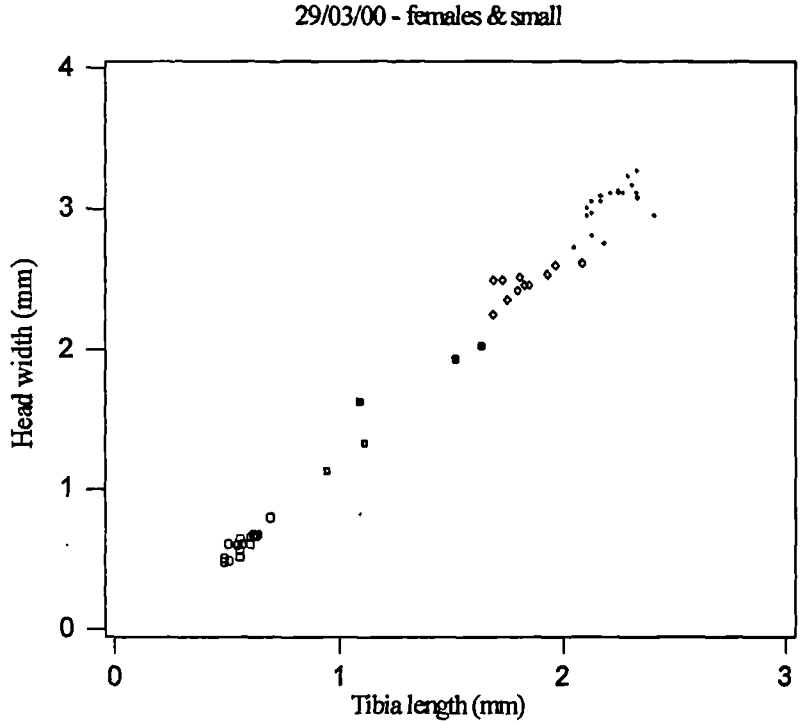


Fig. 9e

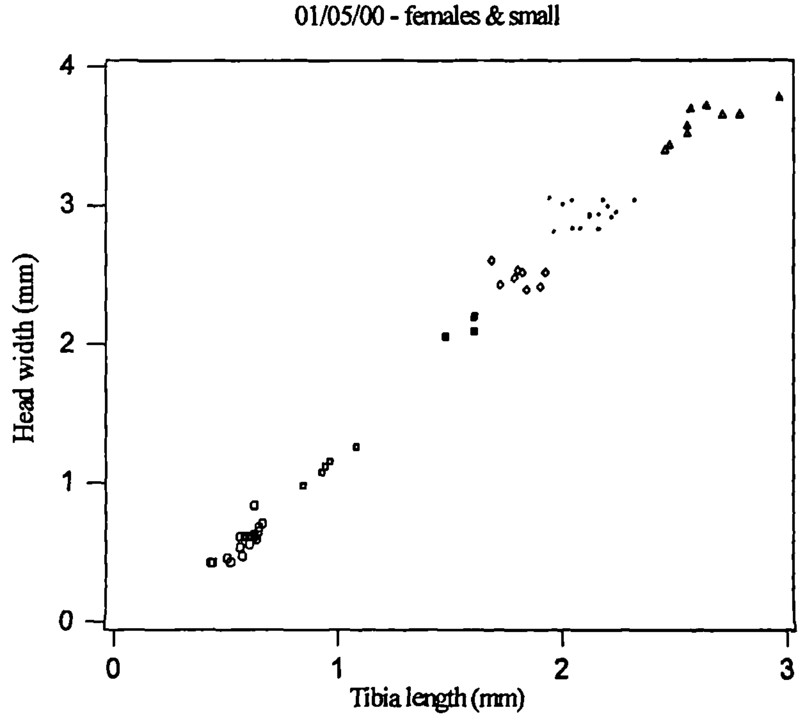


Fig. 9f

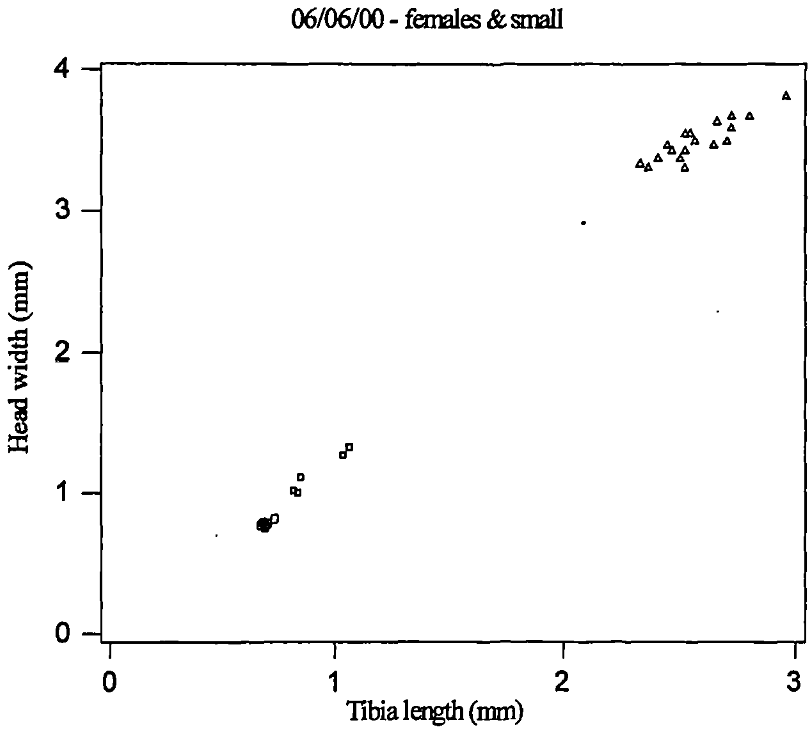

06/06/00 - females & small
