The Ecology and Conservation of the Southern Damselfly (*Coenagrion mercuriale* – Charpentier) in Britain

R&D Technical Report W1-021/TR

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Preface - Purposes (and use) of this Report
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. The Southern Damselfly was among this list and, in 1995, a species action plan was produced for this species.

A Steering Group was inaugurated in April 1997 to co-ordinate and oversee the implementation of this Species Action Plan (SAP). Represented on the group are the Environment Agency, the Countryside Council for Wales, English Nature, the British Dragonfly Society, The Wildlife Trusts. Academics from Liverpool University have been co-opted onto the Group. The SAP highlighted the need for further research into the ecological requirements of this species in Britain (Action 5.5.1). This resulted in the Steering Group commissioning, in1998, a PhD study on the ecology and conservation of the Southern Damselfly. A copy of the thesis is available as R&D Project Record W1-021/PR.

This R&D Technical Report aims to summarise information from the PhD, in an accessible form, on the following;

- Life cycle and development of the Southern Damselfly (Chapter 3)
- Large-scale habitat use (across sites – Chapter 2) and small-scale habitat use (within a site by adults and larvae – Chapter 4)
- Reproduction, mortality and dispersal of the mature adult Southern Damselfly (Chapters 5 and 6).

The main findings of a chapter are contained in a summary section at its beginning.

In view of this information, Chapter 7;

- lists habitat attributes required by the Southern Damselfly in Britain
- recommends management for achievement of favourable habitat condition

- advises on monitoring of the Southern Damselfly

Boxes in each chapter provide definitions of technical terms and site examples. Odonates and plants are referred to by their latin names with the common name provided in brackets where possible on first mention of a species. For clarity, extensive description of methodology and statistical analyses are not included in this report unless relevant and are detailed in W1-021/PR. In addition, only the most relevant references are cited in the text and listed in the table of references. More detailed references can be found in W1-021/PR. In this report, the symbol μ is used to indicate the sample mean (rather than the population mean as is conventional). Means are presented ± the standard error (s.e.).

The Steering Group commisioned a second PhD which began in 2000 to investigate the ecology of the Southern Damselfly in its chalksteam-fen habitats. This is also being managed and co-funded as an R&D project (W1-066)

EXECUTIVE SUMMARY

The Southern Damselfly is rare in Britain and Europe and has declined by around 30% in Britain this century. It occupies two rare biotopes in Britain – small streams on heathlands and old water meadow ditch systems on chalkstreams, both of which have undergone considerable fragmentation this century (though a few sites are found on poor fen).

Prior to this project, there had been numerous, independent studies of the ecology of the Southern Damselfly but these lacked standard methodology or aims and, in 1995, the Species Action Plan for this species highlighted the need for further research into its ecological requirements in Britain.

This R&D Technical Report presents the results of a PhD study on the ecology and conservation of the Southern Damselfly commissioned by the UK Steering Group in 1998. The life cycle and development of this species were investigated as well as reproduction, mortality and dispersal of the mature adult stage. Large-scale habitat use (across sites) and small-scale habitat use (within a site by adults and larvae) were examined. In light of these results, this report recommends management (and monitoring) regimes for the Southern Damselfly in Britain.

The findings of this report on aspects of the species' basic ecology can be summarised as follows:

- The Southern Damselfly requires two years for larval development in Britain
- The flight period of the adults is shorter in Britain than in Europe and daily emergence depends on climatic variables.
- Mortality was consistently low in the mature adult stage and at emergence but high in the egg and immature adult stages.
- Climatic variables influenced mature adult survival, whether individuals were present at the breeding site and whether they engaged in reproductive activity given that they were present
- The Southern Damselfly was found to be relatively sedentary but the field observed dispersal rate was probably sufficient for colonisation events and exchange of individuals to occur frequently between populations in large clusters of sites in Britain.
- Soft-stemmed, submerged and semi-emergent herbs were favoured for oviposition whilst tall emergents with rigid upright stems were favoured for emergence.
- Dispersal seemed highly dependent on aspects of landscape structure.

The Southern Damselfly was found to be restricted in its national and global distribution probably by climatic variables including temperature and by the availability of its biotopes. It is further restricted within these biotopes because it is stenotopic i.e. highly sensitive to a number of habitat factors such as sunlight, shade, water flow and aquatic and bankside vegetation structure. The physical, vegetation and chemical features common to British Southern Damselfly sites can be summarised as follows:

Physical features

- Low altitude and gently sloping ground (< 10% slope)
- Inorganic substrate overlaid with shallow organic peat or silt
- Shallow narrow waterbodies on heathlands, small ditches on chalkstreams
- Slow to moderate water flow
- Proximity to springs or groundwater ensuring permanence of water flow and stable thermal regimes with high minimum winter temperatures. Water arising from soft deposits of sandstone, limestone and clay

Vegetation features

- Remoteness from improved agriculture preventing eutrophication and encroachment of invasive tall emergents and algae

- Open and exposed watercourses
- Medium to high cover of submergent and emergent stream vegetation (low to medium height)
- Herbaceous, perennial stream vegetation
- Shelter on bankside and sometimes within the stream (e.g. *Myrica gale*). .

Chemical features

- Dystrophic to oligotrophic nutrient conditions
- Unpolluted water
- High oxygen concentrations

Many of these features seem to reflect a requirement for a thermally advantageous microclimate, restricting the Southern Damselfly to an early successional stage of its biotopes. This requirement is also reflected in the features selected by individuals at a small-scale - during emergence and oviposition.

In light of these findings on the ecology and habitat requirements of the Southern Damselfly in Britain, the following recommendations are made for management;

- Moderate grazing regimes should be used that reduce establishment of scrub and invasive emergents with heavier animals such as cattle or horses to produce poached watercourse margins and a diversity of tussock structure.
- Intermittent selective hand clearance of vegetation is recommended within watercourses in both biotopes. Cut vegetation from clearance should be deposited on only one bank or area of the site.
- On chalkstream ditches, hand-cutting of bankside herbs and rushes may be beneficial within short stream sections and on a rotational basis.
- Burning 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. Burnt vegetation should be removed from the site to minimise pollution.
- Drop board weirs can be used on water meadow ditch systems to maintain water availability through spring and summer.
- Canalisation, drainage, abstraction and dredging of watercourses and peat cutting should be avoided near watercourses occupied by the Southern Damselfly.
- Nutrient run-off from farmland should be minimised in catchments of watercourses containing the Southern Damselfly populations by minimising the use of artificial fertilisers. Agricultural land, adjacent to Southern Damselfly sites in Britain should be used extensively or a buffer strip of extensively used land, of at least 20m, should be maintained around watercourses.
- Empty sites, within 1-3 km of extant populations should be actively managed to facilitate dispersal.
- Re-introduction to empty habitat patches is not considered a priority for this species in Britain.

In light of the above information on habitat attributes required by the Southern Damselfly, this report suggests upper and lower thresholds for each attribute to allow habitat conditions for this species to be monitored. With regards to monitoring of the species itself, the mature adult stage is the most appropriate life stage to sample. Consideration for each site should be given to the maximum count of individuals normally supported on a site as a species attribute to be met. Monitoring visits should be carried out between early July and mid-July, 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.

Fixed transects (of a known distance) should be walked along waterbodies (or mire where streams are more diffuse) to include areas of both low and high concentrations of individuals. and the time taken to walk transects should be recorded in order to make sure that similar amounts of time are taken on each visit.

Future work should be directed at the habitat requirements and mortality factors of the larval stage – the stage in which 95% of the Southern Damselfly life cycle is spent - and in particular, at the habitat attributes required by the species in its chalkstream biotope. The latter is the subject of a second PhD commissioned by the UK Steering Group in 2001.

CONTENTS

1. INTRODUCTION

Chapter Summary

The Southern Damselfly (*Coenagrion mercuriale*) has been singled out for individual species protection in Britain and Europe since it:

- **has a restricted global and British distribution.**
- **has declined in its British distribution in the last century.**
- **has small population sizes in Britain.**
- **is stenotopic and occupies two scarce and threatened biotopes in Britain.**

Why is the Southern Damselfly in need of conservation?

Very few insects are given individual species protection but are instead conserved as a by-product of the protection of their biotopes (Samways, 1994). Within Britain and Europe, the Southern Damselfly (hereafter referred to as SD in figures and tables) is afforded individual species protection since it fulfils several of the criteria commonly used to assess rarity.

Box 1.1 – some definitions

biotope – the physical local area where a species lives.

habitat – concept emphasizing the interaction between the species and the physical habitat structure where this interaction depends on aspects of a species' behavioural ecology and life-history.

stenotopic – species that are confined to one or a few biotopes e.g. for odonates, stenotopic species are those that are highly sensitive to a number of habitat factors such as sunlight, shade, water flow and vegetation structure.

eurytopic - species that are found across a range of biotopes e.g. for odonates, eurytopic species are not sensitive to as many such factors and can colonise newly formed, sparsely vegetated lentic conditions common in artificial waterbodies.

Odonates as a group are in need of protection

Odonates in general have been declining. Their wetland biotopes have been subject, more than most biotopes (Thomas, 1991), to fundamental destruction due to processes such as drainage, pollution, eutrophication, and inappropriate management (Foster, 1991; Thomas and Morris, 1995). Odonates are restricted to water in their egg and larval stages and use open water areas for breeding (Corbet, 1980). They are generalist carnivores but still require particular shelter, roosting, and egg-laying areas and are thus susceptible to wetland fragmentation (Samways, 1993).

A review of the status in Europe of 164 indigenous odonate species found that 61 were considered endangered, vulnerable or rare under IUCN red data book categories (Van Tol & Verdonk 1988 – the global IUCN status of the Southern Damselfly was vulnerable). Decline or extinction of odonates in Europe was particularly noticed among species of lakes, peat bogs, mesotrophic marshlands and rivers.

Attributes of a species are used to define categories of rarity including geographical range, the size of its populations and the degree to which it is restricted to a particular biotope. Next, we shall discuss why the Southern Damselfly is rare in relation to these attributes as discussed in the following section.

The Southern Damselfly has a restricted global and British distribution

The Southern Damselfly has a restricted distribution at both a national and global level. It is limited to the south and west of Europe (Figure 1.1) and has populations of unknown status in northern Africa.

Populations in Italy and northern Africa consist of different sub-species (*C. m. castellani* and *C. m. hermeticum* respectively) to other European populations. 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).

The Southern Damselfly is on the northern edge of its range in Britain and has a discontinuous distribution, and is again restricted mainly to the south and west of the country. Figures 1.2 and 1.3 show maps of the United Kingdom (UK) distribution at a 10km resolutions. Figures 1.4 and 1.5 show 100m resolution maps for the New Forest and Pembrokeshire in more detail. The information in these figures is derived from a database of 1166 British Biological Records for the Southern Damselfly up to 1999 that was collated from a variety of national and regional sources (listed in W1-021/PR).

Figure 1.1 Global distribution of the SD – (taken from Askew, 1988).

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 (Figures 1.3 and 1.4, Table 1.1). Populations on Anglesey and Oxfordshire occur on poor fen which could be considered to be a third biotope for the Southern Damselfly in Britain. There are large centres of population on water meadow ditch systems along the Itchen Valley and smaller populations along the Test Valley (chalk rivers) which have been discovered relatively recently (Mayo and Welstead, 1983; Stevens and Thurner, 1999; Strange, 1999).

Examination of when the Southern Damselfly was last recorded at each 10km grid reference (symbols on Figures 1.2 and 1.3) 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) Pembrokeshire (Letterston) and Cardiganshire (Llanrhystud). Thus although the Southern Damselfly has been recorded in 35 10km squares since 1975 only 28 of these have been re-recorded since 1990. The rate of this decline is quantified in more detail in the next section.

Existing biological data are not sufficiently accurate to allow the number of discrete populations of the Southern Damselfly in Britain to be determined, but this figure must lie between 100 and 150 populations (Table 1.1).

Table 1.1 Probable number of discrete SD populations in each region of Britain.

Region	No. of different 100m grid squares in which the SD has been recorded since 1990	No. of discrete populations thought to occur in region
Oxfordshire	1	1
Dartmoor	2	2
Devon	4	2
Dorset	16	6
New Forest	59	36
Itchen and Test	40	20+?
Anglesey	8	2 (1 found in 2000)
Pembrokeshire	187	20-40
Gower	6	2
Total	323	92 – 150?

In Europe, the Southern Damselfly has been recorded in at least 260 sites in Germany (Kuhn, 1998; Sternberg et al., 1999), over 400 sites in France (Grand, 1996) and is said to be widespread in Spain (Grand, 1996). Thus it is unlikely that Britain contains up to 25% of the global population of the Southern Damselfly as suggested by previous authors (HMSO, 1994).

Why is the Southern Damselfly restricted to a south-westerly distribution both within Europe and in Britain? As a group, odonates are thermophilic, having originated in the tropics. Thus their distributions are often strongly restricted by climatic factors and an increase in species richness of odonates along a gradient from north to south of Britain has been reported. The edge of the Southern Damselfly's distribution has been said to follow the 2.2ºC February minimum isotherm (Chelmick, 1980) and the species is found in oceanic areas with a relatively mild climate.

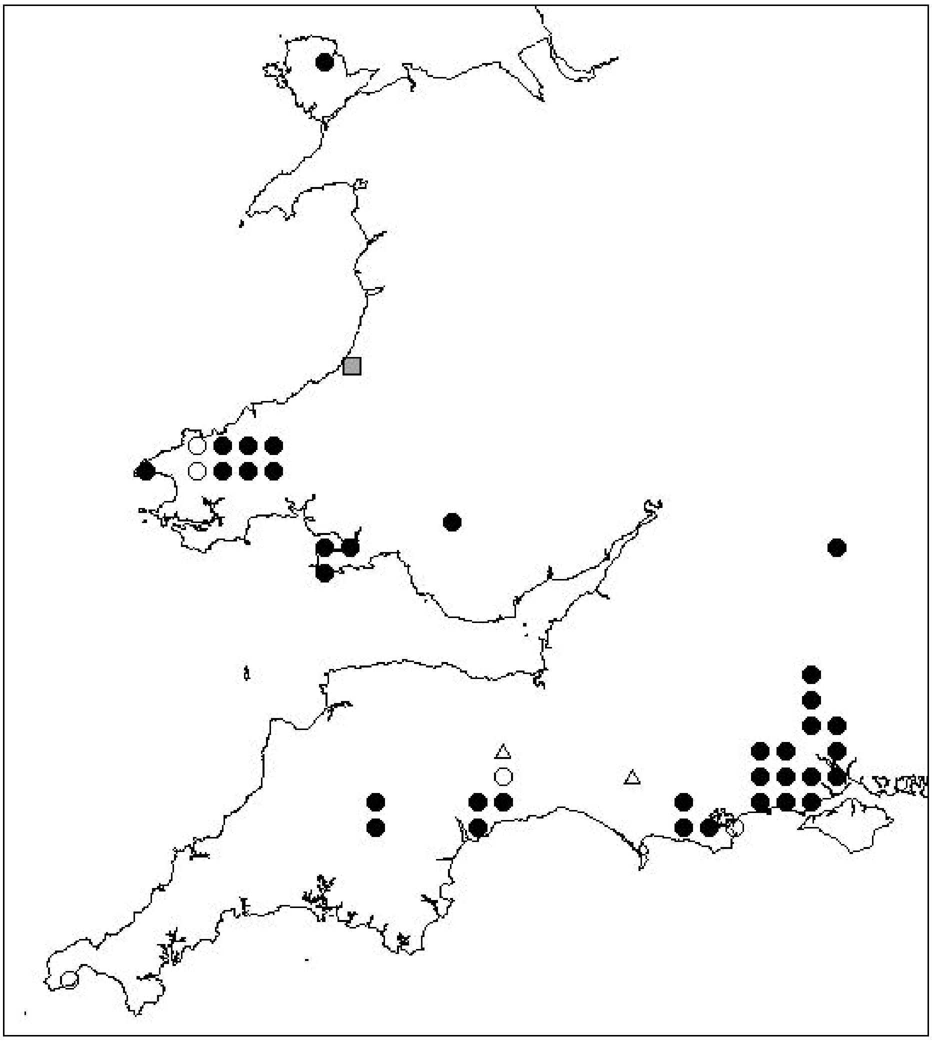


Figure 1.2 Distribution of the SD in the UK at a 10km grid reference resolution. Symbols indicate the 25 year period in which the Southern Damselfly was last recorded at a particular grid reference according to the following key; Closed circles – 1975-1999, open circles – 1950-1974, grey squares – 1925-1949, open triangles – 1900-1924.

Outline of the UK on Figures 1.2 and 1.3 is reproduced with the permission of Ordnance Survey on behalf of the Controller of Her Majesty's Stationery Office © Crown copyright. Unauthorized reproduction infringes Crown copyright and may lead to prosecution or civil proceedings. Environment Agency, GD03177G, (2002).

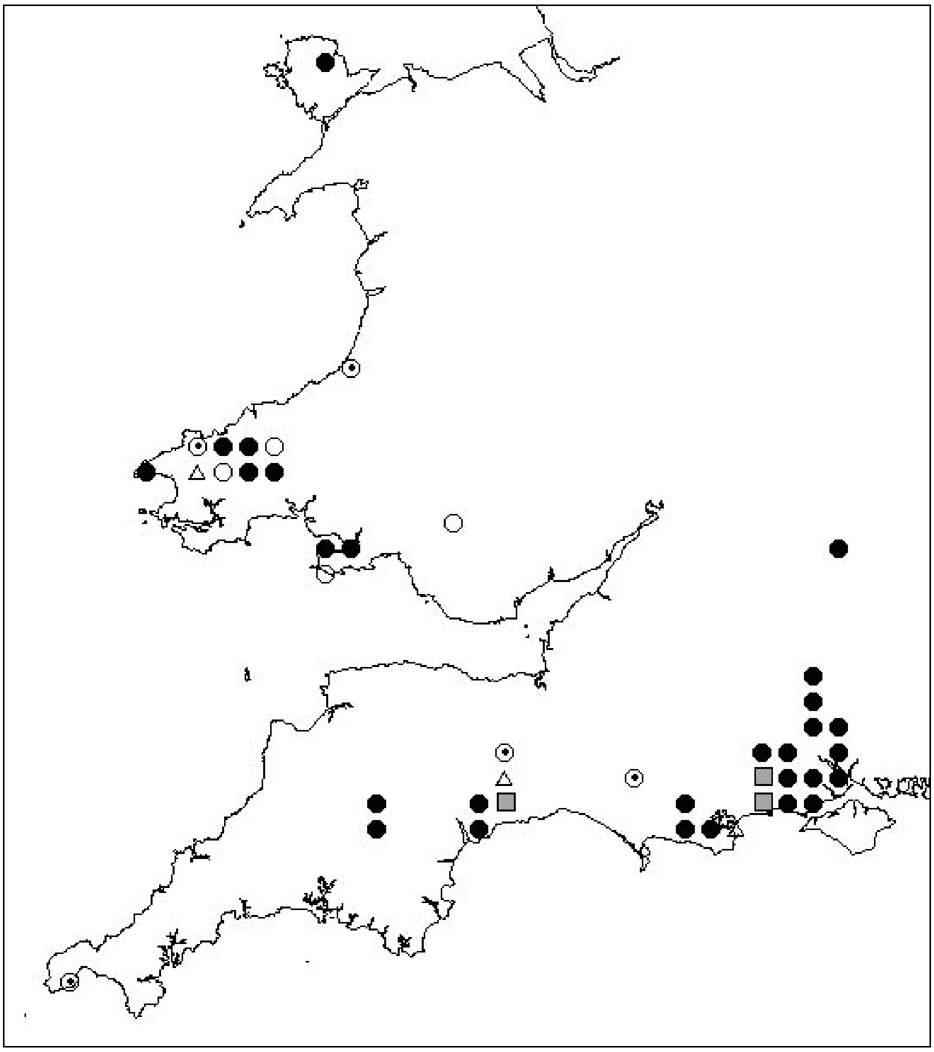


Figure 1.3 Distribution of the SD in the UK at a 10km grid reference resolution. Symbols indicate the decade in which the Southern Damselfly was last recorded at a particular grid reference according to the following key; Closed circles – 1990-1999, open circles – 1980-1989, grey squares – 1970-1979, open triangles – 1960-1969, dotted circles – pre-1960 records.

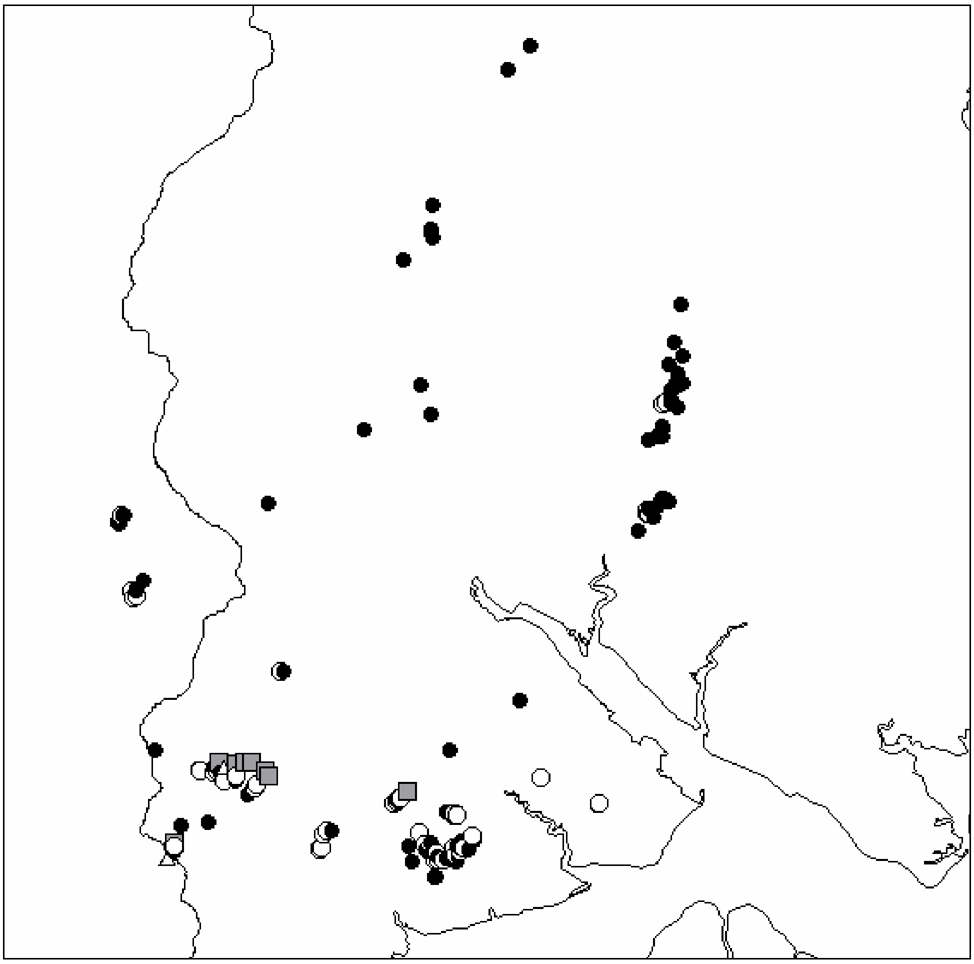


Figure 1.4 Distribution of the SD in Hampshire at a 100m grid reference resolution (see legend of Figure 1.3 for symbols).

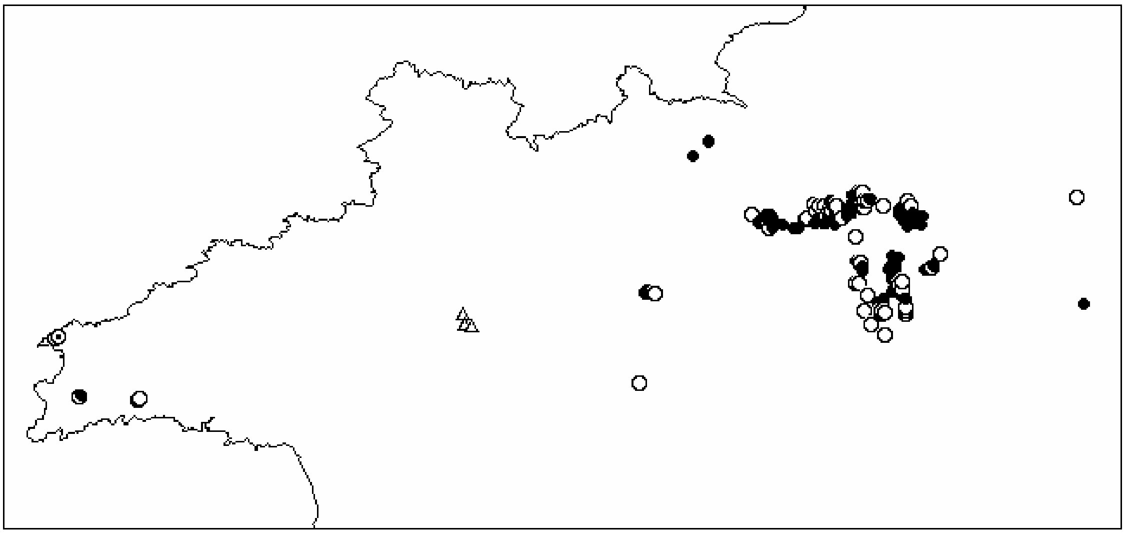


Figure 1.5 Distribution of the SD in Pembrokeshire at a 100m grid reference resolution (see legend of Figure 1.3 for symbols).