Head width (mm)
Tibia length (mm)
0
1
2
3
4
0
1
2
3

Fig. 9g

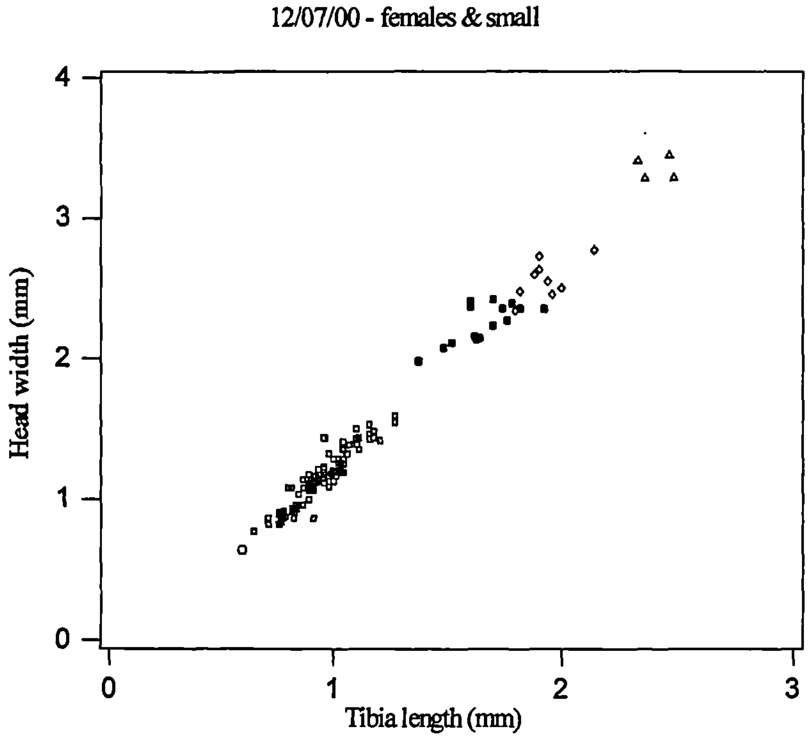
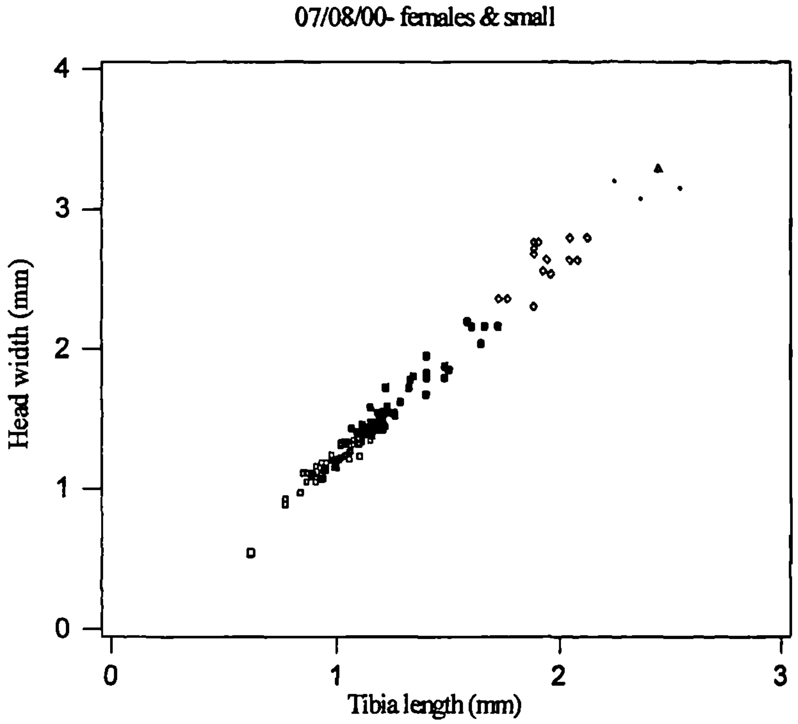
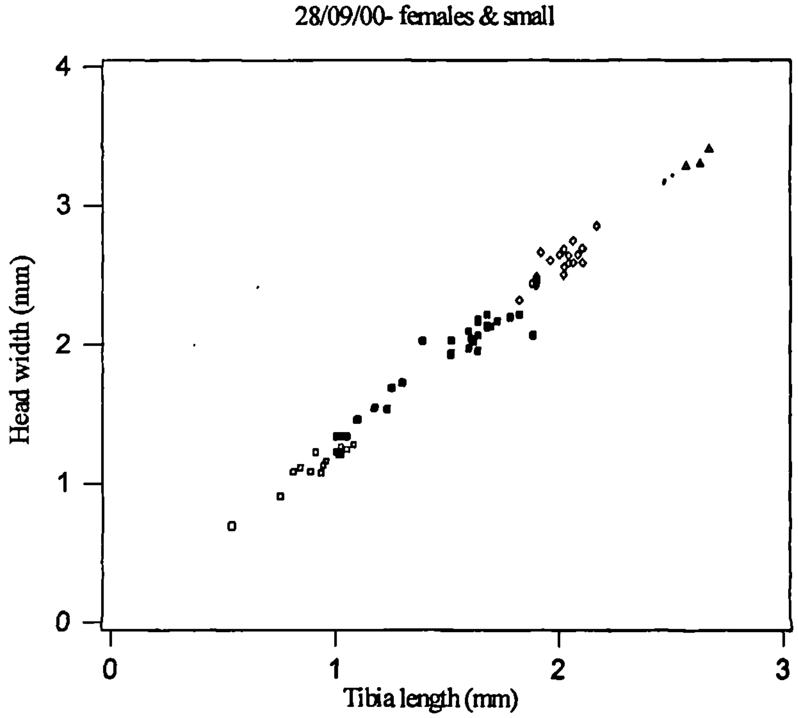

12/07/00 - females & small
Head width (mm)
Tibia length (mm)
0
1
2
3
4
0
1
2
3

Fig. 9h



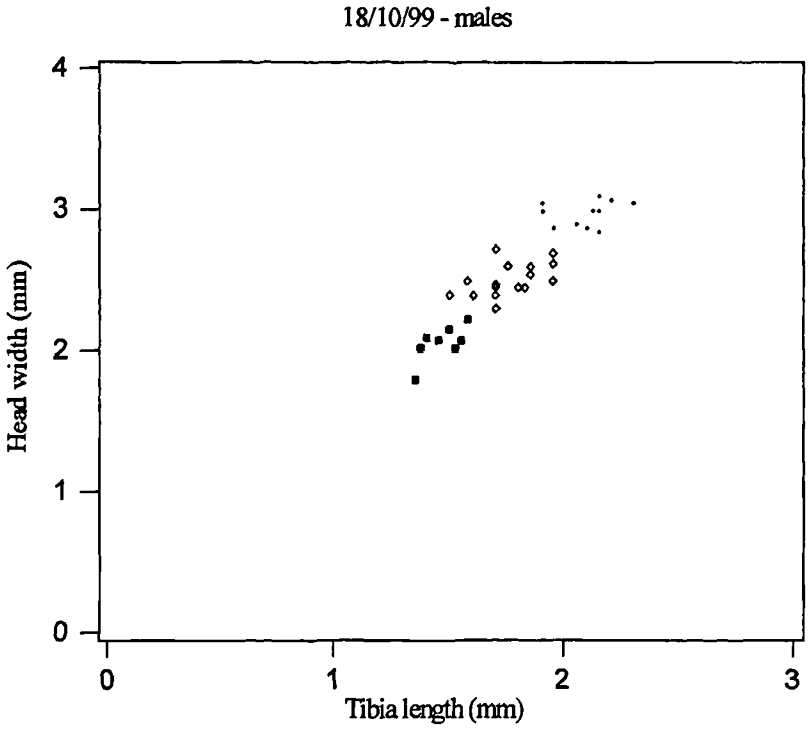
07/08/00- females & small

Fig. 9i



28/09/00- females & small

Fig. 9j


18/10/99 - males
Head width (mm)
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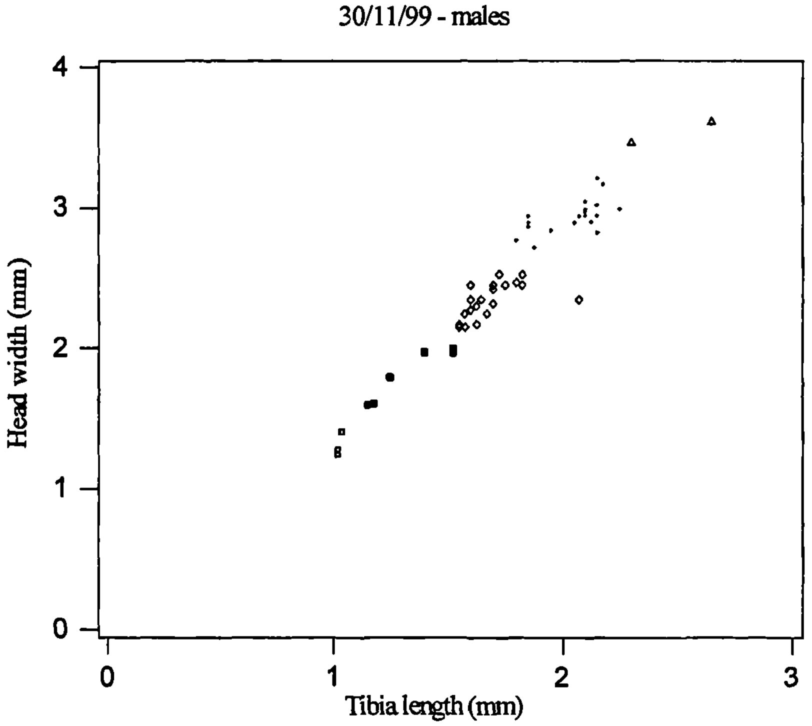
1
2
3
4
Tibia length (mm)
0
1
2
3