Within the New Forest (Figure 1.4), there is a greater incidence of colonies on the southern heaths than on the northern ones (Winsland, 1985). This species' requirement for high temperature is reflected in aspects of its development and habitat use as described in subsequent chapters.

The British distribution of the Southern Damselfly has declined by at least 30% in the last century

It is difficult to quantify the rate of a species' decline using biological records due to variation in recording effort through time, between regions and between habitats. For the Southern Damselfly, there has been a dramatic increase in recording effort through time (Figure 1.6). The number of different grid squares in which the Southern Damselfly is recorded has also increased through time, not due to range expansion, but due to the increase in recording effort since a large proportion of grid squares are newly recorded even in recent years (Figure 1.7).

There is also considerable regional variation in recording effort (up to 1999) at both a 1km and a 100m grid square resolution (see Tables 1.3b and 1.3c - expressed as number of records per grid square for squares recorded since 1990).

The rate of decline (D) of the Southern Damselfly in the last century was calculated for each region as follows;

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

where a is the number of grid squares in which the Southern Damselfly was recorded between 1990 and 1999 and b is the total number of grid squares in which it was recorded. The analysis was performed with all squares (D_{all} assuming that any colony that exists after 1990 also occurred before 1990) but also omitting (from a and b) those squares newly recorded since 1990 (D_{corr}).

Table 1.2 shows the total rate of decline in Britain at each resolution and Tables 1.3 a to c show the rate of decline for each region at each grid square resolution. The Southern Damselfly has undergone at least a 30% decline in its British distribution last century – at a 1km grid square resolution. There are not sufficient data to calculate decline of the Southern Damselfly since 1990 but few populations are known to have gone extinct since then. In contrast, in Baden-Wurttemberg, Germany, 41% of populations (58 out of 141) have disappeared since 1983.

Although a much higher rate of decline in the last century was found at the 100m grid square resolution this is probably an over-estimate. Several six figure grid references are often given a site because the recorder's perception of the colony centre has changed over time and thus they do not indicate site extent.

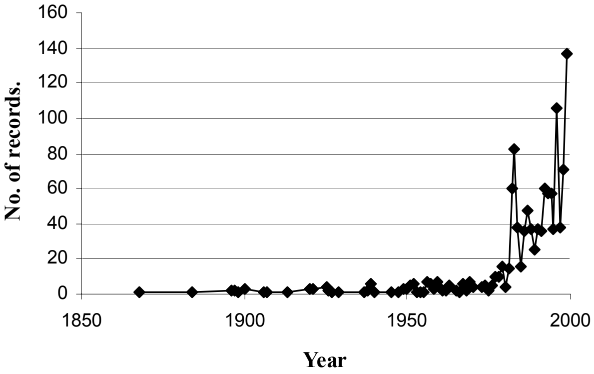


Figure 1.6 Total number of records of the SD in each year.

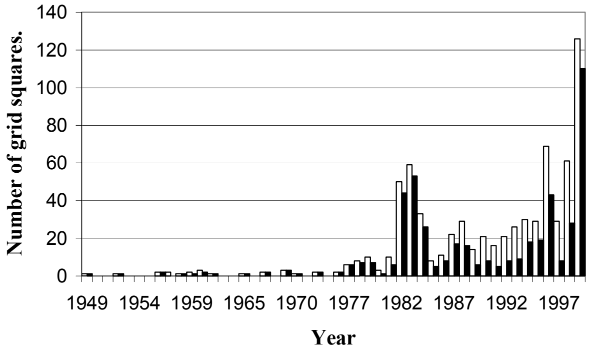


Figure 1.7 Total number of 100m grid squares recorded as occupied by the SD each year (open bars) and the number of squares in which this species was newly recorded in each year (closed bars).

Table 1.2 Percentage decline of the SD in Britain in the last century at 10km, 1km and 100m grid square resolutions.

Resolution	*a*	No. newly recorded since 1990	*b*	D_{all} (%)	D_{corr} (%)
10km	29	8	43	32.6	40.0
1km	103	42	148	30.4	42.5
100m	316	249	479	34.0	70.9

Table 1.3a Analysis of percentage decline of SD distribution at a 10km grid square resolution.

Region code	Region name	a	No. 1st recorded in/after 1990	*b*	D_{all} (%)	D_{corr} (%)
10	Cornwall	1	0	1	100	100
12	St David's	1	0	3	66.7	66.7
20	Dartmoor	2	2	2	0	0
21	Gower	2	0	3	33.3	33.3
22	Pembrokeshire	4	1	8	50	57.1
23	Anglesey	1	0	1	0	0
30	Devon & Dorset	5	2	6	16.6	25
31	Devon	0	0	3	100	100
40	Hampshire	2	0	4	50	50
41	Hampshire & Oxfordshire	11	3	12	8.3	11.1
	Total	29	8	43	32.6	40.0

Table 1.3b Analysis of percentage decline of SD distribution at a 1km grid square resolution.

Region code	Region name	*a*	No. 1st recorded in/after 1990	*b*	D_{all}	D_{corr}	No. of records in *a* squares	No. of record per square
12	St David's	2	0	5	60.0	60.0	2	1.0
20	Dartmoor	2	2	2	0	0	6	3.0
21	Gower	2	0	5	60.0	60.0	7	3.5
22	Pembrokeshire	30	7	40	25.0	30.3	52	1.7
23	Anglesey	1	0	1	0	0	7	7.0
30	Devon & Dorset	13	6	23	43.5	58.8	49	3.8
31	Devon	0	0	2	100.0	100.0	-	-
40	Hampshire	10	4	16	37.5	50.0	24	2.4
41	Hampshire & Oxfordshire	43	23	54	20.4	35.5	69	1.6
	Total	103	42	148	30.4	42.5	-	-

Table 1.3c Analysis of percentage decline of SD distribution at a 100m grid square resolution.

Region code	Region name	*a*	No. 1st recorded in/after 1990	*b*	D_{all}	D_{corr}	No. of records in *a* squares	No. of record per square
12	St David's	2	1	11	81.2	90.0	2	1
20	Dartmoor	2	2	2	0	0	6	3
21	Gower	9	7	16	43.8	77.8	11	1.2
22	Pembrokeshire	180	156	237	24.1	70.4	205	1.1
23	Anglesey	5	3	7	28.6	50.0	13	2.6
30	Devon & Dorset	19	15	43	55.8	85.7	51	2.7
31	Devon	-	-	-	-	-	-	-
40	Hampshire	25	13	49	49.0	66.7	37	1.5
41	Hampshire & Oxfordshire	74	52	114	35.1	64.5	83	1.1
	Total	99	303	163	34.0	70.9	-	-

A large proportion of British populations of the Southern Damselfly are probably small in size

Population sizes have been obtained for few if any Southern Damselfly 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 Figure 1.8.

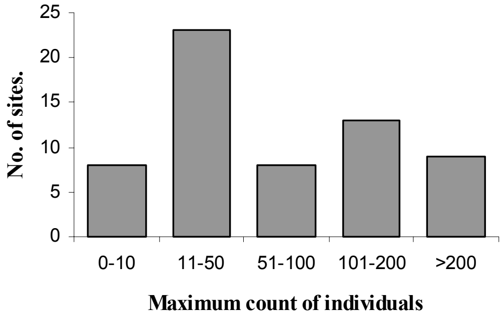


Figure 1.8 Maximum counts of individuals in SD sites in Britain (*n*=61).

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 6). Thus annual population sizes could be up to ten times larger than maximum adult counts and half of the 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. Having said this, maximum counts in 51% of British Southern Damselfly populations were less than 50 and thus these populations are probably small and at risk of extinction from stochastic environmental events.

The Southern Damselfly is stenotopic and is restricted to two main, scarce and fragmented biotopes in Britain

As well as being restricted to the south and west of Britain, the Southern Damselfly's distribution is discontinuous within these areas. This is because this species only breeds in two main biotopes – small streams on heathlands and old water meadow ditch systems on chalkstreams – both of which have undergone considerable fragmentation this 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 in heathland 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 (HMSO, 1995; Ladle, 1991). Changes in the management of water meadow ditch systems have threatened the existence of the ditches in particular (Sheail, 1971) probably limiting the current distribution and continuity of the Southern Damselfy 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.

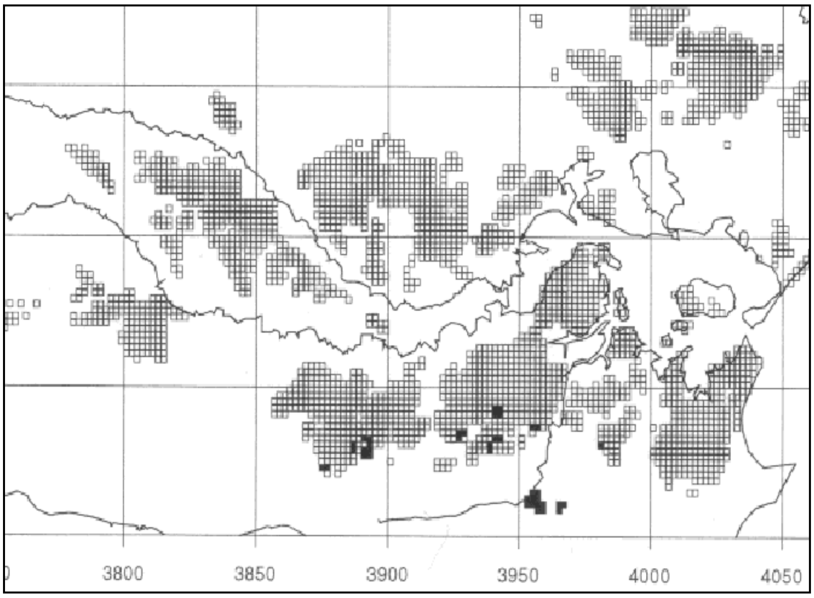


Figure 1.9. The distribution of the SD (closed squares) in Dorset in relation to the distribution of heathland (open squares). This figure was produced by Rob Rose, using the Dorset Heathland Survey, at the Institute of Terrestrial Ecology, Wareham.

As mentioned above, populations in Anglesey and Oxfordshire are found on a third biotope - poor fen.

In Europe, the Southern Damselfly also occupies three scarce biotopes;

- meadow brooks and ditches on the alluvial plains of the Rhône in France and in Bavaria and Baden Württemburg Germany.
- headwaters of major rivers (marshy flatlands) such as the Upper Rhine in Germany, and the Rhône and Durance in France.
- runnels in pre-alpine calcareous spring marshes on the edge of its range in the Alpine region, Bavaria, Germany.

However, the decline of the Southern Damselfly is likely to be due to factors operating at the habitat as well as at the biotope level. This species has a discontinuous distribution even within its biotopes. For example, in Dorset, the Southern Damselfly occupies a very small fraction of available heathland (Figure 1.9) In addition adult and larval populations have a very localised distribution within potential stream habitat on a single site (Corbet, 1957; Evans, 1989; Knights, 1983). Questionnaire data (see Chapter 2) show that the amount of habitat actually used by Southern Damselfly adults ranges from 26-100% of the potential stream habitat present on site. Similarly in calcareous spring mires in Germany, the Southern Damselfly is restricted to 20-100m lengths of stream habitat. These observations suggest that the Southern Damselfly is stenotopic and has very specific habitat requirements within heathland and chalkstream waterbodies and it is these habitat preferences that are the subject of the next chapter.

In addition, the Southern Damselfly may be in greater need of conservation in Britain since it is on the edge of its range here. 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. Thus they are often more prone to extinction on range edges. Since insects are poikilothermic and need to raise their body temperatures above a threshold before activity becomes possible they thermoregulate by selection of appropriate microclimates. Thus small differences in mean temperature can have a large effect on habitat availability for insects in temperate regions and species often occupy narrower niches within biotopes towards the northern edges of their ranges. Thermophilic insect taxa such as dragonflies will be particularly adversely affected at northern range edges. Intraspecific comparisons of the functioning of core and edge of range populations are particularly pertinent in such species (Thomas et al., 1999).

Thus the Southern Damselfly has been singled out for individual species protection in Britain and Europe due to its restricted and declining distribution, the small number and size of its populations, its occupation of only two or three scarce biotopes and its highly specific habitat requirements even within these biotopes.

Legislative Status of the Southern Damselfly

The Southern Damselfly is listed as a priority species for conservation in Britain (UK Biodiversity Action Plan, HMSO 1995) and Europe. Many countries have taken complementary legislative measures for its protection (Box. 1.2). In Britain, very few Southern Damselfly sites occur outside of Special Sites of Scientific Interest (SSSI) or Special Areas for Conservation (SAC). The Southern Damselfly was added to Schedule 5 of the Wildlife and Countryside Act in 1998. The Norfolk Hawker (*Aeshna isoceles*), is the only other resident British dragonfly species to be listed. Although other dragonfly species are listed on the European Community Species and Habitats Directive, the Southern Damselfly is the only resident British dragonfly species to be listed.

Box 1.2 Protection measures for the SD

Legislation or convention.

1. listed on the Bonn Convention for the conservation of Migratory Species of Wild Animals.
2. listed on Appendix II of the Berne Convention, Convention on the Conservation of European Wildlife and Natural Habitats (1979).
3. listed on Annex II of the European Community Habitat and Species Directive (1992) which requires that special areas of conservation (SACs) be designated for animal and plant species of community interest.
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.
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 1996).
6. subject of a UK Biodiversity Action Plan (HMSO 1995).

Species description and identification

The Southern Damselfly, *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 the Southern Damselfly is the smallest. Adult male Southern Damselflies can usually be distinguished from other British blue damselflies by the 'mercury mark' on the 2nd abdominal segment (Figure 1.10). Given variation in this mark, the anal appendages and black spines along abdominal segments 3-5 are more reliable characters for identification (Askew, 1988; Hammond, 1983). There are two female forms or morphs. The more frequent heterochrome (gynomorph) 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 (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 these pale markings described above, and from *Coenagrion pulchellum* by the straight hind margin of the pronotum (Askew, 1988; Hammond, 1983). Additional characters for both sexes include a short, lozenge-shaped pterostigma, and large, rounded, post-ocular spots.

Figure 1.10 Mercury mark found on the 2nd abdominal segment of male Southern Damselflies.

Larval Southern Damselflies can be distinguished from other damselfly larvae on the basis of their caudal lamellae and the shapes of the head and prothorax as described by Gardner (1950) and Corbet (1955).

2. LARGE-SCALE HABITAT USE - WHAT MAKES A SITE SUITABLE FOR THE SOUTHERN DAMSELFLY?

Chapter Summary

- **A wide range of habitat features was found to be common to British Southern Damselfly sites (these are listed in full in Table 2.11). Thus the Southern Damselfly is stenotopic.**
- **The thermal requirements of the Southern Damselfly were reflected in its use of small, exposed, spring or groundwater-fed, waterbodies at low altitudes.**
- **These requirements limit the Southern Damselfly to an early seral stage of succession such that its habitat is maintained by particularly active management regimes.**

Introduction

In this chapter, the large-scale habitat requirements of the Southern Damselfly in Britain are inferred indirectly from examination of:

1. Habitat features that often occurred in sites where populations were found.
2. Habitat features that, when altered had a positive or negative impact on population numbers or persistence.
3. Habitat features that, when altered produced a change in distribution of the species within a site.

Information on such habitat features was obtained from Southern Damselfly site documents, 14 site questionnaires (sample in Appendix 1) and a water chemistry survey carried out in 1998 (see W1-021/PR for details). Documents covered only 76 extant sites including all populations in Dorset, Devon, Gower, the New Forest and Oxfordshire. For Pembrokeshire and the Itchen and Test Valleys only a small fraction of extant populations were covered and for Anglesey, only 1 of 2 extant populations was described.

Box 2.1 – Proximate cues and ultimate factors

Proximately, habitat use is a behavioural consequence of an individual selecting, using cues, where to live (or passively remaining in a habitat). Ultimately, habitat use is determined by natural selection due to the different likelihood of survival and reproduction in different habitats.

Biotope and habitat features examined include 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). Vegetative factors were given particular consideration since plants are used by dragonflies at all stages in their life cycle (e.g. providing cover for larvae, perches at emergence and breeding and substrates for egg-laying - Buchwald 1992) and because macrophytes play a major role in determining habitat structure. Appendix 2 shows selected parts of the site document database – including site name, grid references, sources of literature and some information on habitat factors for each site.

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 this chapter '-' indicates that information was not available for a particular site or region.

The water chemistry survey was carried out in April and May 1998 when 91 water samples were taken from 53 extant and 7 extinct British Southern Damselfly sites. Samples were taken from sources of flushes as well as from streams sections that the Southern Damselfly was known to utilise. Conductivity and pH were measured in the field. Nitrate, ammonia, soluble reactive phosphate, total soluble phosphate, total phosphate, soluble unreactive phosphate and particulate phosphate were measured in the laboratory (see W1-021/PR for details of methods). Since these samples provide only a 'snapshot' of chemical conditions on sites, monthly water chemical samples (and stream dimensions) were taken from Glan-yr-afon Uchaf, Pembrokeshire between 18th October 1999 and 3rd October 2000. These were analysed by the Environment Agency. A datasonde (Hydrolab Datasonde 3 Water Quality Logger) was placed in the stream for two months (from 3rd December 1999 to 12th February 2000) to record temperature, pH and conductivity at half-hourly intervals.

The aims of this examination of habitat features required by the Southern Damselfly across British sites were several:

1. to determine why this species has a discontinuous distribution within its biotopes and to see how stenotopic it is compared to other odonates.
2. to compare habitat use at the edge of its range with that in core European populations.
3. to identify the main threats to Southern Damselfly habitat in Britain.
4. to summarise the proximate features used by the Southern Damselfly across sites (and the possible ultimate factors governing their selection – Box 2.1) to contribute to the identification of habitat attributes that indicate favourable habitat condition for this species (Chapter 7).

In this chapter, documents containing information on British sites are referenced in the text. For European biotopes, information was obtained from Sternberg (1999) and Kuhn (1998) but also from the following sources for;

- meadow brooks and ditches of Baden-Württemburg, Germany – (Buchwald, 1994; Roske, 1995; Buchwald et al., 1989), of the Rhône and Durance, France – (Deliry and Grand, 1998).
- pre-Alpine, calcareous spring marshes, Germany – (Buchwald, 1983; Buchwald, 1994).
- marshy flatlands of the Upper Rhein (Buchwald et al., 1989).

Thus these references are not cited in the text.

Topography and geology

In Britain, Southern Damselfly sites are mainly found at low altitudes

Eighty-two percent of British Southern Damselfly sites occur at or below 90m above sea level (a.s.l.). and the majority are found between 16 and 45m a.s.l. (maximum 285m a.s.l. - Table 2.1). However, the Southern Damselfly is able to occupy higher altitudes further south in its distribution. In Central Europe, it occupies moderate altitudes (mostly below 400m a.s.l. in France and between 400 and 500m a.s.l in sites on meadow brooks and ditches in Germany) but survives at high altitudes of up to 1500m in Spain, 1600m in Switzerland and above 1900m in Morocco. In other edge-of-range populations, in the alpine range in Germany, the species can occupy higher altitudes (between 500 and 920m a.s.l.) since cooler temperatures at higher altitudes may be offset by thermal constancy of the springs feeding these marshes or by selection of habitats exposed to the sun.

In Britain, Southern Damselfly sites are found on very gently sloping ground.

64% of Southern Damselfly sites are situated on slopes of less than 5% (Figure 2.2) and only 3% on slopes of greater than 10%. The Southern Damselfly may be restricted to shallow slopes due to requirements for slow flow (discussed later). Unfortunately, data were not available on aspect of slopes occupied by the Southern Damselfly in Britain.

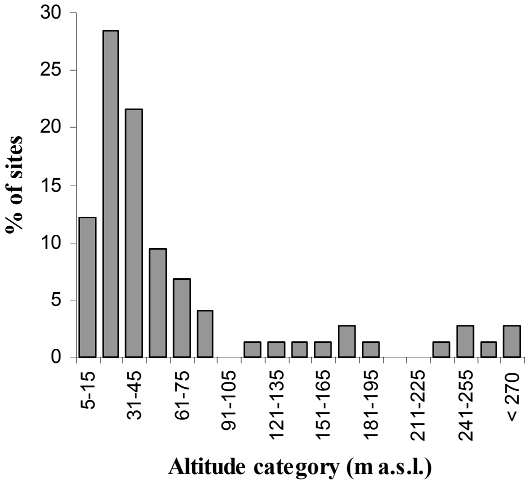


Figure 2.1. Percentage frequency distribution of sites (n=74) across different altitude categories.

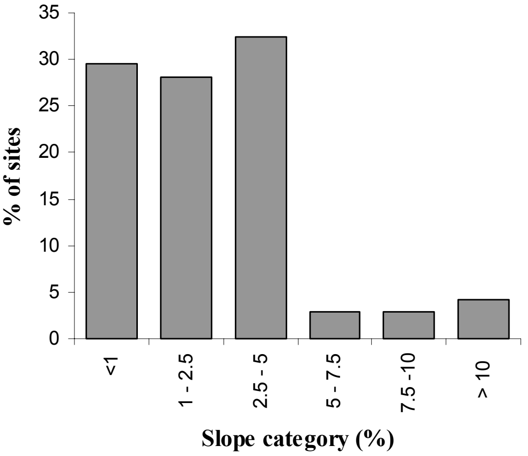


Figure 2.2 Percentage frequency distribution of sites (n=71) across different slope categories (where – 2.5 means up to but not including 2.5).

In Britain, waterbodies occupied by the Southern Damselfly are fed by water emanating from soft, calcareous deposits.

Rock types influence topography, chemical composition of substrate and water, the amount of sediment entering the stream and the physical composition of the substrate. Most heathland streams occupied by the Southern Damselfly 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 2.1). 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 the Southern Damselfly. It is also found under many water bodies occupied in France. These soft rocks are particularly susceptible to weathering especially where most flow is sub-surface (i.e. near springs) and the effect of these processes on water chemistry is discussed later as is the effect of the porosity of chalk on flow regime.

Watercourse type and dimensions.

In Britain, the Southern Damselfly occupies small waterbodies.

Watercourses across most heathland sites in Britain consist of very shallow (<40cm), narrow (usually < 5m wide), slow flowing flushes and runnels (Table 2.2.) 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. 2.2.). In Germany there is similar variation between biotopes in the type of waterbodies occupied by the Southern Damselfly. On pre-alpine spring marshes, the species occupies shallow runnels, 2-20cm in width, that flow very slowly over peat or limestone mud. Occupied 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. They have a gravel substrate.

Waterbodies that occur on meadows, though still small, are often larger than those found on heathlands or calcareous mires and may offer larger areas of habitat, supporting larger populations of this species. 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. Similarly, chalkstream waterbodies in Britain, may support larger populations of the Southern Damselfly than heathland waterbodies.

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 in Europe. Such high temperatures may allow larval development, emergence and oviposition to proceed more rapidly.

Table 2.1. Range of altitude, slope and geology found in SD 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 (James and Wiggers, 2000; Merritt, 1983).
Devon	85-115	0-13%	Springs originate from calcareous sandstone overlaid with acidic pebblebed (Kerry, 1994; Knights, 1983).
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	35-270	0-16%	Clay deposits over laid with peat (Coker and Fox, 1985; Evans, 1989).
Gower	65-100	2-9%	Gravel deposits over laid with peat (Evans, 1989; Merritt, 1983).
Itchen & Test Valley	10-25	0-4%	Chalk reserves originating in gravel (Mayo and Welstead, 1983).

Table 2.2 Watercourse type and dimensions on SD sites in each region.

Region	Watercourse type, water source, flow rate, and substrate	Range of water depth (m)	Range of peat/silt depth (m)	Range of stream width (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)
Anglesey	Shallow, narrow, spring-fed, slow-flowing flushes, runnels and small pools over peat.	-	-	-	-
Pembrokeshire	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 overlaid 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 the Southern Damselfly.	max.1.5	-	0.75-10	-

The Southern Damselfly requires slow to moderate water flow

In Britain, larval Southern Damselfly populations are associated with areas of slow shallow flow on several sites (Waun Fawr - Evans, 1989; Povingdon Heath - James and Wiggers, 2000).

In addition, adult populations have been noted to avoid narrow boggy runnels with no depth at Millersford Bottom West and, at Highbridge, Russell's Meadow, they avoid areas with zero flow (Stevens and Thurner, 1999). On chalkstreams, adult populations have been found mainly 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 dense larval population. Even if flow in the main channel is moderate on chalkstream ditches, 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 (discussed later) were associated with Southern Damselfly populations in Baden Württemburg and in the Upper Rhine region in Germany.

The Southern Damselfly seems to require permanent water flow and proximity to springs or ground water

On heathland sites, watercourses are spring-fed (augmented by groundwater or clay pit outflows) and, on watermeadow ditch systems, are fed by chalkstream carriers (sometimes augmented by springs) (Table 2.2.). Thus the Southern Damselfly requires a permanent water supply on all its British sites and in Europe - on meadow brooks and ditches in Germany and France, and on calcareous spring mires in Germany.

As well as assuring the permanence of water flow in shallow waterbodies, springs maintain a higher than average temperature in winter (4-10 ºC 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 11ºC all year (Crisp et al. 1982, cited in Berrie, 1992). The scarce blue-tailed damselfly (*Ischnura pumilio)*, another species that is on the northern edge of its range in Britain and has a southern distribution here, is also restricted to spring fed watercourses or those near outflows from mineral extraction works (Fox, 1994).

As well as being found in areas with slow shallow flow, larval Southern Damselfly populations in Britain are only found in those portions of waterbodies that receive permanent flow (Evans, 1989; Hold, 1997; Skidmore, 1996).

The permanence of water flow is also indicated by vegetative factors on Southern Damselfly sites. For example, *Rorippa nasturtium aquaticum* and *Ranunculus* sp. occur on chalkstream sites (Tables 2.6-2.7) and indicate relatively high winter and spring water temperatures respectively. Many of the NVC communities associated with the Southern Damselfly 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 the Southern Damselfly, of the presence of particular plant species as cues to the permanence of the water supply is discussed later.

Threats to Southern Damselfly habitat due to reduction in temporal or spatial availability of water were noted on a substantial proportion of extant British sites (Table 2.3). The main causes of reductions in water availability were canalisation or artificial drainage and siltation or headward erosion.

Where populations have been monitored, reductions in water availability have had negative impacts on the population range and adundance of the Southern Damselfly within some British sites. Box 2.2 contains some examples. In Europe, the overall decline of European populations of the Southern Damselfly since the 1950s has also been attributed to drainage. Watercourses occupied by the Southern Damselfly on ditch systems in Baden Württemburg and in calcareous spring marshes, were those that never (or only partially) dried out or froze up. In addition, the Southern Damselfly has expanded its distribution and population size on British sites in response to an increase in water availability. These examples (Box 2.2) suggest that the Southern Damselfly responds positively to the creation of new areas of suitable watercourse adjacent to existing colonies.

Table 2.3 Number of extant British SD sites threatened by different factors.

General Threat	Specific threat -	No. of sites
Reduced water availability 22 sites	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 sites	Nutrient run-off	4
Overgrowth of streams 34 sites	Channel vegetation	7
	Bankside vegetation	27

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.

The Southern Damselfly occupies waterbodies with shallow ditch profiles

Most heathland sites consist of mires or runnels near spring sources (i.e. first order) and the bank usually rises only a few centimetres above the water level. On sites where the stream occurs in deeper gulleys, adults tend to be concentrated in areas where the banks are lowest (Stevens and 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 (see later). 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).

Box 2.2 Examples - population extinctions/reductions due to lack of water availability and population exapansions due to an increase in water availability

Extinctions

- Cosmore Common, Dorset in 1837 after drainage (Prendergast, 1996).
- Afon Brynberian, Pembrokeshire due to the creation of an artifical watercourse in 1983 (Skidmore, 1996).

Reductions

- Blackwell Common, New Forest due to a drought in the late 1980's (Jenkins *et al.* 1996) with a maximum count of one individual being recorded in 1990 (Stevens & Thurner, 1999)
- Outflow mire, Povingdon Heath, Dorset, due to the gradual accumulation of silt from the clay pit outflow since 1995 such that smaller streams were cut off from flow and have dried out (Winsland, 1994b; James & Wiggers, 2000).
- Millersford Bottom East, New Forest - decrease 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).
- Horsebush Bottom, New Forest, the lack of a permanent water supply (and annual drying out) prevents local recruitment to the population though adult populations have been found using the stream for breeding in late summer (Jenkins, 2001)

Expansions

- Povingdon Heath, Dorset due to the creation of an area of mire following flooding of an area of acid peatland by a clay pit outflow (Prendergast, 1996).
- Aylesbeare Common, Devon, where shallow pools, dug at intervals along the runnels in 1993 and 1994 (Kerry, 1994), were rapidly colonised by the Southern Damselfly (by 1998 – pers obs., Kerry, 2000).

The Southern Damselfly occupies waterbodies with inorganic substrates such as clay or gravel

The watercourses in British Southern Damselfly usually have an inorganic substrate such as clay or gravel (Table. 2.1) 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 (Evans, 1989; Knights, 1983)), 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 and Thurner, 1999). Although meadow brooks and ditches in Germany have gravel substrates, all have a 10-30cm layer of mud at their edges. On calcareous spring marshes, a substrate of peat or limestone mud is found. Whilst there has been some suggestion that early instar larvae live in these shallow organic deposits (Corbet, 1957) these are not supported by the larval experiments reported here (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.

Habitat types found on and around streams.

Whilst sites containing the Southern Damselfly in Britain can be broadly divided into those occurring on heathland or on chalkstream water meadow ditch systems, it is necesary 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 (Appendix 2), 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 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 (Figure 2.3). Acid and other types of grassland were also found particularly 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.

Table 2.4 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 (two Dartmoor sites, Hartland Moor and Sluxton Farm, – Table 2.7). Streams next to improved grassland may not be favoured by the Southern Damselfly since grazing stock will prefer this nutrient improved food supply rather than stream vegetation (Evans, 1989).

In contrast, in meadow brooks and ditches in Baden Württemburg, Germany, most Southern Damselfly sites are near intensively used agricultural areas. Here, the type and condition of adjacent agricultural land determines the suitability of the area for the Southern Damselfly, 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, the extent of cutting influences the habitat structure and in turn the microclimate and prey availability (see later). Similarly, the Keeled Skimmer, *Orthetrum caerulescens*, a lotic species that often co-occurs with the Southern Damselfly, prefers extensive wet meadow but will colonise farming land.

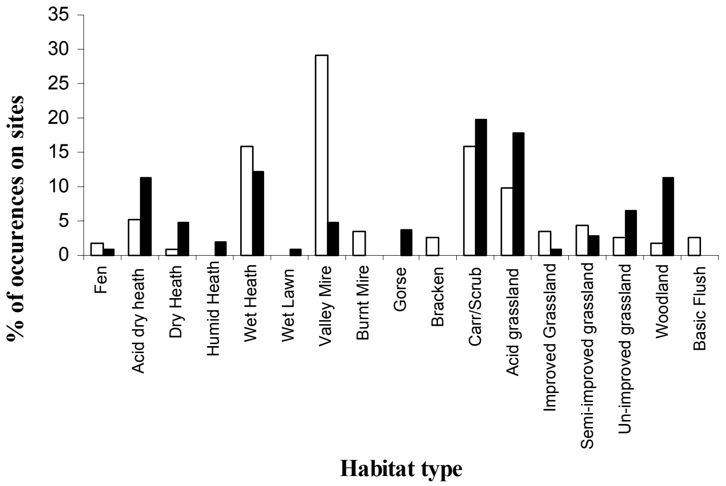


Figure 2.3. Percentage occurrence of different types of habitat in the immediate vicinity of (open bars) and surrounding watercourses (closed bars) on British SD sites (*n*=113).

Table 2.4 Habitat types and NVC communities found on British SD sites.

Region	Habitat type	NVC Communities
Oxford	Calcareous/ poor fen 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, at least 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 fen 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.

Plant species, plant communities and vegetation structure on stream and banksides in Southern Damselfly sites

The most prevalent plant species found near streams and surrounding streams are shown in Tables 2.6-2.7 together with the number of times they were present and formed a main component of the vegetation. Table 2.8 summarises the plant species composition by region.

The Southern Damselfly is not associated with a particular plant species or set of plant species across its range

The Southern Damselfly 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 and Wiggers, 2000). Breeding adults have been associated with *Rorripa nasturtium-aquaticum* agg., *Glyceria maxima* and *Apium nodiflorum* (Stevens and 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. However, *Hypericum elodes* and *Potamogeton polygonifolius* were found in the majority of heathland sites and *Glyceria maxima* was frequent in chalkstream sites (Tables 2.6-2.7). Given that no association has been found between Southern Damselfly populations and a particular plant species' prevalence, it is necessary to consider next what particular plant species indicate about chemical and structural features of the habitat. Such features of the habitat will be discussed in the next two sections drawing on information about plant species and communities as appropriate. The Southern Damselfly is also associated with a range of NVC community types (Table 2.4) with a range of habitat preferences (Rodwell, 1991).

In Britain, the Southern Damselfly requires open watercourses with sparse marginal or bankside vegetation.

For 11 sites where the openness of the water course was discussed specifically, 8 were described as open (Hold, 1997; Kerry, 1994; Smallshire, 1998; Evans, 1989; Stevens and Thurner, 1999; Strange, 1999). Bankside vegetation heights were less than 75 cm in the majority of sites for which there were questionnaire data.

Breeding adults are found in open areas (James and Wiggers, 2000; Stevens and Thurner, 1999; Strange, 1999; Woodman, 1999 – 10 sites), with short to medium edge vegetation (3-10cm Evans, 1989) or where *Juncus* sp. and *Molinia caerulea* tussocks are low (James and Wiggers, 2000; Stevens and Thurner, 1999). 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; James and Wiggers, 2000; Skidmore, 1996) 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 water margins (Strange, 1999).

Overgrowth of streams constitutes a significant threat to Southern Damselfly habitat in Britain

Overgrowth of streams was recorded as a significant threat to habitat on 34 British sites – further indicating the importance of open stream areas. In seven of these sites it was the runnel itself that was choked with vegetation whilst in the remainder the overhanging/bankside vegetation was too dense.

Table 2.5 Frequency of sources of overgrowth in different British SD sites.

Source of overgrowth	No. of sites
'Scrub'	14
Myrica gale	6
Juncus species (*J.acutiflorus*, *J. subnodulosus* and *J. effusus*)	7
Molinia caerulea (where it formed tall tussocks)	7
Schoenus nigricans	2
Sparganium erectum	1
Trees	4

On 23 sites some removal of scrub or trees has taken place recently (sometimes on an annual basis) to open up watercourses and on 22 sites further removal has been recommended. 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).

Scrub or tree removal has resulted in an increase in Southern Damselfly population size or range on several British sites.

On Creech Heath, Dorset, removal of willow, birch and pine scrub, lead to a movement of the population from above the waterfall to below - to an area which previously contained no Southern Damselfly (population count below the waterfall increased from 0 to 164 in consecutive years - Sutcliffe, 1998).

On Aylesbeare Common (Kerry, 1994; Kerry, 1999) 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) following a programme of grazing and clearance. Channels were initially overgown with dense tussocks of *Molinia caerulea* and *Schoenus nigricans*.

Table 2.6 Number of times the most prevalent plant species were present on streams on heathland and chalkstream SD sites (number of times they formed a main component of the vegetation in brackets).

Heathland sites *n*=53	No. of presences	Chalkstream sites *n*=13	No. of presences
Plant species		Plant species	
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 pseudocorus*	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 tenellum	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)	*Alopecurus praetensis*	2 (0)
Carex echinata	5 (1)	*Rumex hydrolapathum*	2 (0)
Sparganium erectum	5 (0)		

Table 2.7 Number of times the most prevalent plant species were present surrounding streams on heathland and chalkstream SD sites (number of times they formed a main component of the vegetation in parentheses).

Heathland sites *n*=53	No. of presences	Chalkstream sites *n*=13	No. of presences
Plant species		Plant species	
Molinia caerulea	*17 (12)*	*Iris pseudocorus*	*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 gallii	6 (0)	*Filipendula 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 erectum*	1
Mentha aquatica	4 (2)	*Urtica dioica*	1
Potentilla erecta	4 (0)		
Rubus sp.	4 (0)		

Table 2.8 Commonest plant species in watercourses and on banksides in each region (frequency of occurrence on SD 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, Succisa pratensis 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), *Sphagnum* 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 tetralix, 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), *Cirsium* sp.. (*C. dissectum* (1), *C. arvense* (1))

A heavy season of winter grazing in 1990 was followed by annual light summer grazing (May to October), producing 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 tenella, Drosera rotundifolia, Pinguicula lusitanica, Potamogeton polygonifolius*. The species expanded still further into the south of the site following clearance of woodland in 1997 (Kerry, 1999).

The majority of British Southern Damselfly sites are grazed and stronghold sites have moderate to heavy grazing regimes.

Table 2.9 shows the range of grazing regimes employed on British Southern Damselfly sites. All but a few 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 and reductions have been attributed to reductions in grazing regime (see Box 2.3). In 6 of 24 sites for which information was available, it was perceived that an increase in grazing intensity was required for maintenance of favourable habitat (Table 2.11). Grazing not only produces open stream areas favoured by the Southern Damselfly but also influences the structure and composition of bankside and edge vegetation as described later.

Box 2.3 Examples - population extinctions due to lack of cessation of grazing regimes

- St. David's Head, Pembrokeshire – after 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).
- Lower sector of Waun Isaf, Pembrokeshire- when grazing ceased, vegetation became rank and species poor, dominated by *Molinia* and rough herbage (Evans, 1989).
- Venn Ottery Common in Devon (Kerry, 1994) due to cessation of any grazing regime.

The Southern Damselfly requires sun-exposed watercourses in Britain and Europe

Exposure to the sun was found in every site occupied by the Southern Damselfly on meadow brooks and ditches in Germany with 70% being unshaded and 20% only partially shaded. In calcareous spring marshes, sections with concentrations of the Southern Damselfly were unshaded or only partly shaded. The average vegetation height was less than 1m, with a height of 20-40cm being optimal for the Southern Damselfly in calcareous spring marshes. Vegetation height in meadow brooks and ditches was always less than 60cm.

Open areas are partly required because shallow larval habitat will warm up quickly when exposed to the sun and to provide sun-exposed 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 Southern Damselfly sites.

In Britain, the Southern Damselfly prefers streams that are well vegetated.

The Southern Damselfly prefers streams that are generally well vegetated in the larval (Evans, 1989; James and Wiggers, 2000; Skidmore, 1996) and adult stages (Stevens and Thurner, 1999, pers. obs.). Breeding adults avoid sparsely vegetated watercourses such as those with gravel substrates (e.g. Hatchet Moor -Stevens and Thurner, 1999; pers. obs.). From questionnaire data, the mean percentage cover of submergent vegetation in areas where adult Southern Damselflies were found in Britain was 29.3 ± 7.0 (n=14, range 0-75%) and that of emergent vegetation was 42.0 ± 5.4 (n=14, range 8-75%). On chalkstream sites, ditches with concentrations of the Southern Damselfly 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 necessity 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 meadow ditches in Germany most Southern Damselflies were found in areas of 40% cover, with none found in areas of less than 10% cover.

Table. 2.9 Grazing regimes found in British SD sites.

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

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 grazing regime excessive.

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 the Southern Damselfly, probably providing cover for larval stages (and sufficient oxygen – see later), oviposition substrate and perching sites for adults.

Structural habitat features that may be indicated by the species composition of the vegetation include

- exposure to sun (see above).
- likelihood of build up of a fringe of emergent vegetation and slow water flow – indicated by silt-trapping, clump-forming species that occur on chalkstreams (*Veronica* sp., *Rorripa nasturtium-aquaticum* agg., *Apium nodiflorum* Haslam, 1978).
- *Sphagnum* sp. and other mosses were found on most heathland sites (even though they were under-recorded) and formed mats that support vascular plant 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).

Soft, semi-emergent, perennial herbs are prevalent on British and European Southern Damselfly sites and may be used as a cue to the permanence of water supply and the stability of temperature and vegetation cover.

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. In contrast to the finding of a range of communities on sites occupied by the Southern Damselfly 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 the Southern Damselfly 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 above. 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 the Southern Damselfly 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 (*Small Red Damselfly*), Cercion lindeni* and *Erythromma viridulum* (Small Red-eyed Damselfly) 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 Southern Damselfly 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.

The Southern Damselfly requires tussocky bankside vegetation for feeding and roosting in the adult stage and requires some degree of shelter from trees or tall scrubs.

The Southern Damselfly uses bankside vegetation in several ways. Tussocky vegetation, including *Molinia caerulea*, *Juncus effusus*, ericaceous species and gorse, is used for feeding and roosting (Hold, 1997; Hopkins and Day, 1997; James and Wiggers, 2000, pers. obs.; Skidmore, 1996; Strange, 1999). It is often found next to watercourses containing Southern Damselfly populations (e.g. 10/15 sites where bankside vegetation is 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, Southern Damselflies have been observed to use reeds (but not scrub or bramble) at heights of 40-50cm for roosting on meadows brooks and ditches and roost up to 10m from the breeding site and up to 100m in large populations. In calcareous spring mires, the optimal bankside vegetation height was 20-40cm reflecting the fact that these runnels are smaller and more easily overshadowed.

Most British sites occupied by the Southern Damselfly 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 the Southern Damselfly 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 Southern Damselfly 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 the Southern Damselfly, being associated with areas used by the species in 13 out of 24 sites in Table 2.9. This process opens up areas of bare silt or mud encouraging the rooting of shallow water plants (Painter, 1999) and emergent herbs (such as *Apium nodiflorum*) (Strange and 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 the Southern Damselfly. Trampled, gently sloping ditches also support a diverse insect fauna in general (Kirby, 1992).

A degree of shelter from trees and shrubs is also found in many sites (referred to as carr/scrub in Table. 2.3). 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, the Southern Damselfly 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 further 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).

Range of chemical parameters found in watercourses occupied by the Southern Damselfly.

Water chemical parameters are given for each sample in Appendix 3 and mean water chemical parameters for each region are given in Appendix 4.

pH, conductivity and temperature

The majority of sites had pHs of 7.0-7.5, though a wide range of pH was found in the watercourses on Southern Damselfly sites (Figure 2.4). This range of pH is similar to that found in the Upper Rhine valley (6.6 – 8.5). pH is seldom the proximate factor determining dragonfly distribution and numerous species show tolerance to a wide range of values similar to that reported here for the Southern Damselfly.

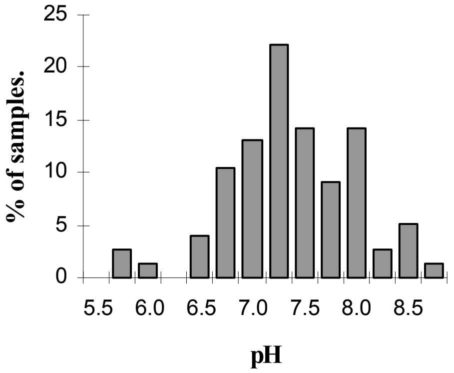


Figure 2.4 Percentage distribution of sites across pH values (*n*=77).

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 and Vodopich, 1992).

However, pH can indirectly affect invertebrates through its effect on vegetation. In Southern Damselfly sites on heathland, the existence of often base-rich water (due to underlying soft calcareous rocks) 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 *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. 2.8).

Consistent with measurements of pH, the base status of NVC communties (from Rodwell, 1991) associated with the Southern Damselfly 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. Figure 2.5 shows that most sites have fairly low values for conductivity (most are less than 150 uS/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 2.9).

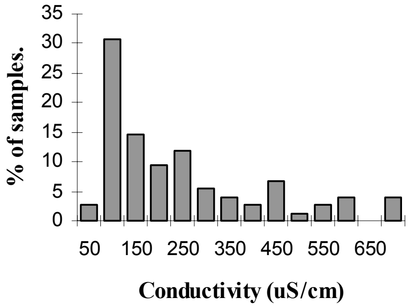


Figure 2.5 Percentage distribution of sites across conductivity values (*n*=75).

The mean and range of pH and conductivity (and other water chemical parameters) across monthly samples is shown in Table 2.9 whilst Figure 2.6a-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 2.10), the range of pH found across months (Table 2.10) and half-hourly periods (Figure 2.6c) was as wide as that found across sites for the Southern Damselfly. Conductivity was less variable within a site than across sites. Both of these parameters and temperature showed considerable diurnal variation (Figure 2.8). 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 pH (Allan, 1995). Photosynthesis, and thus carbon dioxide fixation and oxygen production, occurs only in the day time and proceeds more quickly at higher temperatures.

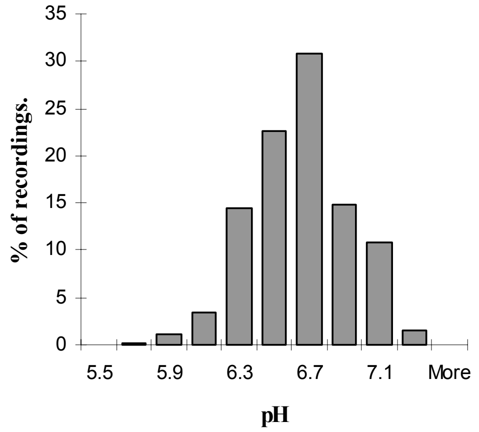


Figure 2.6a Percentage distribution of datasonde recordings over different pHs (Dec 1999-Feb 2000).

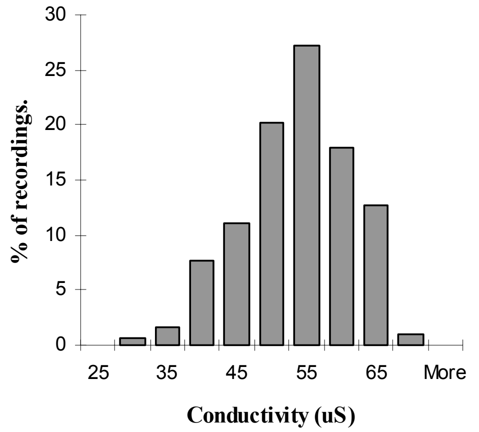


Figure 2.6b Percentage distribution of datasonde recordings over different conductivities (Dec 1999-Feb 2000).

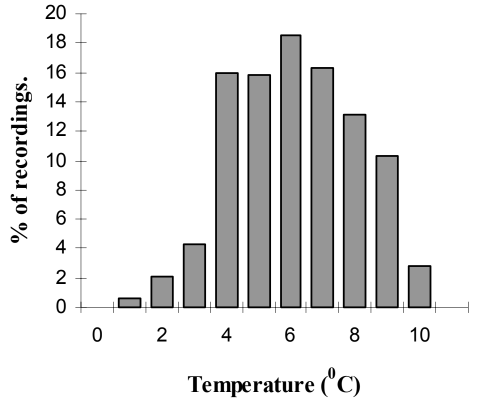


Figure 2.6c Percentage distribution of datasonde recordings over different temperatures (Dec 1999-Feb 2000).

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 the Southern Damselfly 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 the Southern Damselfly 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 (December 1999-February 2000), the temperature always remained above 0°C and mostly lay between 4 and 8°C (Figure 2.6c). 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.

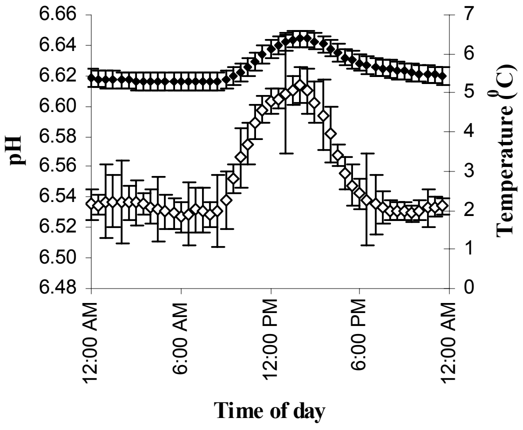


Figure 2.7a Mean (± s.e.) pH (closed squares) and temperature (open squares) in each half hour time period in a day (*n*=70).

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 2.10), compared to those in typical marine and coastal rainfall (from Berner & Berner, 1987 cited in Allan, 1995) though this difference was not as substantial as that between river water concentrations and rain water (Allan, 1995). Higher levels of these ions may result from weathering of rocks that has taken place before springs emerge.

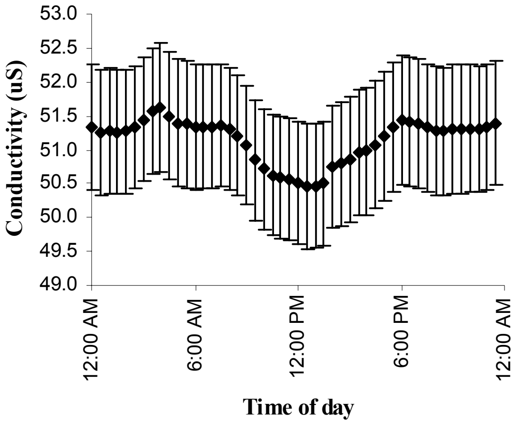


Figure 2.7b Mean conductivity (± s.e.) in each half hour time period in a day (*n*=70).

Stream concentrations of potassium, nitrate and ammonia were similar to rainwater or lower. One consequence of living in such small shallow streams is that Southern Damselflies are subject to considerable monthly variation in stream volume and flow rate (Figure 2.8a-d show monthly variation in width, depth, volume and flow rate for streams at Glan-yr-afron, Pembrokeshire for three larval sampling positions). Despite 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.

Interestingly, 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 (μ = 0.136 ± 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. The highest flow rate was found in September when stream volume was high and the lowest flow rate was found in July when the stream volume was low. 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.

Table 2.10 Mean (± s.e.), range and coefficient of variation (V), for chemical parameters from monthly samples from Glan-yr-afon Uchaf – units are mg/litre unless otherwise stated.

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

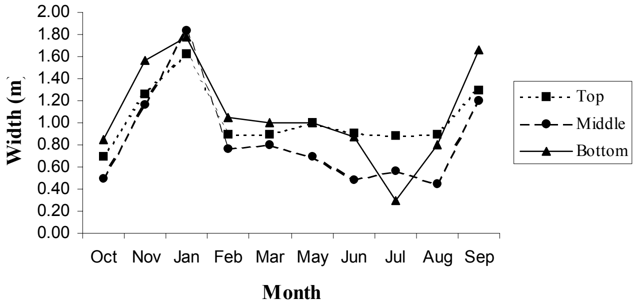


Figure 2.8a Monthly variation in the width of the Glan-yr-afon Uchaf stream – closed squares - top site, closed circles - middle site, triangles – bottom site.