Fig. 9k


30/11/99 - males
Head width (mm)
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1
2
3
4
Tibia length (mm)
0
1
2
3

Fig. 9l

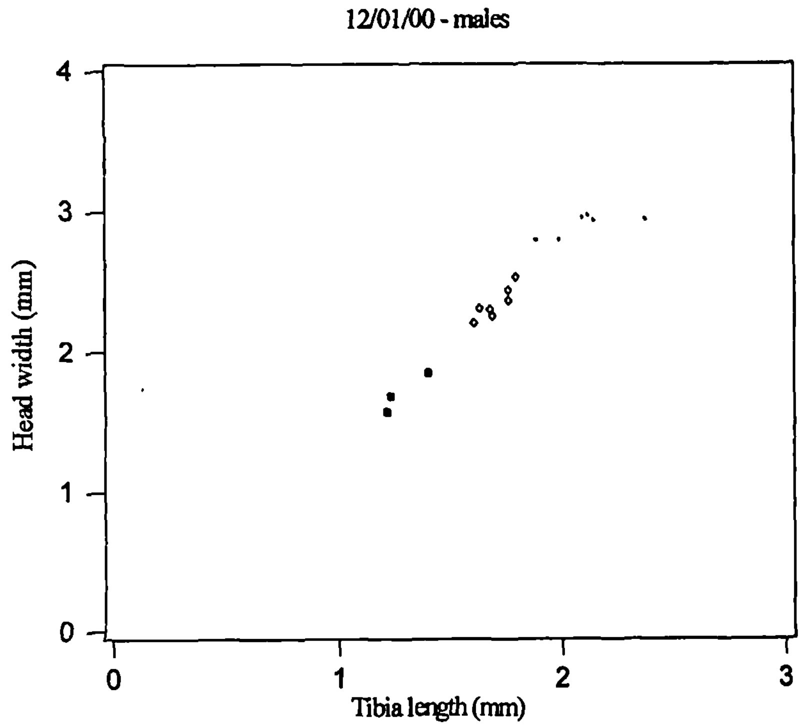
12/01/00 - males
Head width (mm)
0
1
2
3
4
Tibia length (mm)
0
1
2
3

Fig. 9m

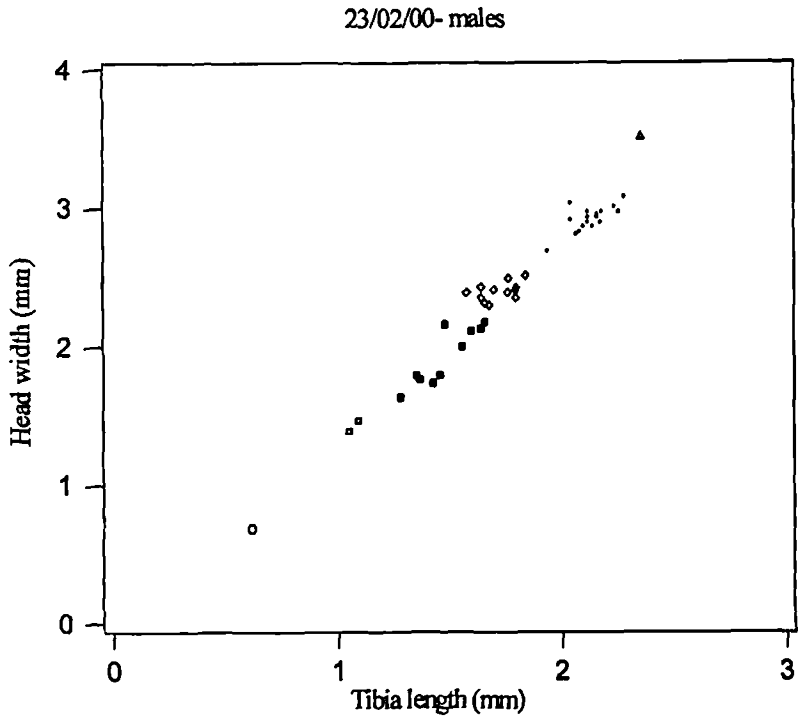
23/02/00- males
Head width (mm)
0
1
2
3
4
Tibia length (mm)
0
1
2
3

Fig. 9n

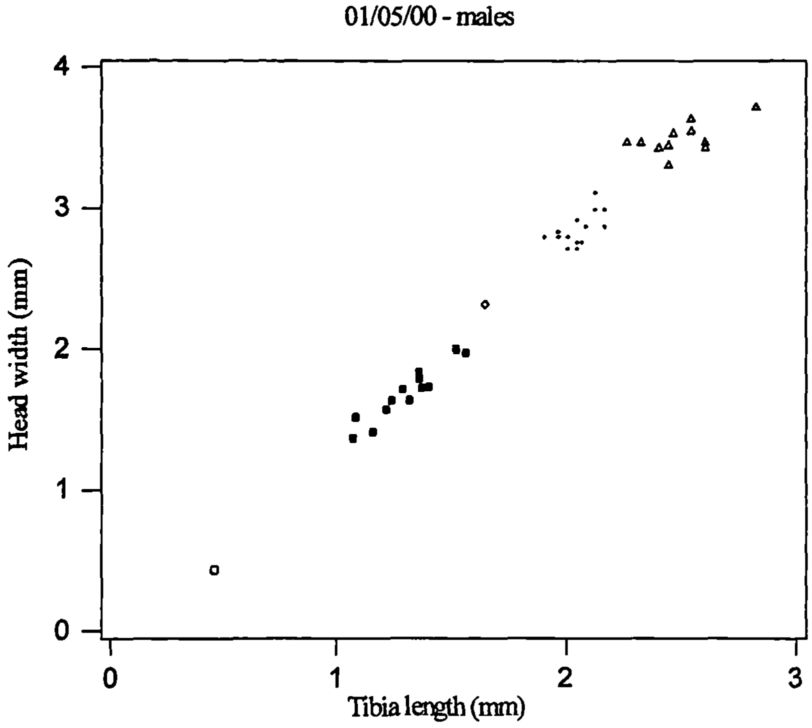
01/05/00 - males
Head width (mm)
Tibia length (mm)
0
1
2
3
4
0
1
2
3

Fig. 9o

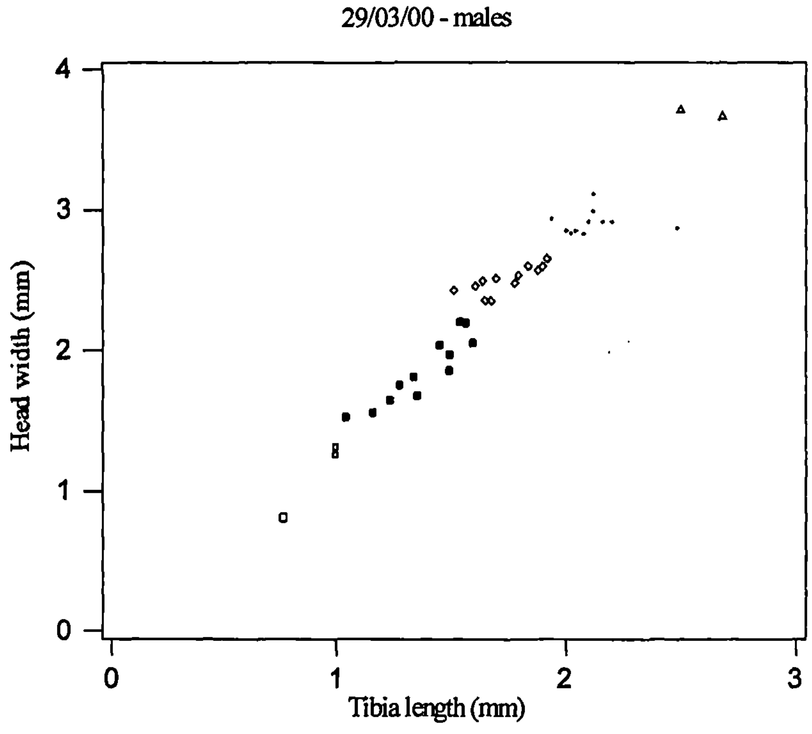
29/03/00 - males
Head width (mm)
Tibia length (mm)
0
1
2
3
4
0
1
2
3