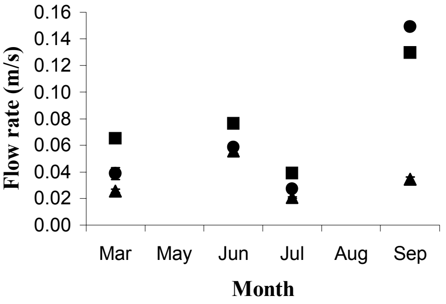


Figure 2.8d Mean flow rate of the Glan-yr-afon Uchaf stream (in m/s) for each position in four months of the larval sampling period. Key as for 2.9a.

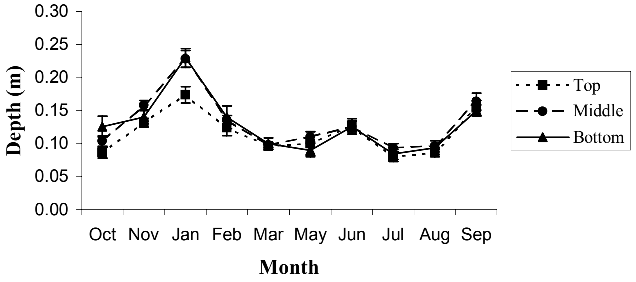


Figure 2.8b Monthly variation in the depth of the Glan-yr-afon Uchaf stream. Key as for 2.9a.

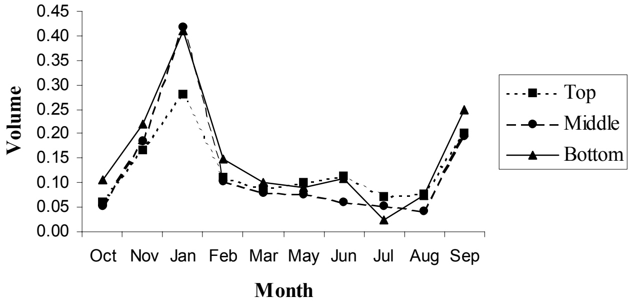


Figure 2.8c Monthly variation in the volume of the Glan-yr-afon Uchaf stream (in m^3). Key as for 2.9a.

Phosphates and nitrates

The Southern Damselfly seems to require oligotrophic or dystrophic conditions since low levels of phosphates and nitrates were found in most British sites.

Levels of all types of phosphate were below 0.025 mg/l in most watercourses occupied the Southern Damselfly (Figure 2.9a-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, Figure 2.10) 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 Sluxton Farm).

The finding of generally low levels of phosphates and nitrates on heathland sites indicates that the Southern Damselfly is found in oligotrophic or dystrophic conditions. This is consistent with the range of plant species found on sites (Tables 2.6-2.7). *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 and around streams may indicate that the Southern Damselfly 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 the Southern Damselfly.

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 fen 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, the Southern Damselfly is also found in oligotrophic and mesotrophic nutrient conditions. The species avoids eutrophic conditions in Germany because in these conditions a bacterial or algal film forms on the water surface and cover of submerged aquatic vegetation decreases. 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, Filipendula 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.

Ammonia

Levels of ammonia were usually low (less than 0.1 mg/litre – Figure 2.11) though a wide range of values, up to 0.55 mg/litre, was 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.

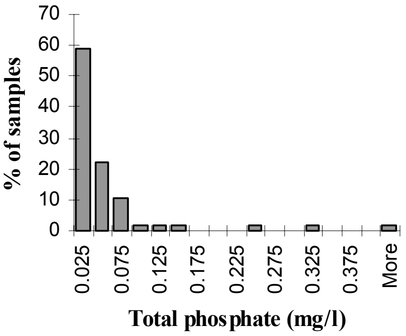


Figure 2.9a Percentage distribution of total phosphate across sites (*n*=68).

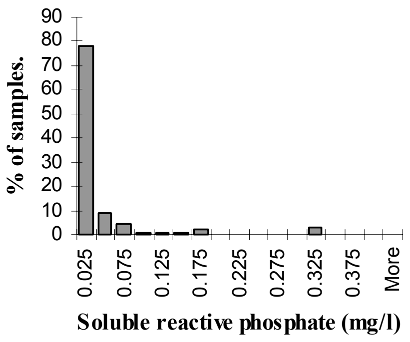


Figure 2.9b Percentage distribution of soluble reactive phosphate across sites (*n*=91).

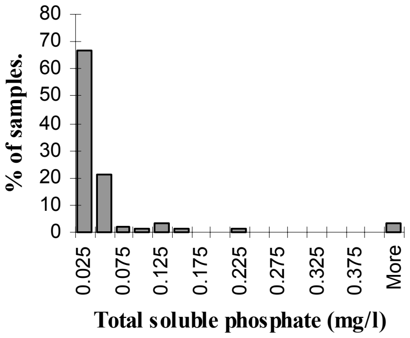


Figure 2.9c Percentage distribution of total soluble phosphate values across sites (*n*=91).

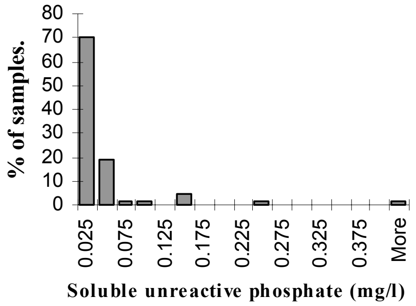


Figure 2.9d Percentage distribution of soluble unreactive phosphate values across sites (*n*=63).

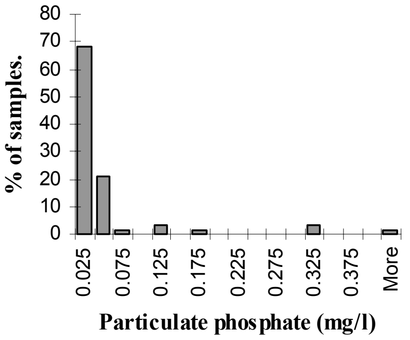


Figure 2.9e Percentage distribution of particulate phosphate values across sites (*n*=66).

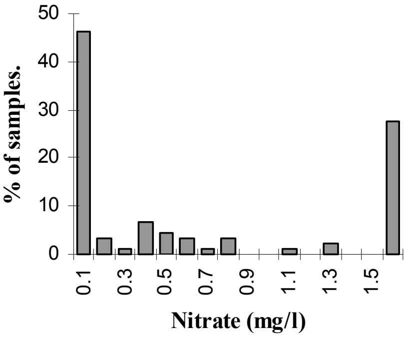


Figure 2.10 Percentage distribution of nitrate values across sites (*n*=91).

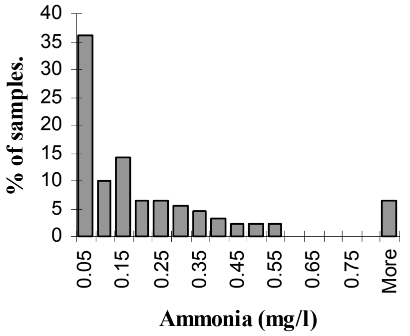


Figure 2.11 Percentage distribution of ammonia values across sites (*n*=91).

Oxygen concentration

The Southern Damselfly requires well-oxygenated conditions in Britain and Europe

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. 2.10) 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, the Southern Damselfly is found in well-oxygenated water with concentrations ranging from 2.5-30 mg/litre. Thelen (1992) found that larval populations of the Southern Damselfly were associated with mean oxygen saturation of 76% on the Upper Rhine. The association of Southern Damselfly populations with areas of flow, high vegetation cover and proximity to springs may reflect this species requirement for well-oxygenated water.

Pollution

The Southern Damselfly requires unpolluted water

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 affected by eutrophication as described above. Defaecation by grazing animals may significantly affect 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 Southern Damselfly is associated with high water quality on European sites. Given the low tolerance of other odonates to pollutants, it is safest to assume that the Southern Damselfly 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 and Wiggers, 2000) exacerbated by siltation due to excessive poaching.

Discussion from document review of large scale habitat use by the Southern Damselfly

Examination of habitat features common to locations of Southern Damselfly populations and features that had positive or negative impacts on population size revealed a range of features used by this species. Table 2.11 summarises the proximate cues or habitat features used by the Southern Damselfly in Britain elucidated in this review. Possible ultimate factors selecting for the use of these features are suggested.

To assess the stenotopy of the Southern Damselfly, it is important to distinguish between those habitat features required by all odonates from those required particularly by the Southern Damselfly. Percentage cover of vegetation, water temperature and shade are important predictors of dragonfly distributions, with Zygoptera usually tolerating a wider range of these factors than Anisoptera (Samways, 1993; Samways and Steytler, 1996).

Since the Southern Damselfly seems to have multidimensional requirements for factors such as sunlight, shade, vegetation structure and water flow, it can be described as a stenotopic dragonfly. Buchwald (1994) points out that all central European lotic odonates require some water current and exposure to sunlight. However, the Southern Damselfly is the only one of these species (apart from the Keeled Skimmer (*Orthetrum caerulescens*) that requires proximity to springs or groundwater in addition to these two factors. This specific preference may arise because the Southern Damselfly requires high oxygen concentrations in the larval stage or because it has higher thermal requirements for larval growth and development.

The Southern Damselfly 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 and Steytler, 1996). However, it is stenotopic in that the plant communities it is associated with indicate proximity to springs or groundwater. Thermal requirements of the Southern Damselfly were reflected both in its European and British distributions (Chapter 1) and in its microhabitat selection within sites (features 1, 4, 5, 7, 9, 11 on Table 2.11). 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 (Cherrill and Brown, 1990a;

Cherrill and Brown, 1990b; Hill et al., 1999; Thomas, 1983; 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 the Southern Damselfly 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 than the core populations and their location near to springs may compensate for exposure to relatively cooler temperatures. In Britain, the Southern Damselfly occupies lower altitudes than those populations on the German range edge and thus are less stenotopic with regards to their use of water bodies (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 the Southern Damselfly to an early seral stage of succession. This is true of many other species on their northern range edges. For example, the silver-studded blue butterfly, *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). Such early seral stages provide particularly unstable habitats (Usher and Jefferson, 1991) requiring very active management regimes (such as grazing, burning, cutting, scrub and channel clearance) to prevent extinction of associated species (Samways, 1994; Warren et al., 1984). The perception of overgrowth of runnels or bankside vegetation as the main threat to British Southern Damselfly sites illustrates the dynamic nature of Southern Damselfly 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, the Scarce Blue-tailed Damselfly (*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). Mobility of the Southern Damselfly is discussed in Chapter 6 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 and 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 and Jefferson, 1991). Appropriate measures to achieve this in Southern Damselfly sites are discussed in Chapter 7.

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) of the sort seen in Southern Damselfly biotopes. In addition, the Southern Damselfly is not only limited by temperature but by other factors such as oxygen and water availability which may not necessarily increase predictably during global warming.

It is necessary to consider whether the small population sizes seen in the Southern Damselfly in Britain (Chapter 1), 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 susceptible to some processes that result in loss of genetic variation. Although minimum viable population sizes have not been investigated for the Southern Damselfly, 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. At least 50% of the Southern Damselfly populations 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 unnecessary in most cases.

Management and monitoring recommendations (including indicators of condition for Southern Damselfly habitat) that arise from this review are described in Chapter 7.

Table 2.11 Summary of the proximate cues/features used by the Southern Damselfly 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 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 features 9, 10, 11, 13, 8, ensure the provision of open stream areas with substrates for oviposition and egg development 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
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	
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	
Vegetation features		
8. Remoteness from improved agriculture?	Prevent eutrophication, encroachment of invasive tall emergents and algae	
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		

3. LIFE CYCLE AND DEVELOPMENT OF THE SOUTHERN DAMSELFLY

Chapter Summary

- **In Britain, the Southern Damselfly has semi-voltine development with no splitting of year groups into different cohorts whilst in some European populations development can be completed in one year.**

- **The growth period of larvae is restricted to the period between April and October but again would presumably be longer further South in this species distribution.**

- **There is no diapause in the egg stage but a facultative autumn diapause in the penultimate larval instar may synchronise emergence in this species.**

- **The flight period is short on this species northern range margin and daily emergence depends on climatic factors as well as season.**

- **Mortality in the different life stages of the Southern Damselfly is discussed further in Chapter 7.**

Length of the life cycle

The Southern Damselfly is semi-voltine in Britain i.e. it has a two year life cycle. This was determined by measuring larvae from ten monthly hand net samples taken from Glan-yr-afon Uchaf, Mynydd Preseli, Pembrokeshire between October 1999 and September 2000. Figure 3.1 shows the percentage distribution of larvae across different head width classes in the October 1999 larval sample. Since eggs hatch without diapause in summer (Corbet, 1955), each peak on the length-percentage histograms corresponds to different year group (cohort) of larvae (rather than slow and fast growing cohorts from the same year group).

Similarly, the absence of a bimodal emergence curve for the Southern Damselfly at Upper Crockford (see Emergence study) indicates that cohort-splitting did not occur. Cohort-splitting is where, in a semi-voltine population, some of the 1st year 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 phenomenon has been observed in the Large Red Damselfly (*Pyrrhosoma nymphula*) and the Emperor Dragonfly (*Anax imperator*) and also in Southern Damselfly populations in mainland Europe. Indeed, most mid-European populations of the Southern Damselfly are also semi-voltine (Sternberg et al., 1999). However, in a German population, when industrial cooling waters substantially increased the water temperature, development was completed in one year (Thelen, 1992). This suggests that, like other odonates, the length of the life cycle of the Southern Damselfly may vary across its distribution depending on climate and the productivity of the habitat.

This chapter describes each stage of the life cycle in turn including duration and mechanisms of development and possible mortality factors operating at each stage – from the egg to the immature adult. Reproduction and mortality of the mature adult stage is discussed in Chapter 5. Small scale habitat use by each stage is covered in Chapter 4 (though some details have already been given in Chapter 2).

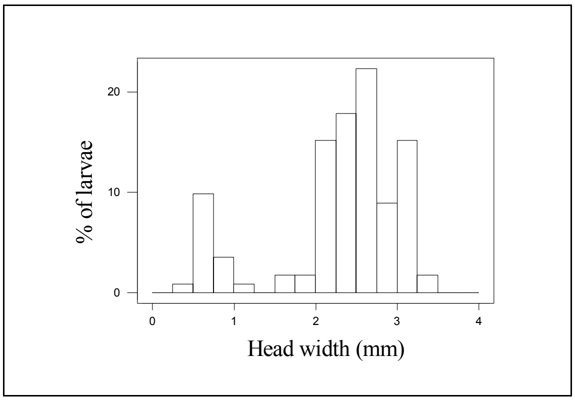


Figure 3.1. Percentage distribution of head width for larvae in the October 1999 sample from Glan-yr-afon Uchaf.

Egg stage - duration and mortality

Female Southern Damselflies lay their 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 (Figure 3.3a). This is known as endophytic oviposition and is common to all damselflies.

Chapter 4 describes experiments on habitat use by ovipositing pairs. Focals were carried out which were observation periods in which focal pairs were followed and observed. For ten focals from Upper Crockford (Beaulieu Heath, Hampshire), four weeks after females were observed to oviposit into plant stems, 20 stems were removed from the stream and dissected for eggs. Eggs are arranged in very regular patterns up stems such that irregularities in the pattern would indicate that more than one female had used the stem for oviposition. Hatched eggs appeared as yellow, split outer cases (chorion) lacking a micropyle. Healthy eggs in an earlier stage of development appeared yellow with a milky interior, sometimes with eye spots at the anterior end. Eggs that had died during the hatch period were transluscent or blackened. On average, 66 % ± 1 of eggs retrieved from each stem had hatched confirming that there is no diapause in the egg stage. 21 % ± 1 were healthy but in earlier stages of development and 14% ± 5 had died during the hatch period.

The presence of healthy but unhatched eggs in these stems indicates that the hatch period can last longer than four weeks (perhaps up to six weeks) in the natural environment and that hatching is not well synchronised within clutches (unlike in the Large Red Damselfly, *Pyrrhosoma nymphula*). The hatch period of the Southern Damselfly is shorter, lasting 21 days, in captivity (Corbet, 1955). The length of the hatch period is within the range found for other damselfly species whose eggs hatch directly (i.e. without diapause) i.e. between 5 and 40 days. Eggs of species that have diapause in the egg stage can take between 80 and 320 days to hatch.

Possible sources of egg mortality in endophytic species include desiccation, infertility, unhatchability, predation, parasitism and over-use of stems (such that eggs might be punctured from repeated oviposition). No stems were found to contain clutches from before the focals (further oviposition into stems was prevented after a focal) and no eggs were observed to have been predated or parasitised. Thus the observed egg mortality can probably be attributed to infertility and unhatchability. None of the 20 stems was found exposed due to drops in water level after the four weeks for which they were left in place. However, the stream margin retreated considerably during the 1999 flight season, exposing other areas known to have been used for oviposition at Upper Crockford. Thus desiccation could represent a significant egg mortality factor for the Southern Damselfly due to the shallow water habitat it prefers.

Larval stage – length of growth period,

Insects have a discontinuous growth pattern due to their rigid exoskeleton. Increases in body size can only occur at the moults when a new cuticle with greater surface area is formed. Thus an individual goes through a step-wise pattern of size increase as development proceeds and can be assigned to a particular developmental stage on the basis of size. Growth in the larval population can then be inferred from changes in the distribution of larvae between size categories through time (as they move from one developmental stage to the next).

In odonates, individuals from field populations, belonging to the same instar, appear as clusters of points when two body measurements are plotted against each other (on an X-Y plot). For species such as the Large Red Damselfly that have synchronous and early emergence, these clusters are relatively discrete and there is one for each instar. For species like the Southern Damselfly that have asynchronous emergence, these clusters are less discrete and may consist of two or three instars. The reasons for this will be explained further later. Therefore, 3-dimensional plots of tibia length, wing bud length and head width (e.g. Figure 3.3), as well as all combinations of X-Y plots, were used to assign larvae from each month to instars.

This was done both for the Southern Damselfly and for the small numbers of Large Red Damselfly co-occurring with them at Glan-yr-afon Uchaf. 1195 Southern Damselfly larvae collected in samples could not be separated into instars but instead were separated into 6 instar groups (A to F) on the basis of these plots. The Southern Damselfly has 13 larval instars in captivity (Corbet, 1955). Figure 3.3b shows a Southern Damselfly larvae from Instar Group D i.e. the ante-penultimate larval instar.

Thus, Instar Group A corresponded to instars 2-6, Group B corresponded to instars 7-8, Group C corresponded to instars 9-10 whilst D, E and F corresponded to the antepenultimate, penultimate, and final instars respectively. For the Large Red Damselfly, 129 larva were collected and were separated into all 12 instars after the pro larva on the basis of such plots. Appendices 5 and 6 respectively contain mean dimensions for instar groups of the Southern Damselfly and for instars of the Large Red Damselfly.

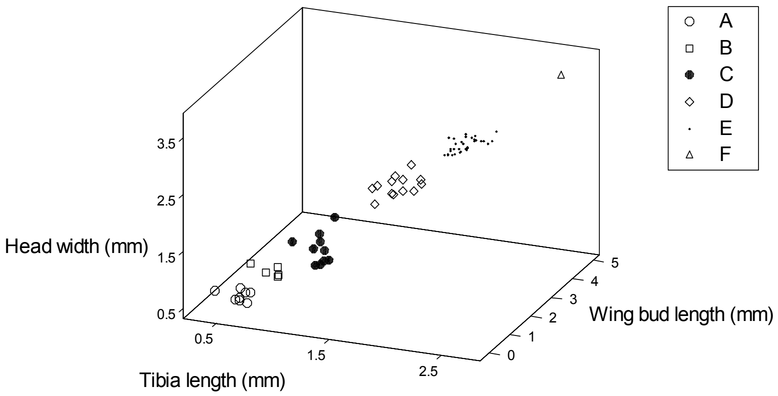


Figure 3.2 Three Dimensional plot of body size variables for females and small Southern Damselfly larvae from November 1999.

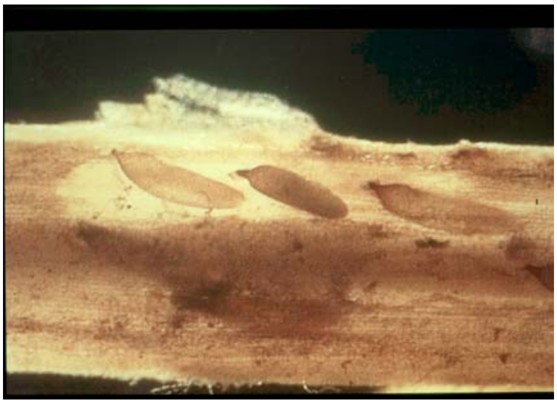


Figure 3.3a Southern Damselfly eggs placed inside a stem of *Hypericum elodes*.

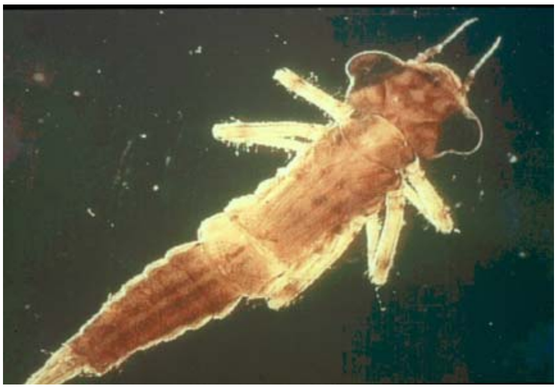
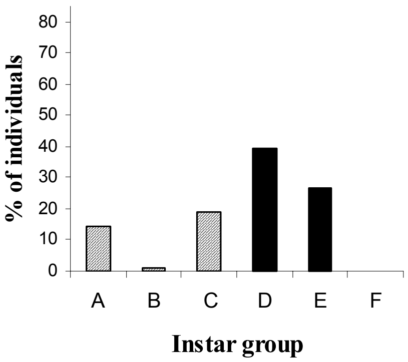


Figure 3.3b A Southern Damselfly larva from instar group D.

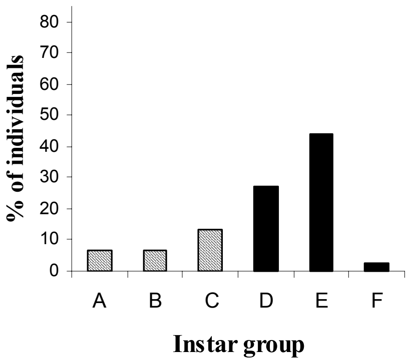
Figure 3.3c A Blue Damselfly final instar exuviae on its emergence perch.

Figure 3.3d Emergence cages used at Upper Crockford in 1999.

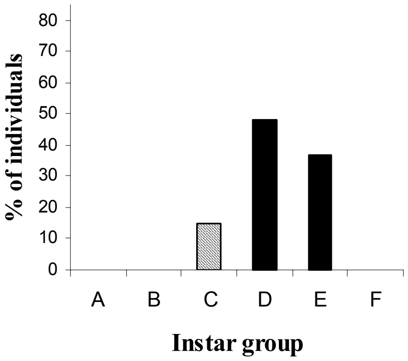
(a) 18/10/99 n=112



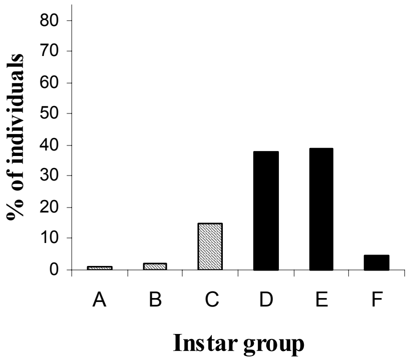
(b) 30/11/99 n=112



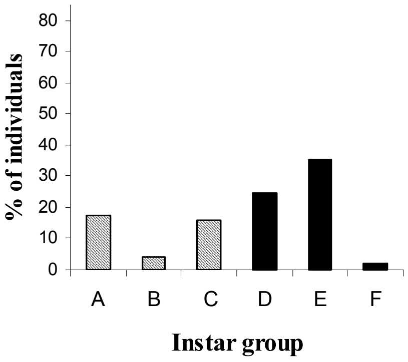
(c) 12/01/00 n=27



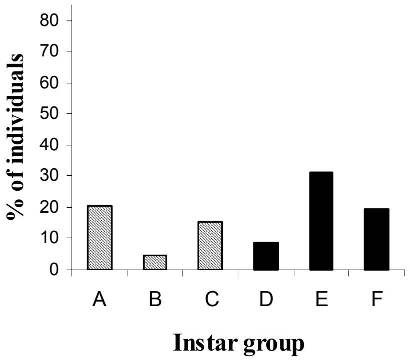
(d) 23/02/00 n=87

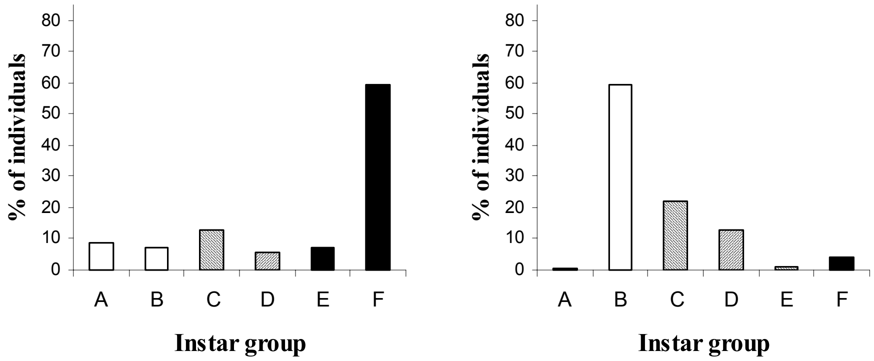


(e) 29/03/00 n=93

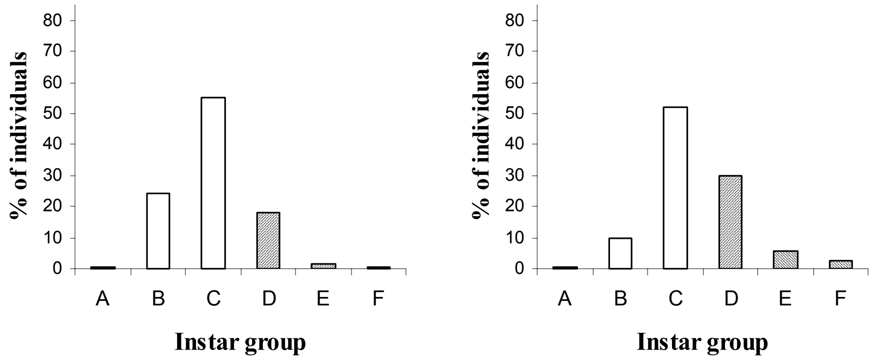


(f) 01/05/00 n=103




(g) 06/06/00 n=71

(h) 12/07/00 n=167


(i) 07/08/00 n=247

(j) 28/09/00 n=162

Figure 3.4 The percentage of Southern Damselfly larvae in each instar group in each month. Cohort 1 (1998-2000) is represented by closed bars, Cohort 2 (1999-2001) by diagonally-striped bars and Cohort 3 (2000-2002) by open bars.