Fig. 9p

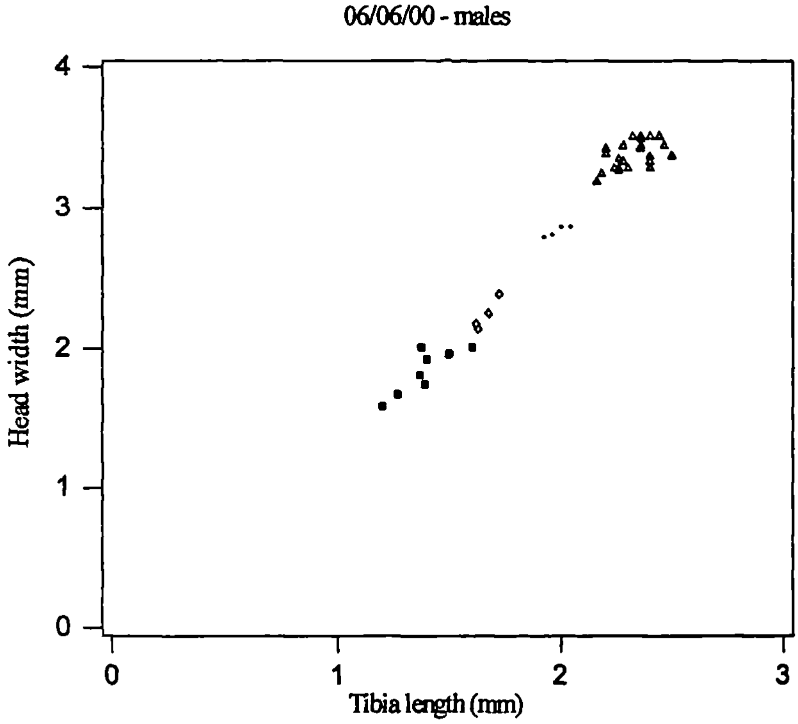
06/06/00 - males
Head width (mm)
Tibia length (mm)
0
1
2
3
4
0
1
2
3

Fig. 9q

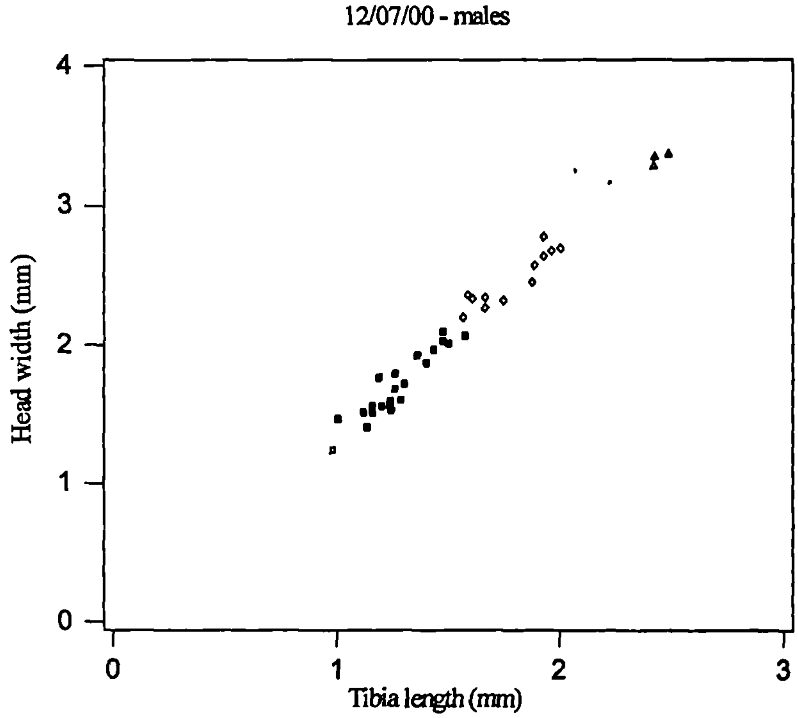
12/07/00 - males
Head width (mm)
Tibia length (mm)
0
1
2
3
4
0
1
2
3

Fig. 9r

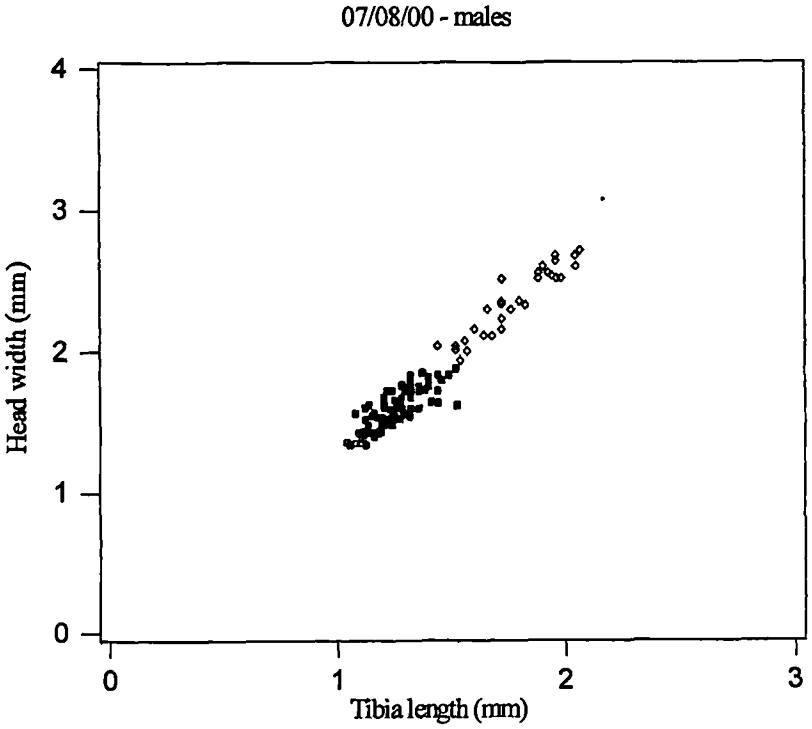
07/08/00 - males
Head width (mm)
0
1
2
3
4
0
1
2
3
Tibia length (mm)

Fig. 9s

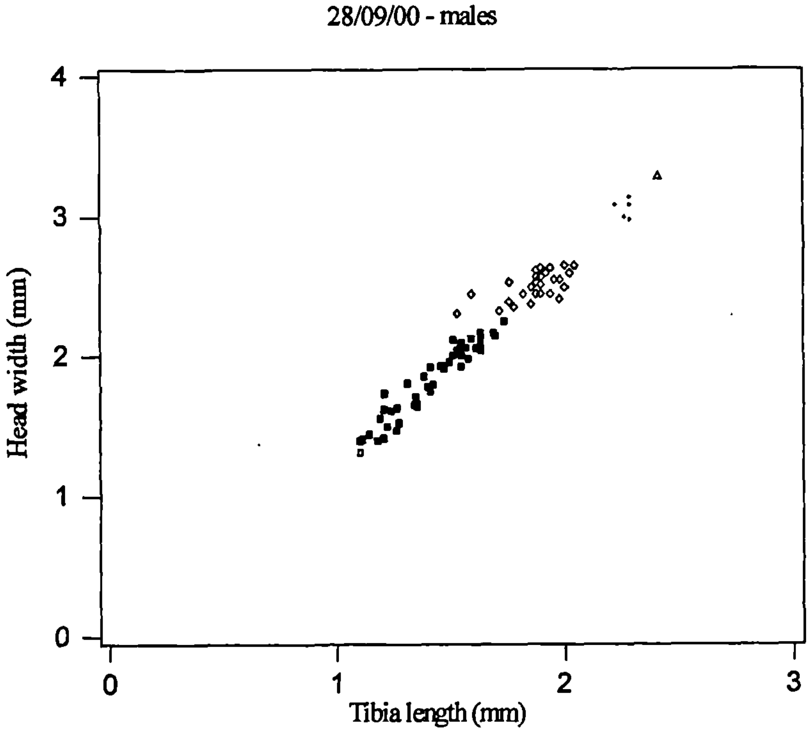
28/09/00 - males
Head width (mm)
0
1
2
3
4
0
1
2
3
Tibia length (mm)

Fig. 9t

Appendix 7 Number of individuals of different invertebrate taxa found in samples from top (T), middle (M) and bottom (B) sampling positions at Glan-yr-afon Uchaf, in March 2000, Total frequency across samples and percentage of the total abundance made up of each taxa are also given.

	Position and sample number											
Taxa	B1	B2	M1	M2	M3	M4	T1	T2	T3	T4	Total	% of total
Chironomid	3	8	8	1	2	5	3	12	18	2	62	31.6
Gammaridae	4	3		1			1	5	2	2	18	9.2
Hydroptilidae		5	3				1	2	2		13	6.6
Dytiscidae									1	1	2	1.0
Corixidae	1		3	2	1		1		1		9	4.6
Hydrometridae			1	2					2		5	2.6
Hydrophillidae			5	1			3	2	2	1	14	7.1
Oligochate							3		1		4	2.0
Lymnaeidae		1						1	1	2	5	2.6
Hydrobidiae			4			1	1	1	2		9	4.6
Limnephlidae	2	3			1c	2	1	1	1		9	4.6
Simulidae		2						1			3	1.5
Hydracarinidae								1			1	0.5
Gerridae		1	2	6		1	1			2	13	6.6
Ephemerellidae	1	1	1			1					4	2.0
Tipulidae		1									1	0.5
Elmidae				1							1	0.5
Baetidae			1					1			2	1.0
Leuctridae								1			1	0.5
Sphaeridae										1	1	0.5
Anisoptera (mainly Libellulidae)	3	2	2	4		2		1	1		15	7.7
Zygoptera (mainly Calyopterygidae)	2	1						1			4	2.0
								Total abundance			196	

Key: c=case, all other numbers refer to frequencies of larval stages.

Appendix 8 Observed (O) and expected (E) frequencies of matings within each age group for males.

Age class/days	*n*	No. of matings		χ^2
		O	E	
1	116	16	17	0.06
2	32	2	5	1.80
3	33	3	5	0.80
4	32	5	5	0.00
5	25	5	4	0.25
6	22	6	3	3.00
7	23	4	3	0.33
8	22	4	3	0.33
9	19	2	3	0.33
10	29	7	4	2.25
11	24	2	3	0.33
12	15	2	2	0.00
13	14	2	2	0.00
14	11	2	2	0.00
15	16	4	2	2.00
16-21	45	6	6	0.00
>22	39	3	6	1.50
			Total	12.98

Appendix 9. Observed (O) and expected (E) frequencies of matings within each age group for females.