Since the Southern Damselfly has a two year life cycle at least two year groups (cohorts) of larvae were present in the samples at any one time. Cohort 1 hatched in 1998, was in instars 9-13 (groups D to F) when sampling began and emerged in summer 2000. Cohort 2 hatched in 1999, was in instars 2-10 (Groups A to C) when sampling began and would have emerged in summer 2001. Cohort 3 hatched in summer 2000 (appearing in June) and would have emerged in summer 2002. Figure 3.4 shows the percentage of Southern Damselfly larvae in each instar group in each month divided into the three cohorts present in the samples.As described above, if growth is occurring in the larval population, this change should be reflected as differences in the proportion of larvae in each instar group between consecutive months. These proportions were compared between months using chi-squared tests (for instar groups C to F since instars A and B were not detected consistently in samples –see Table 3.1).

The lack of significant changes in the distribution of individuals across instar groups between consecutive months from November to March suggests that no larval growth (in terms of instar changes) was permitted in this part of the year. This is probably because some minimum temperature threshold for ecdysis was not attained during this period.

Lower temperature thresholds for growth have been identified in a range of other temperate odonate species e.g. 10-12°C for the Azure Damselfly *(Coenagrion puella),* 8°C for the blue-tailed damselfly (*Ischnura elegans*). These thresholds may be determined by the profound effect of temperature on activity (and thus the availability) of prey and on the feeding rate of invertebrate predators.

Since the size of the chi-squared values (Table 3.1) reflects the degree of difference between instar proportions, they reflect the amount of growth that has occurred. These indicate that a large amount of growth occurs in the larval population between March and August but that some growth also occurs in October.

Table 3.1 Chi-square tests to compare the distribution of individuals across instar groups C to F between consecutive pairs of months (Groups E and F were amalgamated and all χ^2-statistics were distributed with 1 d.f.).

Pair of months	χ^2	p
October versus November	9.63	0.002
November versus January	2.87	0.09
January versus February	0.77	0.38
February versus March	1.29	0.257
March versus May	20.81	< 0.001
May versus June	29.74	< 0.001
June versus July	54.67	< 0.001
July versus August	18.72	< 0.001
August versus September	11.03	< 0.001

Larval stage – seasonal regulation and the location of diapause

The division of the life cycle into active and diapause stages has been crucial to the success of many temperate-zone insects. In odonates, seasonal regulation (i.e. the placement of adult emergence) is achieved by different diapause characteristics of the larvae, and distinct responses to critical day length and temperature thresholds in different instars. In odonates, Corbet (1954) distinguished between

- ‘spring’ species - populations that overwinter and diapause in the final instar and have a closely synchronised and often early emergence
- ‘summer species’ that overwinter in one or more earlier stadia, have less synchronised emergence and emerge later.

To investigate in which instar groups the Southern Damselfly overwinters and to locate diapause within each cohort, the growth of the 2nd year cohort is examined separately.

As shown on Figure 3.4, 2nd year Southern Damselfly larvae overwintered in a range of instars from the ante-penultimate to the final instar (Groups D-F). The percentage of individuals in F, during this period, ranged from 0 to 4% of the cohort. The rest of the individuals were divided equally between instar groups D (mean %= 47.8 ± 4.4) and E (mean %= 49.7± 3.7). This is consistent with the asynchronous emergence curve of the Southern Damselfly (described in the next section).

Between March and May, individuals moved rapidly from instar groups D to E and from E to F, but by the time emergence began in May, 67% of the population were still in the penultimate and antepenultimate larval instars, indicating considerable asynchrony in the cohort. Similarly, in a previous study, Corbet (1957) found that 50% of the cohort has not entered the final instar by the time metamorphosis began. Thus the Southern Damselfly is a ‘summer’ species.

These data can also be used to investigate the mechanism of larval diapause. Corbet (1957) suggested that this type of emergence curve, typical of ‘summer’ species, could be produced by a rising series of lower temperature thresholds for entry into successive larval instars, ensuring that early instars are the first to resume growth in spring as the temperatures rise.

However, in this study, when growth resumed in the 2nd year group in spring, growth resumed in antepenultimate and penultimate instars at the same time i.e. individuals passed rapidly from the ante-penultimate to the penultimate instar and from the penultimate to the final instar. Emergence from the final instar began slightly later in May. If there were a rising series of lower temperature thresholds for entry into successive larval instars, transitions from the penultimate to the final instar would have occurred after transitions between the ante-penultimate and the penultimate instars. Thus the diapause mechanism in the Southern Damselfly does not consist of a rising series of such thresholds.

While there may indeed be a higher temperature threshold for emergence from the final instar than for the preceding two larval transitions, the delayed appearance of this stage may be due to the low proportion of the cohort that overwinter in the final instar (around 4%). The data are not inconsistent with the existence of a facultative diapause in the penultimate instar in autumn. This could be induced by decreasing photoperiod such that larvae entering the penultimate instar in the autumn would tend to remain there for winter but in March and April, ante-penultimate instar larvae would pass rapidly through the penultimate and final instars. A laboratory investigation of the precise effect of temperature and photoperiod on diapause in this species would be pertinent.

The lack of egg diapause in the Southern Damselfly was again evident since Cohort 3 larvae passed rapidly through instars A, B (99% of cohort in July) and C (83% of cohort in September) following their appearance in June.

Larval stage – size structure of the larval population and the consequences for competition and predation

In a semi-voltine population, 1st year larvae co-exist with 2nd year larvae. The degree of size separation or overlap between larvae determines the potential for intraspecific predation or competition between different instars and may in turn affect differential habitat use by instars. Wissinger (1988) found that for two species of libellulids (*Libellula lydia* and *L. luctuosa)* 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 the Southern Damselfly population studied here, 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 degree of size separation can be expressed as a ratio of body size between the largest and smallest co-occuring larval groups (Wissinger, 1988). In the larval Southern Damselfly population studied here, the ratio of mean head width of instar groups A and F ranged from 1.65 (Jan) to 6.16 (May) with a mean of 4.89. 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). Although there is the potential for intraspecific predation, no remains of Southern Damselfly larvae were found in a limited sample of prey obtained from faecal pellets of Southern Damselflies (Harris, 2000). Even if cannibalism itself is rare, interference suffered by small instars in the presence of large conspecifics can reduce growth rates, increase development time and reduced mean head widths over the period of one instar.

One consequence of this interference competition may be spatial separation of large and small instars between different microhabitats. For example the Emperor Dragonfly (*Anax imperator*) hatches in *Potamogeton*, moves to *Litorella* for the first year of larval development and then to *Hypericum* for the second year. However, both in this study and in a European study (Thelen, 1992), larvae of all instars of the Southern Damselfly were found in the perennial plant substrate throughout the year and no larvae were found in the peat layer on the base of the stream. Therefore spatial separation may be 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 ((as observed in the Large Red Damselfly *Pyrrhosoma nymphula,* Bennett & Mill, 1993; Lawton, 1970).

The larval population of the Southern Damselfly, a ‘summer’ species, shows more overall variation in size dimensions than that of the Large Red Damselfly, a ‘spring’ species.

The residuals from a regression of head width on tibia length for the Southern Damselfly larval population showed significantly more variation than those derived from the same regression for the Large Red Damselfly population (Levene’s test statistic=6.71, p=0.010, σ_{cm} = 0.1351, n=1195, σ_{pn}=0.0945, n=116). Within instar groups (using the same groups as those found in the Southern Damselfly), coefficients of variation (V) in head width were larger for Southern Damselfly than for the Large Red Damselfly for groups B to E (Instar group A - V_{cm}=17.6, n=71, V_{pn}=31.1, n=14; Instar group B - V_{cm}=14.2, n=199, V_{pn}=9.7, n=31; Instar Group C - V_{cm}=15.1, n=351, V_{pn}=5.5, n=32; Instar Group D - V_{cm}=6.5, n=273, V_{pn}=3.9, n=19; Instar Group E - V_{cm}=4.8, n=314, V_{pn}=2.0, n=4).

The Southern Damselfly has a long, asynchronous emergence whilst adult emergence, mating and oviposition are well-synchronised in the Large Red Damselfly. Thus the length of the oviposition and hatch periods will be greater for the Southern Damselfly than for Large Red Damselfly, producing broader size distributions in larval populations of the former species even within year classes (Johnson, 1991). As discussed above, broader larval size distributions increase the potential for interference competition between large and small larvae.

Larval stage – prey items

The diet of larval Southern Damselflies sampled at Glan-yr-afon Uchaf in 1999 included Ephemeroptera, Diptera (Chironomidae and Simulidae) and *Gammarus* sp. – though a large proportion of prey items could not be identified. Chironomids made up a large proportion of invertebrates present in an invertebrate sample taken from Glan-yr-Afon Uchaf in March 2000 (Appendix).

Emergence and maturation

Since dragonflies 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). Examination of dragonflies at emergence allows sex ratio, mean body size, numbers and seasonal pattern to be investigated before dispersal or differential adult mortality introduces any biases. While the potential form of the emergence curve in dragonflies depends on the diapause characteristics of the larval stage (and responses of different instars to photoperiod and temperature), the actual form depends on proximate factors such as temperature before and after emergence, barometric pressure and wind. Since emergence in odonates proceeds more quickly at higher temperatures it may be adaptive for individuals to postpone emergence until temperatures are high and stable, to reduce the risk of predation during hardening.

To examine the actual form of the emergence curve of Southern Damselflies in Britain, emergence cages (Figure 3.2c) were used to enclose a fixed area of stream habitat throughout the flight season at Upper Crockford (Beaulieu Heath, Hampshire). This enabled a standard proportion of the emerging Southern Damselfly population, and that of the co-occurring Small Red Damselfly population to be collected on a daily basis.

It has been suggested that emergence 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 and in which individuals are immobile and defenceless. Possible mortality factors at emergence include competition for perches, predation and desiccation or deformation. Thus for the Southern Damselfly in this study, incidences of death and deformation of tenerals were also recorded from the emergence cages.

Having been collected, newly emerged (teneral) Southern Damselflies were retained in pots and left to harden. 'Teneral' refers to the condition of the adult, up to 24 hours after emergence, when the body is soft and the wings are shiny (Figure 3.3c shows the final instar exuvia of a Blue Damselfly larva). They were measured (left forewing length) and marked the next day and released near the cage in which they had been marked. Within a few hours of emergence, odonate tenerals normally leave the water area and spend some days (the pre-reproductive period) in surrounding vegetation, feeding and roosting before sexual maturity is attained (Corbet, 1980). It is useful to estimate the duration and percentage mortality of this period to interpret the dynamics of adult populations. The time required for maturation depends on food availability and external weather conditions. It is often longer in females than males if the former require relatively more food for the provisioning of eggs. The length of this period was examined in the Southern Damselfly by carrying out a daily mark-release recapture exercise on the sexually mature adults along the stream to try to recapture those individuals released as tenerals.

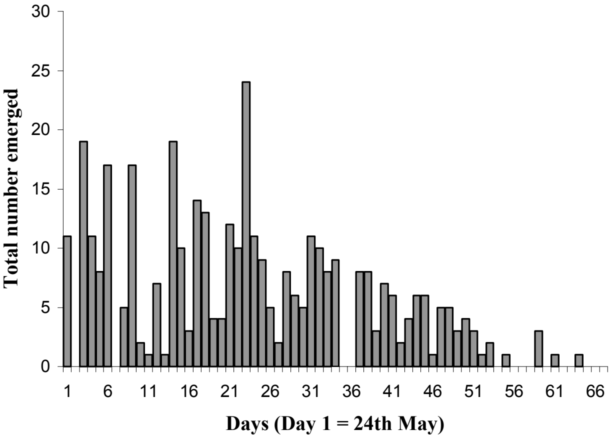


Figure 3.5 Daily emergence of the Southern Damselfly.

Form of the emergence curve

The total number of Southern Damselflies and Small Red Damselflies emerging on each day through out the flight season are shown in Figures 3.5 and 3.6 respectively.

The synchrony of emergence is measured by calculating EM_{50} i.e. the time, in days since emergence began, by which 50% of the annual population has emerged.

In the Southern Damselfly (SD), emergence lasted 60 days (between May 24th and July 26th) and EM_{50} was 22 days. Peak emergence occurred on the 15th June. In the Small Red Damselfly (SRD), the emergence period was shorter lasting only 50 days (from 12th June to 29th June i.e. from Day 20 to Day 67). EM_{50} was 30 days and the 12th and 18th July (Day 50 and Day 56 respectively).

Consistent with the diapause characteristics of their larval stages, both species show an asynchronous emergence pattern. Their values for EM_{50} are similar to those for 'summer' species.

For example, the Southern Hawker (*Aeshna cyanea*) has an EM_{50} of 25 days. In contrast, (*Lestes rectangularis*) has an EM_{50} of 7 days.

The shape of the emergence curves (Komologorov-Smirnov, Z=7.908, p<0.001) and the median day of emergence differed between the two species (median$_{SD}$ = day 23; median$_{SRD}$ = day 47.5; Wilcoxon two-sample test, W=143998.5, p=0.653). In particular, the emergence of the Southern Damselfly was slightly more synchronised than that of the Small Red Damselfly. Corbet (1957a) found, when sampling the larvae of the two species together, that a higher proportion of Southern Damselflies than Small Red Damselflies overwintered in the penultimate instar in their 2nd year and so only had to pass through two stadia before emergence.

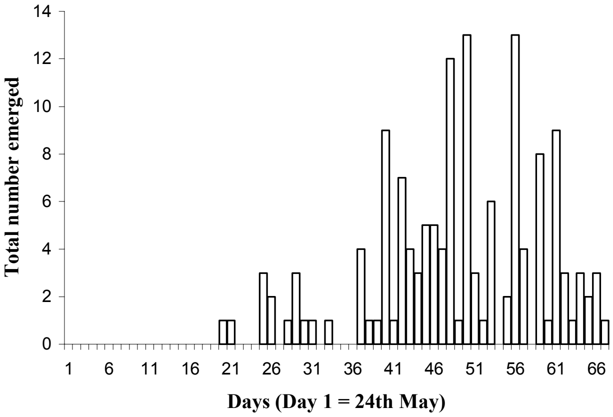


Figure 3.6 Daily emergence of the Small Red Damselfly.

It is also interesting that the initial rate of emergence in the Small Red Damselfly was slower than that of the Southern Damselfly, and seemed to increase only after the rate of emergence decreased in the Southern Damselfly population (Figure 3.7). Since both species use the same habitat for emergence at Upper Crockford, it is plausible that there is selection for temporal separation of emergence between them to avoid interspecific competition between emerging adults.

As with most other dragonflies, there was no difference between males and females in the pattern of emergence for either species Specifically, median day of emergence did not differ between the two sexes for either the Southern Damselfly (males – median = day 23; females - median = day 24; Wilcoxon two-sample test, W=74443.0, p=0.8) or the Small Red Damselfly (males - median = day 47; females – median = day 48; Wilcoxon two-sample test, W=14214.5, p=0.653).

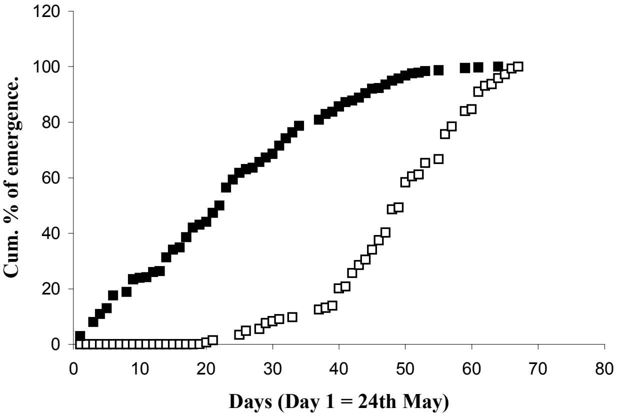


Figure 3.7 Cumulative percentage emergence curves of the Southern Damselfly (closed squares) and the Small Red Damselfly (open squares) in 1999 (from cages 1-10).

The shape of the emergence curve did not differ between males and females for the Southern Damselfly (Komolgorov-Smirnov, Z=1.034, p=0.235, n_1=293, n_2=217) or the Small Red Damselfly (Komolgorov-Smirnov, Z=0.544, p=0.928, n_1=119, n_2=115).

Effect of season and climatic variables on daily emergence

Weather variables during the flight season in 1999 were obtained from a British Atmospheric Data Centre meterological station in Everton (SZ302937, 7km away from the Upper Crockford study site). For each 24 hour period, these were the duration of sunlight, the amount of rain, and the minimum and maximum temperature both in that period and in the previous 24-hour period.

We wanted to investigate the effect of weather variables on the actual form of the emergence curve whilst controlling for the effect of season. The numbers of Southern Damselflies emerging on each day (log-transformed) were regressed against the day of the study (Figure 3.8). The residuals from this regression for each day were regressed against eight weather variables (sun, rain, maximum and minimum temperature from that day and from the previous 24 hour period) using a forward stepwise regression procedure. The same analysis was not performed on the Small Red Damselfly since numbers emerging could not be normalised by any transformation.

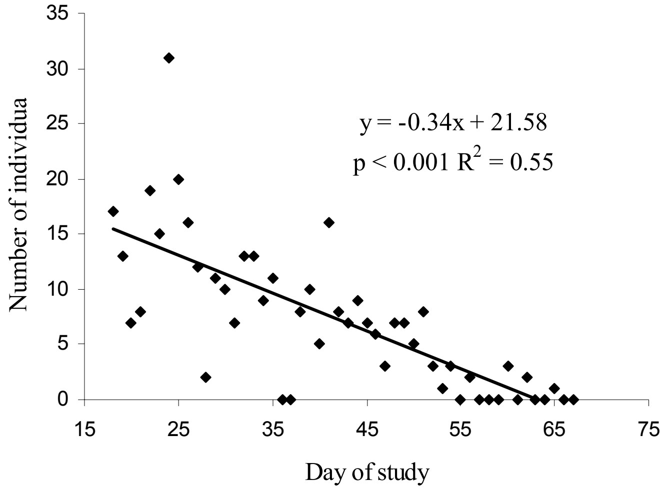


Figure 3.8 Regression of number of Southern Damselflies emerging on each day against day of study.

Having controlled for the effect of season, the residual daily emergence in the Southern Damselfly was positively related to the duration of sunlight on the previous day (Sun Prev - Table 3.2). When the actual number of emerging Southern Damselflies was regressed against Day of emergence and Sun Prev (using an 'enter' multiple regression where all variables are forced into the model), the regression model accounted for 64.3% of the variation in daily emergence (Table 3.3). This suggests that both amount of sunlight and day of season were important in determining daily emergence in the Southern Damselfly.

Since weather variables are often inter-related, it is difficult to confirm which weather variable is most important in influencing daily variation in emergence, but some relationship between temperature and daily emergence is suggested by these results.

This positive relationship has been found in another damselfly species (*Lestes eurinus)* that inhabits small, shallow, sun-exposed waterbodies similar to those occupied by the Southern Damselfly. In such exposed waterbodies, the probability that a particular temperature threshold for emergence or hardening) is reached and maintained on any given day is likely to depend on the level of insolation. There is also a lack of thermal lag between ambient and water temperatures.

There is also some evidence that the Southern Damselfly may have the ability to postpone emergence (for considerable periods) following metamorphosis. In some individuals, the adult labium has been found retracted in the larval prementum for three weeks before emergence, a condition which lasts 2 to 3 days in most other dragonflies (Corbet, 1955).

Table 3.2 Stepwise regression model for variation in residual daily emergence in the Southern Damselfly.

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	*ß*	s.e.	*T*	*p*
Constant	-4.917	1.632	-3.012	0.005
SunPrev	0.0651	0.019	3.440	0.002

Table 3.3. 'Enter' multiple regression model for variation in daily emergence in the Southern Damselfly.

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	*ß*	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

Mortality and deformity at emergence

The frequencies of emerging Southern Damselflies affected by different causes of mortality are shown in Table 3.4. Deaths whilst hardening in pots before marking 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*=0.94 (Yates correction)). The most common forms of deformity were bent abdomens (found in 7 tenerals and 2 mature adults) and crumpled wings (found in 11 tenerals and 5 mature adults). The proportion of deformed individuals in the teneral adult population (22 out of 510) was significantly larger than the proportion of individuals in the mature adult population (7/2694) (χ^2=74.032, 1 d.f, p < 0.001 (Yates correction)).

Table 3.4 Frequency of deaths at emergence due to different causes in the Southern Damselfly.

Cause of mortality	Males	Females	Total
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 (% in parentheses)	5 (1.7)	3 (1.4)	8 (1.6)

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). Percentage mortality of the Southern Damselfly at emergence was low, even including deformed individuals, compared to other odonates where estimates range from between 3.3% and 28%. 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 mortality (Corbet, 1999). Causes of mortality in the Southern Damselfly 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 the Southern Damselfly compared to that occurring in other life stages.

Length and mortality of the maturation period

As often observed in odonates, the rate of recapture of the Southern Damselfly after marking as teneral adults was very low at 4.8% (22 out of 462). 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). This may indicate that the pre-reproductive adult stage consititutes a period of high mortality but may also reflect the difficulty of monitoring diffuse breeding habitat in stream-dwelling odonates. Mark-recapture effort was concentrated on the breeding stream. Teneral recapture rates may have been lower than those of mature adults of the Southern Damselfly since tenerals utilise tussocks for roosting and maturation.

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, all individuals recaptured 8 days or more after emergence were sexually mature and one individual matured in 5 days. 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.

A maturation period of between 5 and 8 days for the Southern Damselfly, falls within the range documented for other zygopterans i.e. 2 days to one month (Corbet, 1980). For example, in another coenagrionid, the Large Red Damselfly, this period lasts 13-14 days. It is also consistent with the 4-5 day maturation period described in populations of the Southern Damselfly in Baden-Württemburg. Although the data for *C. mercuriale* obtained in this study do not represent the full range of maturation periods for the population, 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.

Regional variation in flight period

The dependence of emergence on temperature (seen above) restricts the temporal niche of the Southern Damselfly within a season on the edge of its range. In edge of range, Alpine populations in Germany, the flight period lasts from mid-June to mid-August whilst, in most regions of Britain, it lasts from late May to early August (Table 3.5). The flight period in core populations in the Mediterranean is much longer, lasting from early April to early November (Grand, 1996 and refs therein). Such widening of temporal niches in favourable climates is common in odonates (Sternberg, 1994). In 1999, peak emergence of the Southern Damselfly at Upper Crockford occurred in mid-June and the flight period extended from mid May to late July. Jenkins (1991) found considerable variation in flight period between years at Upper Crockford and between adjacent populations on the same stream system. This variation can also probably be attributed to the temperature dependence of emergence.

Table 3.5 Geographical variation in flight period of the Southern Damselfly.

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 Erddreiniog	edge	8th June - 24th July	47	1998	(Colley and 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.

4. SMALL SCALE HABITAT USE BY ADULTS FOR OVIPOSITION, EMERGENCE, REPRODUCTION AND BY LARVAE

Chapter Summary

In this chapter, the oviposition behaviour of Southern Damselflies is described as follows:

- **Pairs oviposit in several plant stems with several bouts of oviposition per stem. Most only oviposit into one plant species and each pair oviposits for 11 minutes on average.**
- **Females always submerge up to their wings during oviposition but submerge completely in 15% of ovipositions. This behaviour may serve to place eggs further down in the water column to prevent egg dessication.**
- **5% of pairs were affected by predation during oviposition.**
- **The Southern Damselfly performs non-egglaying 'test' oviposition bouts that last around 40-50 seconds and probably serve to test the physical suitability of a stem for laying.**
- **The number of eggs laid on a stem increases with the duration of oviposition.**

Habitat used by the Southern Damselfly for oviposition had the following features:

- **Unshaded, open areas of shallow, slow water flow over dark peat substrate.**
- **Proximity to tussockes for shelter but absence of dense or tall emergent vegetation.**
- **Plant species used for oviposition were herbaceous, soft-stemmed, submergent or semi-emergent perennials with thin cuticular layers in their stems.**

Habitat used by the Southern Damselfly for emergence had the following features:

- **Unshaded, open areas of shallow, slow water flow with floating mats of aquatic vegetation.**
- **Plant species used for emergence had rigid, upright stems (with collenchyma) which resist movement.**

Introduction

For organisms to persist they must select habitat that meets the ecological needs of all the stages of their life cycle. 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 for survival and reproduction (ultimate factors – see Box 2.1). 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, investigations of the cues used by mature adults for selection of habitat for oviposition and emergence by the Southern Damselfly are described. Habitat use by adults for roosting and reproduction and by larvae is also considered.

Habitat selection by odonates

Although some adult dragonflies home to the water body from which they emerged, most species carry out active habitat selection. Wildermuth (1994) has suggested that odonate species respond to the features of their habitat in a hierarchical manner as indicated in the following scheme:

- When flying at decimetres above the habitat, adults respond to the biotope e.g. wet heathland/valley mire for the Southern Damselfly.
- At 0.5-5m above the habitat, they respond to features of the larval water body e.g. small stream or runnel for the Southern Damselfly.
- At 0-0.5m above the water they respond to the features of the oviposition or perch site.

More general cues are likely to be detected visually while tactile or thermosensory cues will be used only at the final stages of the hierarchy.

As discussed in Chapter 2, vegetation is used at all stages of the dragonfly life cycle (Buchwald, 1992) and macrophytes are likely to feature highly among the proximate cues used for habitat selection. Even pioneer dragonfly species (such as the Black-tailed Skimmer (*Orthetrum cancellatum)* and the Broad-bodied Chaser (*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, when investigating the proximate cues used by different life-stages of the Southern Damselfly, many aspects of plant structure were considered.

Habitat selection for oviposition

As discussed in Chapter 3, female Southern Damselflies lay their eggs directly into submerged plant stems. In focals at Upper Crockford in June and July 1999, marked ovipositing pairs were followed from when they arrived at the stream after copulation throughout their period of oviposition. The proximate cues used by the Southern Damselfly at the ultimate stage of the hierarchy were investigated by measuring the utilisation of a stem for oviposition once a pair had landed. Stem utilisation i.e. the duration and number of oviposition bouts on a stem was then related to a variety of habitat factors measured around the stem. Focals were carried out on pairs in caged and natural situations. Stems in natural situations were left in the stream for four weeks to investtigate hatch period (Chapter 3). Stems from cages were removed immediately after the focal for dissection to obtain data on egg deposition rate. Given the difficulty of tracking pairs across boggy habitat (39 of 80 focals attempted were completed), caged focals permitted the entire oviposition period of pairs to be observed without disturbance.

The habitat variables were measured for the oviposition period on each stem were as follows;

- time of day
- water (5cm below water surface) and air temperatures (10cm above water surface)
- pH near stem
- plant species
- length of stem above water
- diameter of stem
- vegetation patch size (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)
- distance of the stem from the nearest discernible area of flow
- distance of the stem from the nearest tussock.
- the depth of water by the stem

General oviposition behaviour

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 (Figure 4.1) with several bouts of oviposition on each stem (Figure 4.2). Most pairs oviposited into one plant species during the oviposition (Figure 4.3). Whilst changes in position between stems could be s strategy for distributing eggs between several sites, especially in populations which are heavily predated during the egg stage or during oviposition, they most probably occur in the Southern Damselfly after unsuccessful attempts at oviposition.

Oviposition behaviour by a pair lasted 670.8 ± 49.4 seconds (i.e. 11.2 minutes) on average (*n*=36) and ranged from 244 to 1471 seconds. This is shorter than the mean duration of oviposition in another damselfly, the Large Red Damselfly (*Pyrrhosoma nymphula*) that oviposits for 22.8 minutes and may reflect the fact that Southern Damselfly females do not seem to lay all their eggs in one oviposition episode. The number of eggs laid by a pair was 90.5 ± 22.3 eggs on average and ranged from 23 to 337 eggs (*n*=13).

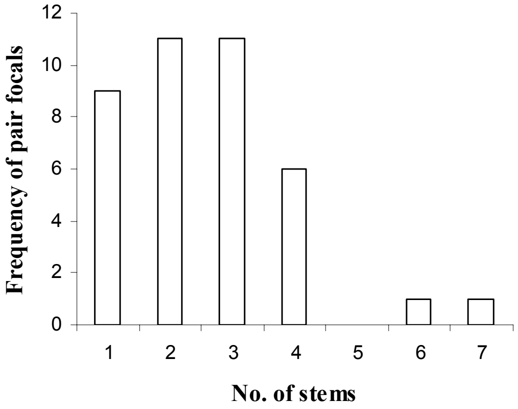


Figure 4.1 Frequency distribution of the number of stems used by pairs during the oviposition period (*n*=39).

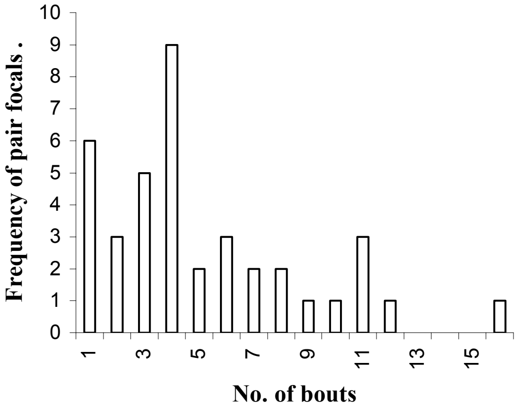


Figure 4.2 Frequency distribution of the number of bouts of egg laying by pairs during the oviposition period (*n*=39).

Submerged oviposition

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.

Submerged ovipositon has been observed in other British (Evans 1989, Jenkins 1997, Woodman 1999) and European populations of the Southern Damselfly. In other damselflies such as *Enallagma hageni* this behaviour allows females to avoid harassment by males during oviposition.

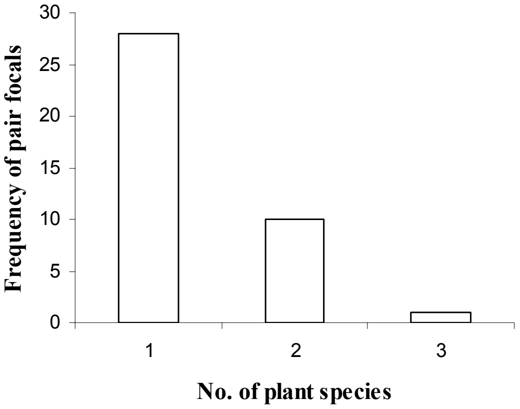


Figure 4.3 Frequency distribution of the number of plant species used by pairs during the oviposition period (*n*=39).

However, in the Southern Damselfly, oviposition occurs in tandem and tandems are rarely broken up by conspecific males. In addition, while a descent below the water surface of 5cm would be sufficient to hide from males, female Southern Damselflies descend up to 10cm and were observed to lay eggs at a depth of 8.7cm. This suggests that this behaviour serves to place eggs far down in the water column and increases the surface area of stem available for oviposition allowing more continuous bouts of oviposition to occur. Most importantly, it decreases the likelihood of desiccation of eggs as water levels drop during the summer. In another damselfly, *E. hageni*, no eggs were found to hatch from exposed sedge stems whilst 96.3% of eggs hatched from submerged stems.

Drying out of oviposition sites may constitute a significant risk to the Southern Damselfly since this species utilises shallow water bodies that are subject to considerable fluctuations in dimensions. For example, at Upper Crockford in 1999, the width of the stream reduced by some five metres in places during June and July.

Predation during oviposition

In three focals, oviposition was terminated when the female was caught in sundew. 5% (2/39) of Southern Damselfly 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.

Non egg laying 'test' bouts

In the Southern Damselfly, as in other damselflies eggs were not deposited during short initial periods of abdominal contact with the stem e.g. these contacts last around 40 seconds in the White-legged Damselfly (*Platycnemis pennipes*). The duration of these non egg-laying 'test' bouts in the Southern Damselfly can be predicted from the y-intercept of a regression of the total duration of oviposition against the number of eggs laid (Figure 4.4), for stems with only one oviposition bout. The value of the *y* intercept on Figure 4.4 is 8.82 with a 95% confidence interval of between 6.74 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 Figure 4.4, the length of a non-egg laying test bout is likely to lie close to the lower limit of the 95% confidence interval. Almost 30% of all oviposition bouts observed were less than 50 seconds (i.e. near the lower limit of the 95% confidence interval - Fig 4.5), suggesting that many bouts are non-egg laying 'test' bouts.

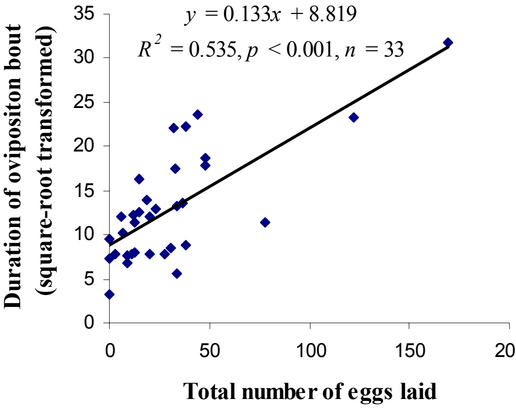


Figure 4.4 Relationship between duration of an oviposition bout on a stem (in seconds) and the total number of eggs laid into it – for stems where only one bout of oviposition was recorded.

Similarly, in a French population of the Southern Damselfly, Martens (1999) found that 54.9% of oviposition bouts lasted less than 20 seconds and females touching the substrate for up to 77 seconds laid no eggs.

Why does oviposition behaviour occur without egg-laying? It has been suggested that egg flow may stop during oviposition though a constant increase in the number of eggs laid with oviposition duration has been found in the White-legged Damselfly. Females may be checking for the presence of predators near the stem. However, the proportion of Southern Damselfly pairs affected by predators was lower than that found for other dragonflies such that predators are unlikely to account for the termination of bouts before eggs are laid in many pairs. Thus in the Southern damselfly, non-egg laying bouts probably reflect unsuccessful attempts at oviposition due to the physical properties of the environment. When several bouts of oviposition occurred on one stem, the female often terminated oviposition bouts by shifting her ovipositor relative to the stem. She often performed rapid probing movements with the ovipositior in a variety of positions until a 'suitable' position was found. The same movements often preceded movement to a different stem. Such unsuccessful attempts at oviposition would necessitate the frequent changes between stems seen in Southern Damselfly pairs. In light of this behaviour, only those plant species on which oviposition is performed for more than 50 seconds should be considered suitable for oviposition.

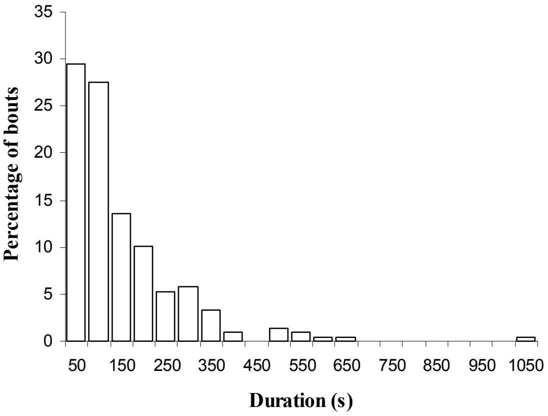


Figure 4.5 Percentage distribution of duration for all bouts (*n*=207; bar labels indicate the upper limit of the class interval).

Measures of site utilisation for oviposition

Total duration of oviposition on a stem was 247.3 ± 21.9 seconds on average (*n*=195) and ranged from 10 to1073 seconds. Total number of eggs laid on a stem was 44.12 ± 8.39 eggs on average (*n*=30) and ranged from 0 to 353 eggs. Deposition rate (calculated from 29 stems into which one bout of oviposition occurred) was 14.06 ± 2.66 eggs per minute on average and ranged from 3 to 65.81. This deposition rate is amongst the highest noted for damselflies since most deposit less than 10 eggs per minute.

Since several bouts of oviposition often occurred on the same stem (Fig 4.6), site utilisation for oviposition was measured by adding up the duration of all bouts of oviposition on a stem to give a total duration of oviposition per stem.

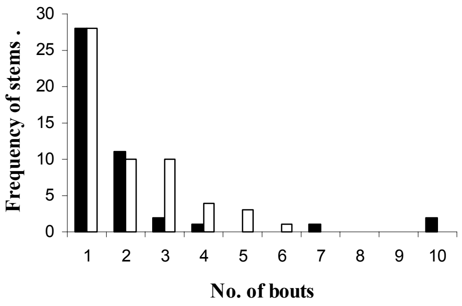


Figure 4.6 Frequency distribution of stems on which different numbers of bouts of egg laying were performed, from caged (closed bars, *n*=45) and natural (open bars, *n*=56) focals.

As expected, there was a significant positive relationship between total duration of oviposition on a stem and total number of eggs laid on a stem (Fig 4.7) indicating that total duration of oviposition was a good measure of site suitability for oviposition. Since the existence of non egg-laying bouts may lead to an over-estimation of the total duration of oviposition on some stems, those bouts that lasted for less than 40 seconds were removed as a correction. However, this correction resulted in a different value of total duration of oviposition for only six stems.

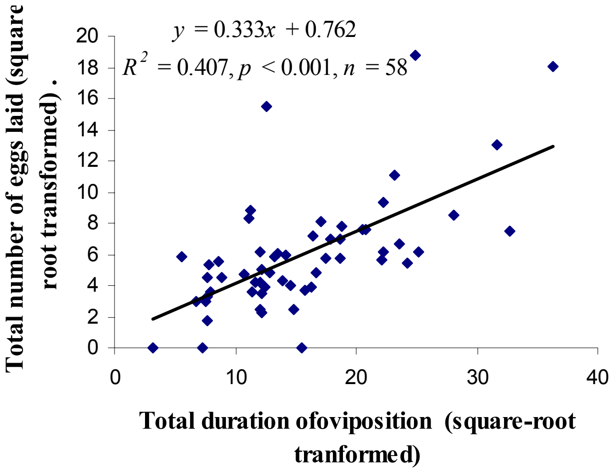


Figure 4.7 Relationship between total number of eggs laid and total duration of oviposition on a stem (all stems).

Thus, this experiment produced two measures of site suitability for oviposition i.e. total duration of oviposition on a stem and total number of eggs laid on a stem.

Effect of habitat variables on site utilisation for oviposition

In stepwise multiple and logistic regression analyses, none of the measured habitat factors could be used to predict the total duration of oviposition or the numbers of eggs laid (see W1-021/PR for details of the analysis). This may be partly because the difficulties of tracking pairs and recovering stems resulted in a low sample size (large sample sizes are required for solutions to multiple regression models). Secondly, these factors may act earlier in the hierarchy described by Wildermuth (1994) i.e. they can generally be assessed visually before a pair lands and may constitute general cues that are unimportant in governing the amount of oviposition that occurs once a pair has landed. As we shall see in the next section, the time spent ovipositing having landed is most likely to be determined by the physical properties of the stem.

Oviposition behaviour occurred at a range of values of these factors. It occurred at a range of pH (5.5 - 7.9, μ=6.67 ± 0.05) and air (13.8 - 28.5 °C, μ=23.05 ± 0.36) and water (18.1 - 29.9, μ=24.96 ± 0.30) temperatures. The water in which oviposition occurred was always shallow (1.5 - 25 cm, μ=8.19 ± 0.55) with 75% of ovipositions occurring at depths less than 10cm.

The Southern Damselfly seems to require slow flow for oviposition in Britain. At Upper Crockford, the distance of oviposition from discernible water flow (0.01 – 0.3 m/s) ranged from 0 to 4m (μ=62.1 ± 10.1) but 75% of ovipositions occurred within 80 cm of flow. In British chalkstream populations ovipositon occurred in discernible flow of not less than 0.029m/s (Strange 1999). In other damselflies, preferences for areas of flow during oviposition has been attributed to a few factors. Increased flow reduces the boundary layer of still water around the egg, allowing oxygen to diffuse into it more rapidly. In *Calopteryx maculata*, less algae was found to build up on the surface of stems (containing eggs) in fast flow. Such a build up would reduce the rate of oxygen supply to eggs or prevent hatching. The larval stage of the Southern Damselfly may also have particularly high oxygen, and thus flow, requirements.

The distance from the nearest tussock ranged from 0 to 2m (μ=61.4 ± 6.6). Such shelter probably improves the accuracy of probing and oviposition movements and allows oviposition to proceed more quickly.

In addition oviposition always occurred on areas of stream with a dark brown peat rather than light gravel substrate. Another shallow bog dragonfly, *Somatochlora arctica* prefers to lay on *Sphagnum* over dark brown peat due to sunlight absorption by the peat that produces water temperatures of up to 20ºC. A similar mechanism may occur in shallow waters occupied by the Southern Damselfly and may allow processes such as oviposition and emergence to proceed quickly. Ditches and brooks used by the Southern Damselfly in south-west Germany, all have a layer of mud at least at their outer edges and on spring mires, the calcareous tufa substrate is coated with organic silt. In addition, high concentrations of Southern Damselfly larvae in Pembrokeshire were associated with a peat substrate that was at least 30 cm in depth (Evans, 1989).

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). Eggs were placed from 0.9 cm to 8.7 cm below the water (μ=3.8 ± 0.54, n=16), reflecting the distances attained when females submerge to oviposit. Egg clutches covered between 3mm and 52mm of the stem (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).

In summary, oviposition occurred in unshaded, open areas of shallow, slow-flowing water over dark peat without dense or tall emergent vegetation.

Frequency of plant use for oviposition

The Southern Damselfly 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. The mean percentage cover across cages or in the natural environment were used to generate expected frequencies of plant use according to plant abundance. Chi-squared tests were then used to compare the frequency of plant use with plant abundance.

There is a significant difference between the observed (O) and expected (E) use of five plant species in cages (χ^2=21.26, 4 d.f., $p < 0.001$; including only those species for which expected frequency of use was two or more – see Figure 4.8a). In natural focals, there is again 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 – see Figure 4.8b). Plants which contribute substantially to the chi-squared value are those which are used either more of less often than their abundance for oviposition (Table 4.1).

- *Eleocharis palustris* (Spiked Rush), *Myrica gale* (Bog Myrtle) and *Molinia caerulea* (Purple Moor Grass) were avoided for oviposition in caged and natural situations.
- *Hypericum elodes* (Bog St John's wort) was favoured for oviposition in caged and natural situations. *Potamogeton polygonifolius (*Bog Pond Weed*)* and *Juncus articulatus* (Jointed Rush) were also favoured for oviposition in natural situations.

Are the plants that are chosen for oviposition by the Southern Damselfly being used as direct cues due to their favourable physical properties for oviposition? Or do they constitute indirect cues to other required properties of the habitat?

If the plants are being used as direct cues then they should share common physical properties that are useful for oviposition. Indeed plant species chosen for oviposition were 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* have a subcuticular layer of collenchyma cells.

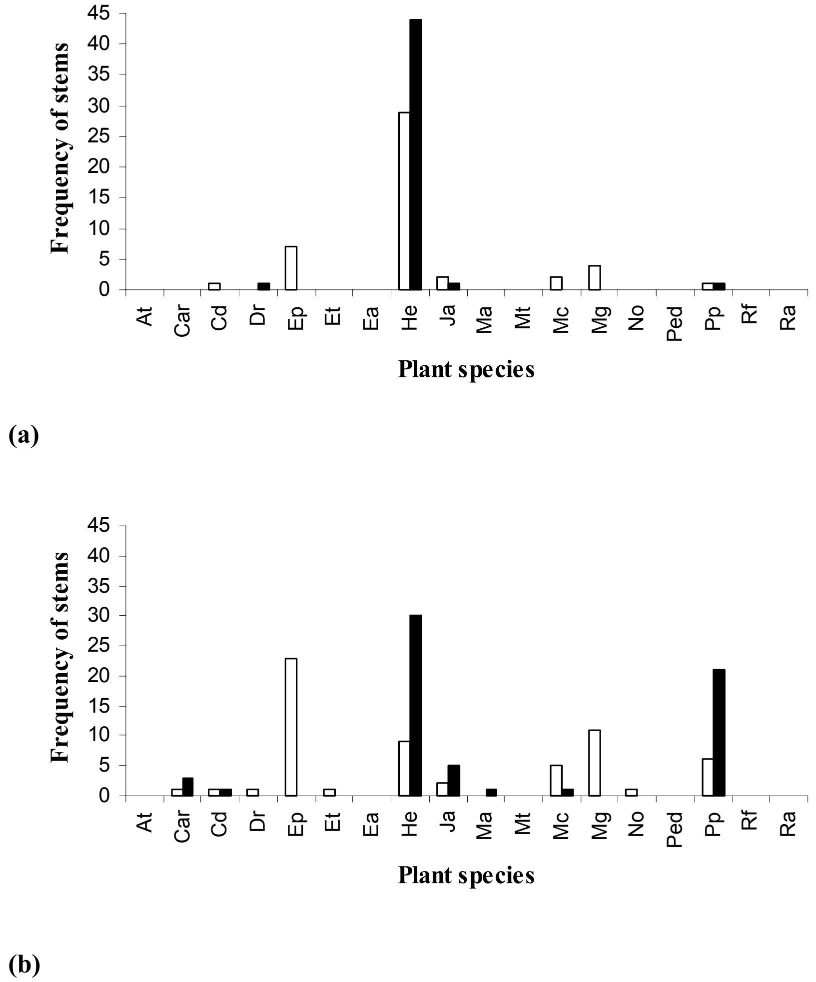


Figure 4.8 Observed (closed bars) and expected (open bars) frequency of plant use for oviposition for (a) caged focals and (b) natural focals.

Plant species key for Figs 4.8 and Table 4.4: 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 angustifolium*; He - *Hypericum elodes*; Ja - *Juncus articularis*; Jb - *Juncus bulbosus*; Mc - *Molinia caerulea*; Mg - *Myrica gale*; No - *Narthecium ossifragum*; Ped - *Pedicularis* sp.; Pp - *Potamogeton polygonifolius*; Rf - *Ranunculus flammula*; Ra - *Rhynchospora alba.*

Table 4.1 Chisquare test of difference between observed and expected use of plant species for oviposition.

	Stem frequency from caged focals			Stem frequency from 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
		χ^2=	21.26		χ^2=	128.20

The failure of eggs to hatch out of tougher stems has been cited as a possible cause of egg mortality in another coenagrionid, the Large Red Damselfly. 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 e.g. *Drosera rotundifolia*, *Anagallis tenella* and *Carex* sp. The stems and petioles of *Hypericum* and *Potamogeton,* in particular, extend laterally under the water surface and have systems of side shoots which may facilitate their use for underwater oviposition in particular.

Table 4.2 lists the 23 plant species that have been used for oviposition by the Southern Damselfly 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. 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, given that early instar damselfly larvae are capable of movement from the oviposition site to a different sub-habitat, oviposition habitat selection probably most closely reflect the habitat features required for egg development and efficient oviposition rather than those for larval development.

If the plant species were being used as indirect cues, they would all indicate a particular habitat property that was useful for oviposition. In fact the plants in Table 4.2 and those used at Upper Crockford 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 be 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 and Mountford, 1997)

To confirm which physical properties of plant stems influence oviposition behaviour in the Southern Damselfly, it would be advantageous to carry out choice experiments. 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.

Plant communities used for oviposition

As well as using a range of plant species, the Southern Damselfly used a range of plant communities for oviposition at Upper Crockford. Table 4.3 shows a similar distribution of oviposition and stream quadrats between a range of communities. 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. The most common NVC plant community in both oviposition and stream quadrats was S19, or *Eleocharis palustris* swamp.

Table 4.3 Plant communities of oviposition (O) and stream (S) quadrats.

NVC Code	Name of community	No. of quadrats O	S
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

These communities are found in moist to wet situations that range from oligotrophic to eutrophic peats. Buchwald (1994) found that Southern Damselfly populations were associated with 6 plant community types in south-west Germany, all of which contained herbaceous plants and that such communities were less likely to be present in the vicinity of intensively used agricultural land.

Table 4.2 Growth form, season and plant group of species used for oviposition by the Southern Damselfly in Britain and Europe.

Plant species	Plant type	Number of observations 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 4.2 continued.

Plant species	Plant type	Number of observations UC	BH	BC	E	Source no.
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
Solanum 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

Habitat selection for emergence

To examine emergence perch use in both the Southern Damselfly and the co-occurring Small Red Damselfly, exuvia were collected from the emergence cages at Upper Crockford (described in Chapter 3) at the end of the emergence period. The plant species, proximity to flow and height of exuvia on stem were noted. The exuviae were sexed and identified to species using the larval keys mentioned in Chapter 1. Seventy exuviae of the Southern Damselfly were collected and 64 of the Small Red Damselfly. Chi-squared tests were again used to compare the frequency of plant use for emergence from exuviae with plant abundance.

To examine habitat use, each cage was treated as a quadrat in which the percentage cover of each plant species, average peat and water depths, and flow rate (given sufficient depth for operation of electromagnetic flow meter) were recorded.