Age class/days	*n*	No. of matings		χ^2
		O	E	
1	76	30	22	2.91
2	12	4	4	0.00
3	8	4	2	2.00
4	7	1	2	0.50
5	11	4	3	0.33
6 to 10	36	5	10	2.50
11 to 15	18	3	5	0.80
16 to 20	15	3	4	0.25
> 20	14	4	4	0.00
			Total	9.29

Appendix 10 Logistic regression analyses for probability of moving more than 0m (Distance$_0$), at least 50m (Distance$_{50}$) and at least 200m (Distance$_{200}$) on moves 1 to 3 – New Forest (LR=likelihoos ratio).

Distance$_0$, movement 1

	$B \pm s.e.$	LR	d.f.	G	p	n_0	n_1	e^B
Constant	0.016 ± 0.126		1		< 0.001			1.02
t_1	0.156 ± 0.030	-432.38	1	36.16	< 0.001	238	424	1.17

Model χ^2=36.16, p< 0.001, 1 d.f.

Distance$_{50}$, movement 1

	$B \pm s.e.$	LR	d.f.	G	p	n_0	n_1	e^B
Constant	-1.222 ± 0.128		1		< 0.001			0.30
t_1	0.131 ± 0.023	-422.97	1	36.91	< 0.001	439	223	1.14

Model χ^2=36.91, p < 0.001, 1 d.f.

Distance$_{200}$, movement 1

	$B \pm s.e.$	LR	d.f.	G	p	n_0	n_1	e^B
Constant	-3.612 ± 0.561		1		< 0.001			0.00
t_1	0.238 ± 0.047	-60.02	1	26.98	< 0.001	650	12	1.27

Model χ^2= 26.98, p < 0.001, 1 d.f.

Distance$_0$, movement 2 – no variables added to model

Distance$_{50}$, movement 2

	$B \pm s.e.$	LR	d.f.	G	p	n_0	n_1	e^B
Constant	-1.021 ± 0.204		1		< 0.001			0.36
t_1	0.154 ± 0.051	-167.30	1	9.82	0.002	162	93	1.17

Model χ^2=9.82, p = 0.002, 1 d.f.

Distance$_{200}$, movement 2 – no variables added to model

Distance$_0$, movement 3

	$B \pm s.e.$	LR	d.f.	G	p	n_0	n_1	e^B
Constant	-0.336 ± 0.324		1		0.300			0.72
t_1	0.310 ± 0.113	-76.51	1	11.68	0.001	44	71	1.36

Model χ^2=11.68, p = 0.001, 1 d.f.

Distance$_{50}$, movement 3

	$B \pm s.e.$	LR	d.f.	G	p	n_0	n_1	e^B
Constant	-1.622 ± 0.328		1		< 0.001			0.20
t_1	0.260 ± 0.078	-71.47	1	13.25	< 0.001	79	36	1.30

Model χ^2=13.25, p < 0.001, 1 d.f.

Appendix 10 continued.

Distance$_0$, movement 1- no variables added to model

Distance$_{50}$, movement 1- no variables added to model

Distance$_{200}$, movement 1- no variables added to model

Distance$_0$, movement 2

	B ±*s.e.*	LR	d.f.	*G*	*p*	n_0	n_1	e^B
Constant	0.143 ± 0.270							1.15
t_1	0.137 ± 0.046	-166.45	1	9.71	0.002	121	120	1.15
Age (mid-point)	-0.105 ± 0.044	-164.79	1	6.39	0.011			0.90

Model χ^2=10.91, p=0.004, 1 d.f.

Distance$_{50}$, movement 2

	B ±*s.e.*	LR	d.f.	*G*	*p*	n_0	n_1	e^B
Constant	-1.919 ± 0.257		1		< 0.001			0.15
t_1	0.109 ± 0.042	117.48	1	6.74	0.009	195	46	1.12

Model χ^2=6.74, p =0.009, 1 d.f.

Distance$_0$, movement 3

	B ±*s.e.*	LR	d.f.	*G*	*p*	n_0	n_1	e^B
Constant	-1.815 ± 0.528		1		0.051			0.16
Date (mid-point)	0.056 ± 0.028	-66.54	1	4.345	0.037	48	48	1.06

Model χ^2=4.35, p =0.037, 1 d.f.

Distance$_{50}$, movement 3

	B ±*s.e.*	LR	d.f.	*G*	*p*	n_0	n_1	e^B
Constant	-1.807 ± 0.386		1		< 0.001			0.16
t_1	0.114 ± 0.058	-50.43	1	3.93	0.048	75	21	1.12

Model χ^2=3.92, p =0.048, 1 d.f.