Emergence perch use

The Southern Damselfly and the Small Red Damselfly both emerge in an upright position usually in the morning. Final instar Southern Damselfly larvae leave the water by ascending emergent vegetation in shallow water rather than by walking onto shore as has been seen in some other damselflies. The mean perch heights for the Southern Damselfly (μ =3.64 ± 0.36, n=74) and the Small Red Damselfly (μ =2.35 ± 0.18, n=68) are consistent with those of other damselflies i.e. 5-10cm above the water surface.

For both damselfly species, the difference between observed and expected perch use (Figure 4.9-4.10) was significant (Table 4.4; SDF; χ^2=285.84, 7 *d.f.*, p < 0.001; SRD; χ^2=106.90, 7 *d.f.*, p < 0.001). For both species *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 Europe, exuviae of the Southern Damselfly have been found on other rigid emergents such as *Schoenus* sp. *Juncus subnodulosus*, *J. alpinus, Carex* sp. but also on softer herbs such as *Berula erecta, Solanum dulcamara*, *Mentha aquatica* and *Nasturtium officinale*.

Table 4.4.Chisquare test of difference between observed and expected use of plant species for emergence.

	Frequency of perch use					
	SDF			SRD		
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 Southern Damselfly and the Small Red Damselfly and the Keeled Skimmer all emerged from the same stream habitat. This is in contrast to suggestions by naturalists (Winsland, 1993) that the Southern Damselfly seldom uses the same stretches of stream as other dragonflies even where it occurs on the same site. The mean density of individuals emerging from one square metre through the season was 52.2 (se 10.8) for the Southern Damselfly and 21.6 (se 5.35) the for Small Red Damselfly, indicating that the Southern Damselfly is the dominant species on this site. Estimates of density for both species are considerable higher than estimates for other damselflies e.g. 4.7-8.7/m^2 for the Large Red Damselfly) Whilst these species may exist in higher density populations, the estimates may be high for purely methodological reasons.

Table 4.5. shows habitat variables measured in each cage and 'suitability' of each cage for emergence of the Southern Damselfly. Emergence cages were designated as 'suitable' or 'unsuitable' according to whether more (suitable, coded as 1 on Table 4.5) or less (unsuitable, coded as 0 on Table 4.5) than the mean proportion of emergence occurred within the cage. Table 4.6 shows Wilcoxon two sample tests comparing suitable and unsuitable cages for the Southern Damselfly with regards to a variety of habitat variables. Although 'suitable' cages for Southern Damselfly 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. Thus, the effect of habitat variables on emergence was not successfully quantified in this experiment. This is because, in order to investigate emergence patterns in the Southern Damselfly (Chapter 3), the emergence

cages were all placed in habitat that was presumed to be broadly 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 need to be positioned in a wide range of habitats.

Habitat that was broadly suitable for emergence of the Southern Damselfly was unshaded, shallow (mean water depth = 6.73 cm ± 6.70cm), open, and slow-flowing (between 0.01 and 0.30m/s) and had floating mats of *Hypericum elodes* (mean % cover = 50% ± 4.4%), *Potamogeton polygonifolius* (mean % cover = 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. (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. How these habitat features relate to those that determine the distribution of adults within and between sites is described above. On a Devon site, most exuviae were found in sites with slow to medium flow and none was found in sites that were heavily shaded *by Myrica gale, Phragmites* and trees (James and Wiggers, 2000).

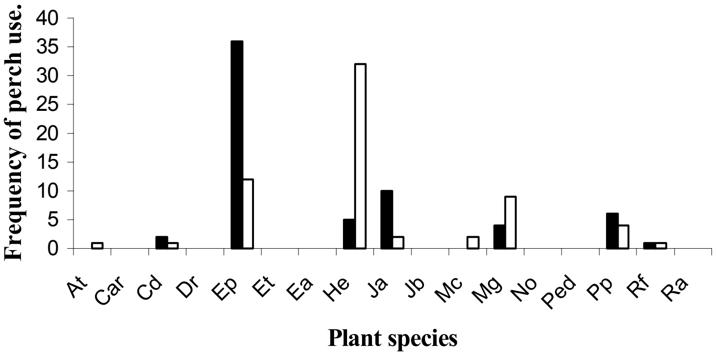


Figure 4.9 Observed (closed bars) and expected (open bars) frequency of perch use by the Southern Damselfly.

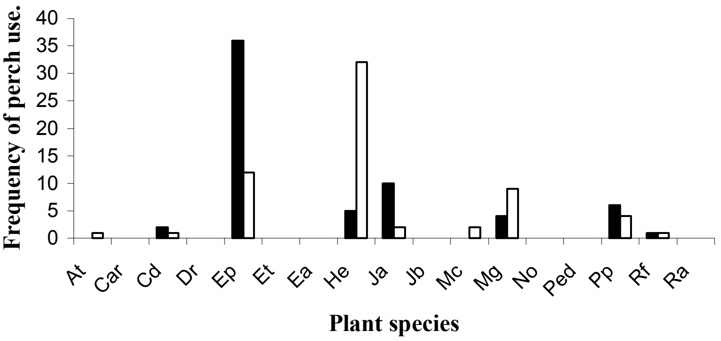


Figure 4.10 Observed (closed bars) and expected (open bars) frequency of perch use by the Small Red Damselfly (key to plant species given in the legend to Figure 4.8).

Table 4.5. '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 SDF
		Hypericum elodes	*Juncus Articulatus*	*Eleocharis palustris*					
1	65	53.2	0	31.9		4.67 ± 1.67	M29(38)	c22.313	1
2	50	28.3	0	37.7	23.40 ± 5.50	7.33 ± 1.59	M29(50)	c22.313	1
3	95	14.3	0	21.4	*	2.67 ± 0.54	M29(32)	c22.313	0
4	60	51.7	0	17.2	*	7.33 ± 2.38	M29(49)	c22.313	1
5	60	25.3	2.5	19	30.20 ± 1.83	8.33 ± 1.01	M29(46)	c22.313	0
6	90	64.5	10.8	16.1	16.80 ± 1.24	8.00 ± 1.39	M29(43)	c22.313	1
7	70	50.6	0	25.3	*	6.17 ± 0.82	M29(59)	c22.313	0
8	60	47.1	0	11.7	*	5.33 ± 0.97	M29(48)	c22.313	0
9	90	68	2.9	19.4	*	3.50 ± 1.35	S19b(47)	c22.312	1
10	60	52.6	0	10.5	*	10.01 ± 1.25	S19a(39)	c53.14a	0
15	90	56	0	24	17.80 ± 1.02	10.83 ± 1.59	M29(55)	c22.313	0
16	30	60.6	6.1	15.2	8.20 ± 2.42	9.33 ± 1.74	M29(28)	c22.313	1
17	90	74.8	9.4	0	41.20 ± 5.09	8.83 ± 1.91	M29(46)	c22.313	1
18	80	36.5	7.3	31.2	*	5.00 ± 2.88	M29(58)	c22.313	0
19	80	66	9.4	7.6	*	6.83 ± 2.83	M29(55)	c22.313	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 4.6. Wilcoxon two sample tests comparing 7 suitable(s) and 8 unsuitable (us) emergence cages for the Southern Damselfly.

Variable	Median_{us}	Median_{s}	*W*	*p*
% vegetation cover	70.00	65.00	16	0.62
Water depth	3.17	7.33	48	1.00
% cover of *Eleocharis palustris*	21.43	16.68	59	0.61
% cover of *Hypericum elodes*	47.06	62.57	36	0.02
% cover of *Cirsium dissectum*	0.00	0.24	48	0.40
% cover of *Juncus articulatus*	0.00	4.48	43.5	0.15
% cover of *Molinia caerulea*	1.04	0.00	57.5	0.46
% cover of *Potamogeton polygonifolius*	19.91	17.65	52	0.19

Habitat use by mature adults

The Southern Damselfly copulates occurred in tussocks of vegetation near the stream rather than in areas of open water at both Aylesbeare (*n*=15) and Upper Crockford (*n*=22). In addition, under poor weather conditions, mature and immature adults spend a huge proportion of their lifespan sheltering in tussocks. At Aylesbeare, where individuals were observed throughout their mature adult lifespan, only a fraction of the individuals known to be alive on a given day (due to subsequent recapture) were actually present on site (Fig 4.11). This is consistent with the association of adult populations with tussocky vegetation across Southern Damselfly sites (Chapter 2). Shelter-belt vegetation may be a particular requirement for the existence of adult populations in edge-of-range populations subject to poor weather conditions.

Habitat use by the larval stage

Current information on habitat factors required by the larval stage has already been described in different parts of Chapter 2, but it is useful to summarise them here;

- Shallow, slow flow (Evans, 1989; James and Wiggers, 2000).
- Permanent flow (Evans, 1989; Hold, 1997; Skidmore, 1996).
- Shallow peat, not deeper than 30cm (Evans, 1989; Knights, 1983) or silt on chalkstream sites (Hold, 1997)
- Open, clear watercourses with abundant submergent aquatic vegetation (Evans, 1989; James and Wiggers, 2000; Skidmore, 1996).

Though Corbet (1957) suggested that early instars live in shallow organic deposits, in this study and that of Thelen (1992), all larval instars were found in submerged aquatic vegetation. Indeed, the hydrophyte portion of the vegetation seemed to be a requirement for larval development on meadow brooks and ditches in Germany. Here, larvae were concentrated where there was emergent aquatic vegetation as well as submergent aquatic vegetation.

In conclusion, many of the thermally advantageous habitat factors used by populations at a broad scale (Chapter 2) were also selected by different life stages at a small scale. This is discussed further in Chapter 7.

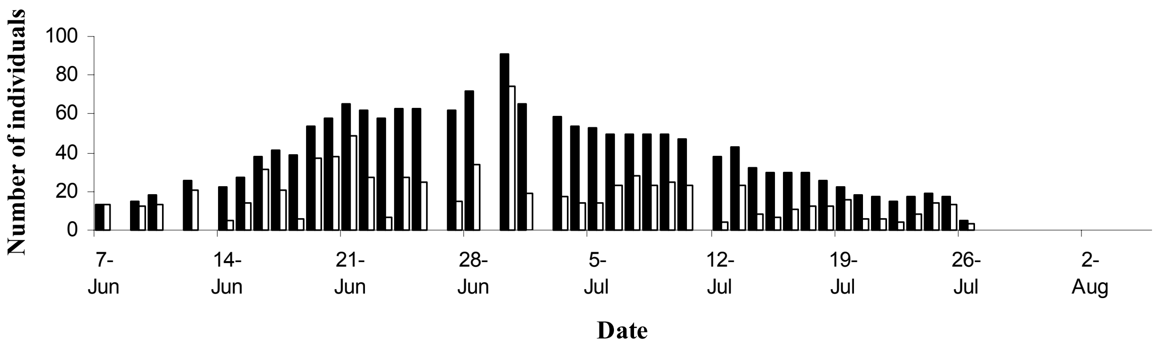


Figure 4.11 The number of individuals alive (closed bars) and the number of individuals present at the Aylesbeare breeding site (open bars) on each date in 1998 (for days when mark-recapture took place).

5. REPRODUCTION AND MORTALITY IN THE MATURE ADULT SOUTHERN DAMSELFLY

Chapter Summary

In this chapter, aspects of the reproductive behaviour and mortality of the mature adult Southern Damselfly were described and can be summarised as follows:

- **A Southern Damselfly copulation lasts for only 20-25 minutes.**
- **General and reproductive activity of Southern Damselflies peaks in the middle of the day.**
- **Only a small fraction of individuals alive on a given day are actually present at the breeding site. Daily activity of both males and females increases with sunlight and temperature as well as decreasing with season.**
- **The amount of sunlight also determines whether reproduction occurs on a day given that damselflies are present.**
- **Lifetime mating success and the mated proportion was found to be low for both sexes in a small population where bad weather conditions permitted only short and infrequent visits to the breeding site.**
- **Females contain an average of 146 eggs in the morning before oviposition and may divide a clutch between two oviposition episodes and two males.**
- **Survival was high and constant in the mature adult stage and there was no difference in survival between males and females.**
- **Males were much more likely to be recaptured than females.**
- **Daily maximum temperature seemed to have a negative effect on survival in this stage.**

Introduction

This chapter describes various aspects of reproductive behaviour in the Southern Damselfly. It draws on data from pair focals carried out at

Upper Crockford in 1999 and at Aylesbeare in 1998. At Aylesbeare, during the daily mark-release recapture exercises, all reproductive activity was observed throughout the mature adult lifespan of individuals. These data are used to examine the dependence of activity and mating success on climatic variables. Some general description of reproductive behaviour is provided since this impinges directly on monitoring strategies.

Duration of reproductive behaviours

Copulations last around 20-25 minutes in the Southern Damselfy (Table 5.1). From when pairs arrived at the breeding site after copulation until the point at which they split after oviposition lasted 69.9 ± 16.0 minutes on average (ranging from 43.0 to 130.4 minutes). For nine pairs from Upper Crockford, timed from before copulation, Figure 5.1 shows the mean percentage of the total period spent in 1) copulation, 2) tandem between copulation and oviposition, and 3) searching for oviposition sites and oviposition itself. 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. 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%).

Diurnal variation in activity

There was a peak of damselfly activity (in terms of number and percentage of individuals present) in the middle of the day (Figures 5.1 and 5.2, *n*=8 days) at Upper Crockford. A peak in reproductive activity also occurred in the middle of the day (i.e. paired individuals on Fig 5.3, *n*=8 days). Females are seen more often in tandem than unpaired. Although mean temperature also peaked in the middle of the day (Fig 5.4, *n*=8 days), it tended to remain high through the afternoon whilst damselfly numbers and reproductive activity decline through the afternoon.

Table 5.1 Mean (± s.e.) and range of total copula duration (minutes) for pairs from Aylesbeare and Upper Crockford.

Site		*n*	μ ± s.e.	Range
Aylesbeare		2	19.5 ± 0.6	-
Upper Crockford	All	22	23.1 ± 1.6	14.2 – 45.0
	Caged	15	22.0 ± 1.6	15.0 – 40.0
	Natural	7	25.6 ± 3.8	14.2 – 45.0

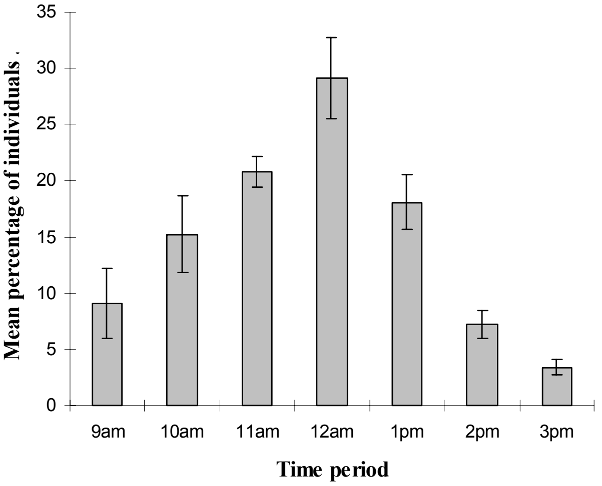


Figure 5.1 Mean percentage of day's individuals (± s.e.) present in each time period.

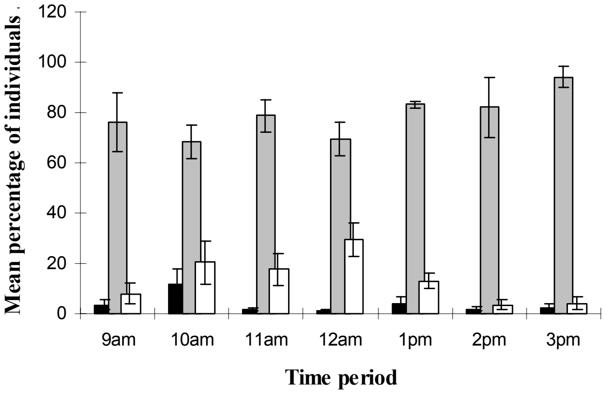


Figure 5.2 Mean percentage of individuals (± s.e.) that are unpaired males (grey bars), unpaired females (black bars) and paired (open bars) in each time period.

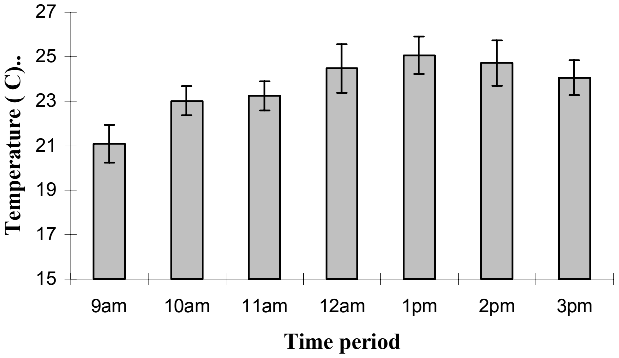


Figure 5.3 Mean temperature (± s.e.) in each time period.

Table 5.2 Mean ± s.e. and range (in minutes) of time spent in different reproductive behaviours for 9 pairs from Upper Crockford 1999.

Time period	$\mu \pm$ s.e.	Range
Total period	68.0 ± 8.5	39.6 – 102.6
1) Copulation	24.2 ± 2.4	15.0 – 40.0
2) Tandem between copulation and oviposition	13.4 ± 3.5	3.0 – 39.0
3) Oviposition or searching for oviposition sites	30.5 ± 5.5	8.3 – 58.0

Daily variation in activity

Since only a fraction of the individuals known to be alive on a given day (due to subsequent recapture) were actually present at the breeding site, the amount of damselfly activity on a given day was expected to depend on prevailing weather conditions and season. Since mark-recapture exercises had only been performed when damselflies were flying on site, this analysis investigates how weather variables and season affect the activity of damselflies, given that weather permitted damselflies to fly 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 at least one damselfly was flying (hereafter referred to as MACTIVITY for males, FACTIVITY for females). The daily sex ratios at the stream varied from 6:1 to 1:1 (males:females). Males exceeded females in the number of individuals present (paired *t*-test, t=-8.036, p<0.001, 49 d.f, Table 5.3); 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 5.3). Thus the analysis of the effect of weather on activity was performed separately for males and females.

Table 5.3 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	10.1 ± 1.2	3.9 ± 0.6
Sum of the hours spent at the breeding site by all individuals	51	20.2 ± 3.6	6.5 ± 1.0

Rainfall - in mm (RAIN), sunlight - in 0.1 hours (SUN) and average daytime temperature in 0.1 °C (TEMP), all for each 24 hour period were obtained from a British Atmospheric Data Centre climate station in Exmouth 10km away from Aylesbeare (SY027819). In a stepwise multiple regression, with FACTIVITY as the dependent variable, and the weather variables and day of season as the independent variables revealed that SUN had a positive relationship with FACTIVITY but only explained 9.9% of the variation in female activity (Table 5.4a). In, a stepwise multiple regression with MACTIVITY as the dependent variable, SUN was added first to the model followed by TEMP and DAY and this model explained 44.6% of the variation in MACTIVITY (Table 5.4b). Thus male activity increased with the duration of sunlight and temperature but declined as the season progressed. 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 lifetime mating success (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.

Table 5.4a 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.		F	p
Regression	1		4.39	0.043
Residual	40			
Total	41			
$R^2 = 0.099$				
Coefficients	B	s.e.	t	p
Constant	4.17	1.72	2.43	0.02
SUN	0.05	0.02	2.10	0.043

Table 5.4b 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.		F	p
Regression	3		10.21	<0.001
Residual	38			
Total	41			
$R^2 = 0.446$				
Coefficients	*B*	s.e.	t	p
Constant	-3.55	3.32	-1.07	0.291
SUN	0.02	0.01	3.44	0.001
DAY	-0.05	0.02	-3.00	0.005
TEMP	0.05	0.02	2.38	0.023

Daily variation in reproductive activity

A stepwise logistic regression procedure, comparing days when mating occurred to days when mating did not occur revealed that probability of mating activity (given that damselflies are present at the breeding site) is also influenced by weather variables. SUN was added as a significant predictor of the probability that mating occurred on a day given that damselflies were present (Table 5.5).

Table 5.5 Logistic regression analysis of the probability that mating will occur on a particular day (given that damselflies are present at the breeding site – LR = likelihood ratio).

	B ± s.e.	LR	G	*p*	n_0	n_1	*Exp (β)*
C	-1.84 ± 0.72						
SUN	0.03 ± 0.01	-29.1	13.3	0.0003	20	22	1.03
Model χ^2=13.30, p< 0.001, 1 d.f.							

Thus external weather variables had a significant effect on whether Southern Damselflies were active on a particular day and on whether damselflies mated on a particular day. Such effects of weather on activity, especially reproductive activity, are widespread in dragonflies. For example, in the Black Darter (*Sympetrum danae*), body-surface temperature had a positive exponential effect on flight activity (within the range 20-40°C) and also decreased time spent per mate during oviposition and copulation.

Visiting patterns to the stream and intervals between consecutive matings

During the field season at Aylesbeare in 1998, 116 males were marked (of which 86 (74.1 %) were recaptured – these are termed resident males) and 77 females were marked (of which 45 (58.4%) were recaptured – these are termed resident females).

The was a lack of continuously suitable conditions for reproduction. Weather conditions permitted only short visits of only an hour and a half to the breeding site by both sexes. Males spent longer at the breeding site in their lifetime though their visits were not significantly longer than those of females (Table 5.5, Figure 5.6). Only 2 males and females separated from their first partner for marking, mated twice on a day

Weather conditions permitted reproductive activity on only 22 days and the intervals between these days ranged from 1 to 4 days (μ = 2.2 ± 0.3). The fact that some females had an interval of one day between matings suggests either that it is possible to mature a clutch of eggs in one day in good weather or that females are dividing their clutch between two males or two days.

Thus 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 – Table 5.5, Figure 5.7), or the mean duration of visits to the breeding site.

The restriction of both sexes to short, infrequent visits prevented males from cycling between mates faster than females as is common in dragonfly populations. This affects the distribution of mating success. 72 matings were recorded. Mean lifetime mating success (i.e. number of matings throughout an individual's lifetime) was 0.62 ± 0.10 for all males but was 0.83 ± 0.13 when only resident males were included. Mean lifetime mating success for females was 0.76 ± 0.10 for all females but was 1.07 ± 0.15 when only resident females were included.

Table 5.6 Mann-Whitney tests (U on table) and Wilcoxon two-sample tests and between males (M) and females (F) for total hours spent at the breeding site in their lifetime, mean duration of visits to the breeding site, mean interval between matings per individual and interval between matings (with mean (± s.e.) and range).

Variable	Sex	*μ ± s.e.*	Range	U or W	*p*	*n*
Total hours spent at breeding site in lifetime	M	4.5 ± 0.4	1 – 20	U =	<0.001	115
	F	2.6 ± 0.2	1 – 9	3073.5		75
Mean duration of visits to breeding site	M	1.6 ± 0.1	1 – 7	U =	0.08	115
	F	1.4 ± 0.1	1 – 4	3785.5		76
Mean interval between matings*	M	4.6 ± 0.8	1 - 12	W =	0.133	17
	F	7.8 ± 1.5	1 - 18	247		16
Interval between matings*	M	4.0 ± 0.6	1 – 9	W =	0.134	29
	F	7.6 ± 1.7	1 – 30	664		21

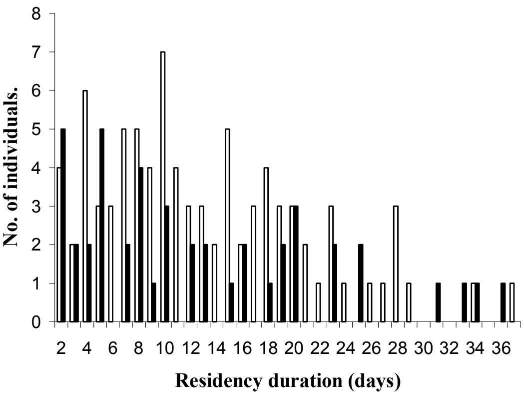


Figure 5.5 Frequency distribution of residency durations of males (white bars, *n*=86) and females (black bars, *n*=45) seen more than once.

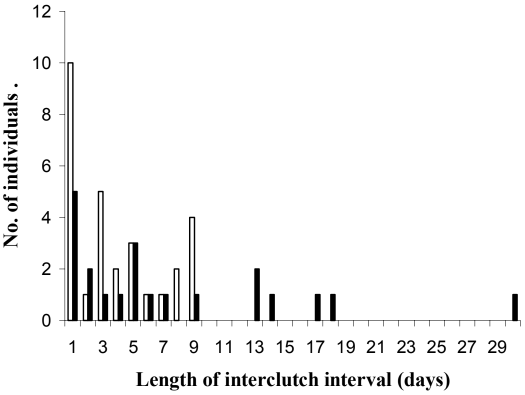


Figure 5.6 Frequency distribution of the total hours spent at the breeding site in their lifetime for males (open bars, n=115) and females (closed bars, n=76).

Due to the restriction by the weather of both males and females to short, infrequent visits, 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 the Southern Damselfly (χ^2 test for difference in LMS between males and females – all individuals χ^2=4.53, p=0.34, 4 d.f. with amalgamation of individuals that mated four or more times, residents - χ^2=4.83, p=0.30, 4 d.f.). The distribution of mating success across the populations did not differ from a random distribution (i.e. a Poisson distribution) for males (residents: χ^2=6.03, p=0.89. 3 d.f., mating success > 3 pooled) or females (residents:χ^2=0.00, p=1.00. 3 d.f.) as shown in Figure 5.8 and 5.9.

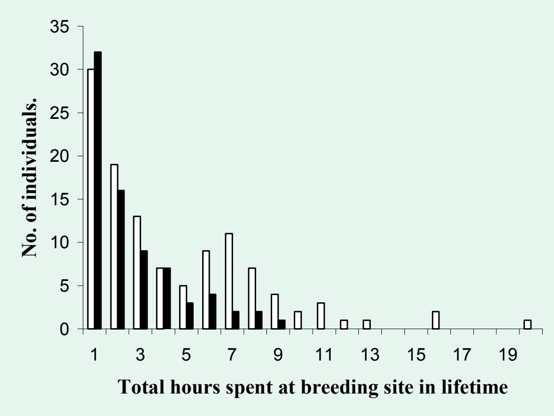


Figure 5.7 Frequency distribution of the interval between consecutive matings for males (open bars, *n*=29) and females (closed bars, *n*=21).

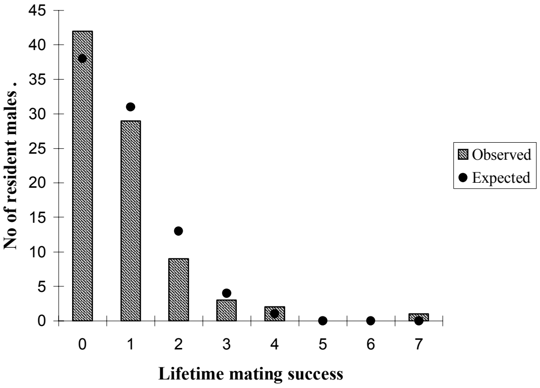


Figure 5.8 Observed and expected (from Poisson distribution) Frequency distribution of lifetime mating success for resident males.

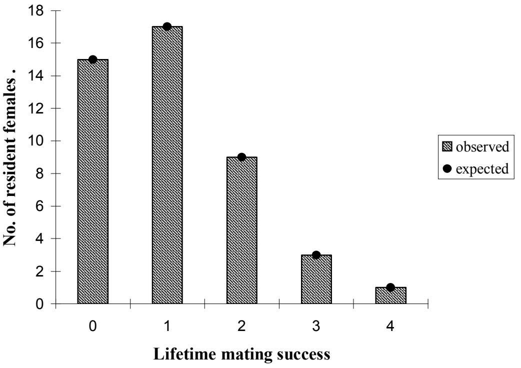


Figure 5.9 Frequency distribution of lifetime mating success for resident females.

Such an equal distribution of LMS between sexes has been attributed in another damselfly, *Ischnura gemina,* 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 the Southern Damselfly, '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.

The unmated proportion is low for females and high for males in most dragonfly populations e.g. 31% of males and 1% of females remained unmated in a population of *Enallagma hageni*. In this study, a high proportion of both sexes remained unmated in their lifetime.

Clutch size and oviposition behaviour

Females were collected at Upper Crockford in 1999:

1. before copulation in the morning
2. after copulation
3. after the oviposition period (from focals)

In the laboratory, head width and left forewing length were measured, sperm presence in the spermatheca and bursa was noted following their dissection and any mature eggs (larger and lighter coloured than immature eggs) in the abdominal cavity were counted.

Figure 5.10 – Figure 5.12 shows the frequency distribution of the total eggs contained in the abdomens of females in categories 1-3 respectively. The mean number of eggs in females collected in the morning before oviposition was 146.1 ± 16.0 and ranged from 7 to 360 eggs. The mean number of eggs left after oviposition was 12.67 ± 4.94 and 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 them between two. This is supported by the fact that a substantial portion of females observed in pair focals laid 50 eggs or less in an oviposition episode.

Although there was no significant relationship between clutch size and body size (head width) in the Southern Damselfly (F=1.80, p=0.197, R^2=0.091, 19 d.f.), large clutch sizes (>200 eggs) were only found in the largest individuals (head widths >4mm), indicating that maximum clutch size may be limited by space available in the abdomen. Mean egg length was 0.981 ± 0.003mm (ranging from 0.833-1.133, n=325). Larger females also produced larger eggs (F=7.82, p=0.009, R^2=0.207, 31 d.f.) that may be better provisioned for embryonic development, increasing offspring survivorship.

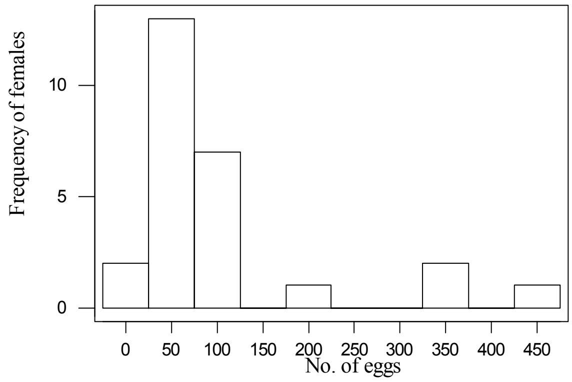


Figure 5.10 Frequency distribution of number of eggs laid by females during oviposition focals (*n*=27, all focals ended with a natural pair split) derived from plant stem dissections.

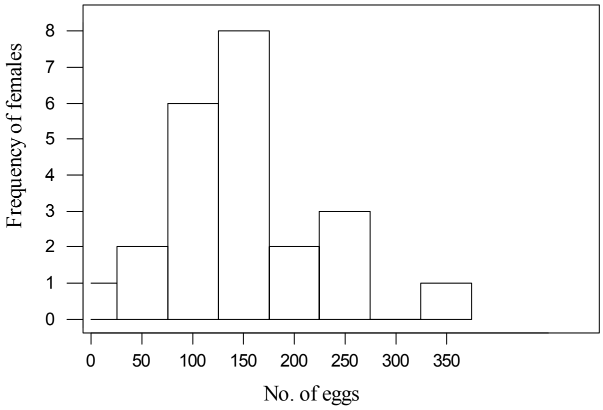


Figure 5.11 Frequency distribution of number of eggs found in females before oviposition (*n*=23).

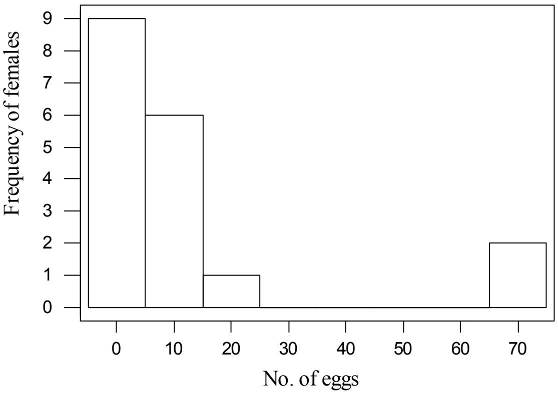


Figure 5.12 Frequency distribution of number of eggs found in females after oviposition (*n*=18).

The mature adult stage

Mark-release-recapture experiments on mature adults at the stream were carried out on three different sites. Survival was examined in these populations using mark-recapture models (Cormack-Jolly-Seber) that separately estimate survival and recapture probabilities – accounting for the fact that the likelihood of recapture can also vary between individuals or occasions. These have rarely been used to estimate survival in odonate populations, making a full explanation of this type of analysis pertinent here.

In this approach, capture histories are constructed from recapture data that record whether an individual was present or absent on a particular occasion. The Cormack-Jolly Seber (CJS) model is fitted iteratively in Program Mark using maximum likelihood methods and two types of parameter are estimated

- the probability that a marked animal survives from one occasion to the next (survival probability ϕ)
- the probability that a surviving marked animal that has not emigrated permanently is observed in the study area (recapture probability p).

Survival and recapture is expected to depend on characteristics of the individual and to vary over time depending on season, life-history or prevailing climatic variables. Having determined that the CJS model fits the dataset, the effect of these variables can be examined within Program Mark by fitting models with different combinations of their main effects and interactions. It is possible to chose the best model on the basis of an information-theoretic measure called Akaike's Information Criterion (AIC_c: Akaike, 1985). This approach is explained fully in W1-021/PR but here it is sufficient to state that a model containing a variable, such as body size, is considered to fit the data better if it has an AIC_c at least two lower than the model with the next lowest AIC_c. Thus ΔAIC_c is presented i.e. the difference in AIC_c between the model in question and the model with the lowest AIC_c.

For the mature adult Southern Damselfly, 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 climatic variables. Models with these variables were thus examined in Program Mark and ranked on the basis of their AIC_cs. Table 5.7 shows the variables included in the models and the subscripts used to indicate them. Plus signs indicate that the model includes only main effects while an asterisk indicates that it includes interaction terms.

Table 5.7 Model subscripts used in capture-mark-recapture analyses.

Subscript	Meaning
Parameter	
ϕ	survival probability
p	recapture probability
Variables	
t	Time-dependence (day-to-day variation)
s	Sex-effect
b	Body size (left forewing length (mm))
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)

The analysis was performed on mark-recapture data from a small, isolated population on Aylesbeare Common in Devon. Here, between June and August 1998, 223 mature adults were marked in daily recapture exercises on this population. In addition, the analysis was performed on data from a large, non-isolated population, Glan-yr-afon Uchaf (Mynydd Preseli, Pembrokeshire) where estimates of survival may be biased downwards by permanent emigration from the study area. At this site, around 2000 mature adults were marked in daily recapture exercises between June and August (Hopkins & Day, 1997).

Survival analysis for Glan-yr-afon Uchaf

Table 5.8 shows the five best models fitted to the dataset for Glan-yr-afon Uchaf, (containing 1110 mature males, 370 mature females). In the best model, survival probability is time-dependent and recapture probability depends on sex, time and body size with an interaction between sex and body size (i.e. $\phi_{(t)}\ \rho_{(t+s*b)}$). The model for the recapture probability including only sex and time (2^{nd} on Table 5.8) had an AIC only 1.39 larger indicating that both models provided a similar fit to the data. 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.

Table 5.8 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

In practice this means that, at Glan-yr-afon Uchaf:

- Males had a higher probability of **recapture** than females (Figure 5.13a - β=1.772 ± 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).
- Body size had a positive relationship with probability of **recapture** (β=0.339 ± 0.184) i.e. larger individuals are more likely to be recaptured than small individuals.
- Probabilities of **recapture** seem to vary substantially between occasions. Since equal recapture effort was employed on each recapture occasion, this time dependence is most likely explained by variation in external weather conditions. Here, 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.

- Mean **survival** probability was 0.882 ± 0.029 (ranging from 0.495 to 1).
- **Survival** probabilities varied substantially between occasions again probably due to weather variables.

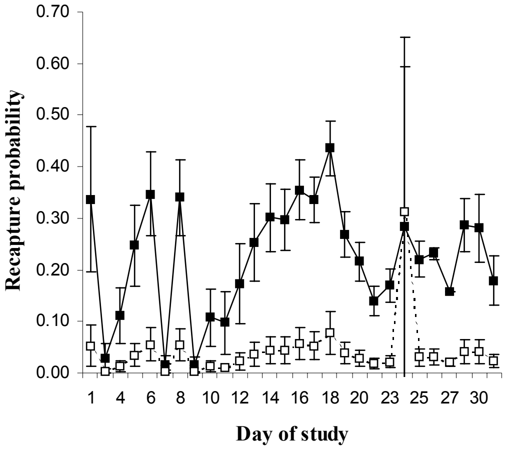


Figure 5.13a Maximum likelihood estimates (± s.e.) for recapture probabilities of Southern Damselfly males (black squares and solid lines) and females (white squares and dashed lines) on each day of the study Day 1=10th June) - calculated from the model ϕ(t) ρ(t+s*b).

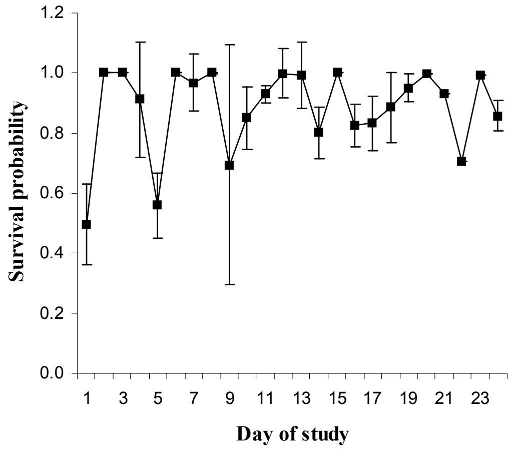


Figure 5.13b Maximum likelihood estimates (± s.e.) for survival probabilities of the Southern Damselfy on each day of the study (Day 1=10th June) - calculated from the model ϕ(t) ρ(t+s*b).

For comparison, residency duration was calculated as the interval between first and last recapture since this is the measure of survival commonly used by investigators of odonates. There was a significant difference between males and females in residency duration in both sites when all individuals were included in the analysis (μ_m ± s.e.= 3.71 ± 0.14, n_m= 1474, range$_m$=1-38; μ_f ± s.e.=1.99 ± 0.14, n_f= 514, range$_f$ =1-25; Komolgorov Smirnov Z=4.02, 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 (μ_m ± s.e.= 8.56 ± 0.28, n_m= 530; μ_f ± s.e.=7.36 ± 0.58, n_f= 80, Komolgorov Smirnov Z=0.77, p=0.376).

Survival analysis for Aylesbeare Common

Table 5.9 shows the five best models fitted to the Aylesbeare dataset (containing 69 males and 42 females for which a body size measurement was available). In the best model, survival probability is dependent on maximum temperature and recapture probability depends on sex, time and body size with no interaction between sex and body size.

Table 5.9 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

In practice, this means that at Aylesbeare;

- Males had a higher probability of **recapture** than females (Figure 5.14a - β=2.082 ± 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).
- Body size had a positive relationship with probability of **recapture** (β=0.632 ± 0.159) i.e. larger individuals are more likely to be recaptured than small individuals.
- Probabilities of **recapture** seems to vary substantially between occasions. Since equal recapture effort was employed on each recapture occasion, this time dependence is most likely explained by variation in

external weather conditions as described above.

- 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.

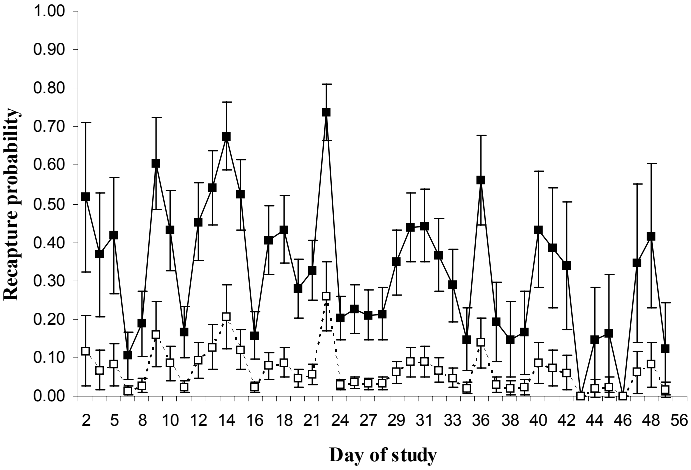


Figure 5.14a Maximum likelihood estimates (± s.e.) for recapture probabilities of Southern Damselfly males (black squares and solid lines) and females (white squares and dashed lines) on each day of the study (Day 1=7th June) - calculated from the model $\phi_{maxt}p_{s+size+t}$.

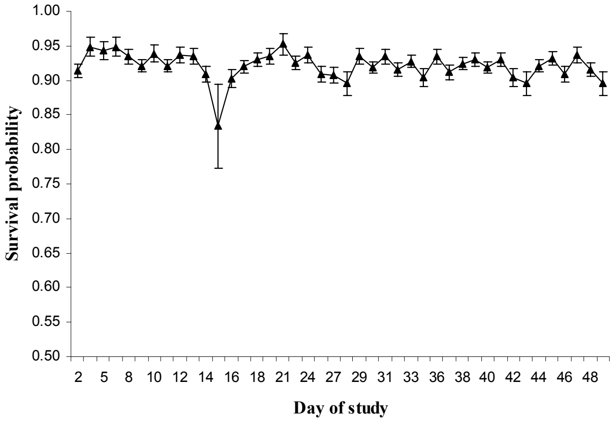


Figure 5.14b Maximum likelihood estimates (± s.e.) for survival probabilities of *C. mercuriale* on each day of the study (Day 1=7th June) - calculated from the model $\phi_{maxt}p_{s+size+t}$.

Conclusions from survival analyses

Survival was high and constant in the mature adult stage of the Southern Damselfly. For example, at Aylesbeare, it ranged from 0.83 to 0.95 due to weather conditions. Survival through the mature adult stage in this species is probably higher than through the other stages of its life cycle and the larval stage probably suffers the highest mortality. Causes of mortality in the mature adult stage may include starvation, water logging, predation, and accumulation of physical damage (Corbet, 1999). The values for survival probability for the Southern Damselfly found in these two sites were intermediate in the range found in previous damselfly studies for males i.e. from 0.73 for *Ischnura posita* to 0.94 for *Lestes temporalis* (Corbet, 1999).

Males and females did not differ in survival probability in either population. Most previous authors have claimed that male dragonflies have higher survival than females in both the pre-reproductive and reproductive periods. But, unlike in 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.

Males and females differed in recapture probability in the Southern Damselfly, probably partly due to the brighter colouration of males but also due to behavioural differences between the sexes. The latter will be discussed more in Chapter 6. In addition, large individuals were more likely to be recaptured than small ones. In the large population, at Glan-yr-afon Uchaf, males and females differed in residency duration but not in survival probability. In the small population, at Aylesbeare, 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 in 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 damselflies of 7.6 days (range 3.8-23.3, Corbet, 1999).

At Aylesbeare, 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 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). For example, the greater mortality suffered by females compared to males during the pre-reproductive period has been attributed to the fact that the former are more active in foraging to gain mass for reproduction.

6. DISPERSAL IN THE MATURE ADULT SOUTHERN DAMSELFLY

Chapter Summary

This chapter examines dispersal traits of the Southern Damselfly in two British sites and can be summarised as follows:

- **The maximum within-patch and between-patch movements of the Southern Damselfly were 610m and 1060m respectively. The between patch migration rate was 1.3% at Crockford and 11.4% at Glan-yr-afon Uchaf.**
- **The rate and extent of mobility of the Southern Damselfly in these two British sites was greater than that observed in previous studies and was comparable to that of other similarly sized odonates.**
- **The Southern Damselfly can move considerable distances in a short period of time.**
- **Dispersal was influenced by landscape structure – being more likely between sites that were closer together, within patches rather than across intervening habitat (for short-medium distance movements) and in the absence of scrub boundaries.**
- **Actual colonisation distances are probably greater for the Southern Damselfly than those observed in the field. Given the current configuration of British sites, frequent dispersal events and recolonisations are likely within the four largest clusters (New Forest, Test and Itchen Valleys and in Pembrokeshire) but are relatively unlikely in small, isolated site clusters.**
- **There was no sex, size or age bias in dispersal.**

Introduction

Dispersal is an undirected movement (in contrast to migration) away from the habitat of origin and plays a vital role in both local and metapopulation dynamics. When a population occupies a patchy habitat it may form a network of smaller, local populations called a metapopulation (Hanski & Gilpin, 1991). Dispersal determines the probability that empty habitat is colonised and affects the probability of extinction, via processes known as the 'rescue effect' and 'genetic rescue'. In butterflies, studies show that by these processes dispersal influences the persistence and (re)founding of local populations and in turn, influences metapopulation persistence (Thomas & Hanski, 1997 and references therein).

Box 6.1 – some definitions

rescue effect - decreased probability of extinction due to stochastic environmental causes in small local populations due to the direct increase in abundance of the recipient populations.

genetic rescue - the replenishment of genetic variation and reduction in inbreeding depression due to an influx of migrants.

Since dispersers reach new habitats by chance and the majority of emigrants never locate another patch, dispersal usually carries a high per capita mortality. For example, between 15-35% of butterflies have been estimated to die between patches. Natural selection may favour individuals that remain in the population even if population persistence or the rate of recolonisation events are reduced 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. 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. 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 because they are restricted to water for most of their life cycle. Despite this, dispersal has been poorly documented in odonates relative to other orders of winged insects. Odonates (and butterflies) are rare among terrestrial arthropods in that flight is multifunctional being used both within patches (for location of food, mates and oviposition sites) and between patches for dispersal. Temporary emigration for roosting and maturation is common in female and teneral odonates. Since most studies on odonate dispersal have focussed on within-patch movements or movements between adjacent waterbodies, between-patch movement has been regarded as uncommon in odonates. However, expansions in species' distributions, in response to factors such as deforestation, development of agriculture and mining areas and global warming, have been observed in odonates and suggest that some species are capable of movement across unsuitable habitat. Direct evidence of between-patch dispersal is required for odonates.

In this study, both within and between-patch dispersal is examined directly in the Southern Damselfly, using field mark-release-recapture datasets, collected in 1997 by Graham Hopkins and Kieron Day, from two stronghold populations in Britain. 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 individuals occupying a shifting habitat mosaic (Thomas and Hanski, 1997). 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. Although, habitat and non-habitat was not mapped explicitly 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.

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. 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. In territorial species, dispersal is more likely in females or in males that do not hold territories. Thus in odonates, phenotypic correlates of dispersal may reflect phenotypic correlates of other aspects of behaviour that require movement (or non-movement).

Extinction and colonisation events have rarely been directly observed in the Southern Damselfly. Here, the spatial configuration of British sites is described in relation to the field observed dispersal ability of the Southern Damselfly. This permits speculation on the likely extent of dispersal between populations in Britain and its effect on the persistence of this species (i.e. the processes of extinction and colonisation) in different parts of its British range.

Study sites

Mark-release-recapture experiments were carried out, at Glan-yr-afon Uchaf in Pembrokeshire and on the Crockford Stream system, Beaulieu Heath, New Forest (hereafter referred to as Glan-yr-afon and Crockford respectively). In each site, *within patch movements* were examined within main stream sections and *between patch movements* were examined between the main patch and a series of peripheral patches around it. The location of sampled and unsampled habitat and areas of scrub is shown for each site in Figures 6.1 and 6.2). Due to the different configuration of sampled habitat, the two sites provided different opportunities for dispersal and different probabilities of observing it.

In Glan-yr-afon Uchaf, 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 Crockford 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 - site 3 (620m from site 2, 1060m from site 1), site 4 (1090m from site 2, 1470m from site 1), and site 5 (1190m from site 2, 1560m from site 1). Thus, the maximum observable within-stream movement was greater in the Crockford than in Glan-yr-afon Uchaf, whilst the maximum observable between-stream movement was also greater at Crockford (3km versus 1.5km). However, in Glan-yr-afon Uchaf, 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 Glan-yr-afon Uchaf, most ‘peripheral’ patches were separated from the ‘main’ one by a mixture of valley mire and wet heath. In Crockford, 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.

Mark-release recapture protocol.

Fieldwork was carried out between 6th June and 31st July 1997 at Crockford, and the following standard protocol was adopted between 18th June and 26th July 1997. When weather permitted damselfly activity, a four hour mark-recapture exercise was performed in sites 1 and 2. Each subsection was searched for twenty minutes. Unmarked Southern Damselfly individuals were each given a unique mark and sex, age (teneral or mature adult), left forewing length, and subsection were noted. The individual was released in the middle of the subsection in which it had been found (enabling the distance between subsequent recaptures to be measured). For recaptured individuals, identity, date, subsection and age were noted. Mature adults seen for the first time were scored as being one day old so that age on subsequent recapture could also be calculated. Sites 3, 4 and 5 were searched for marked individuals at less frequent intervals throughout the season.

Fieldwork was carried out at Glan-yr-afon Uchaf 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. Most peripheral patches were searched every day for individuals though patches further away received less attention.

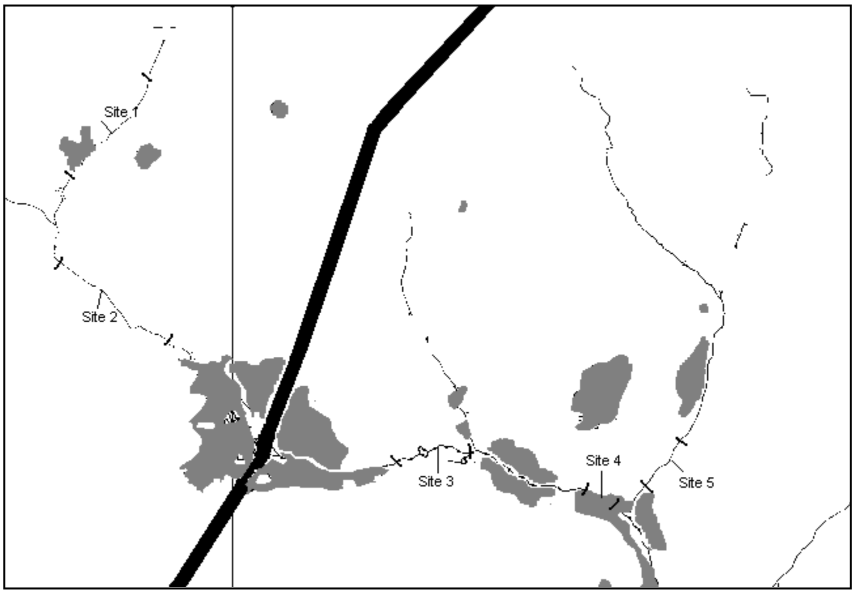


Figure 6.1 Map of Crockford study area. Extent of lengths of sampled stream (sites 1-5) indicated by short black lines across the stream. Grey shaded areas indicate scrub. Black area shows position of road across site.

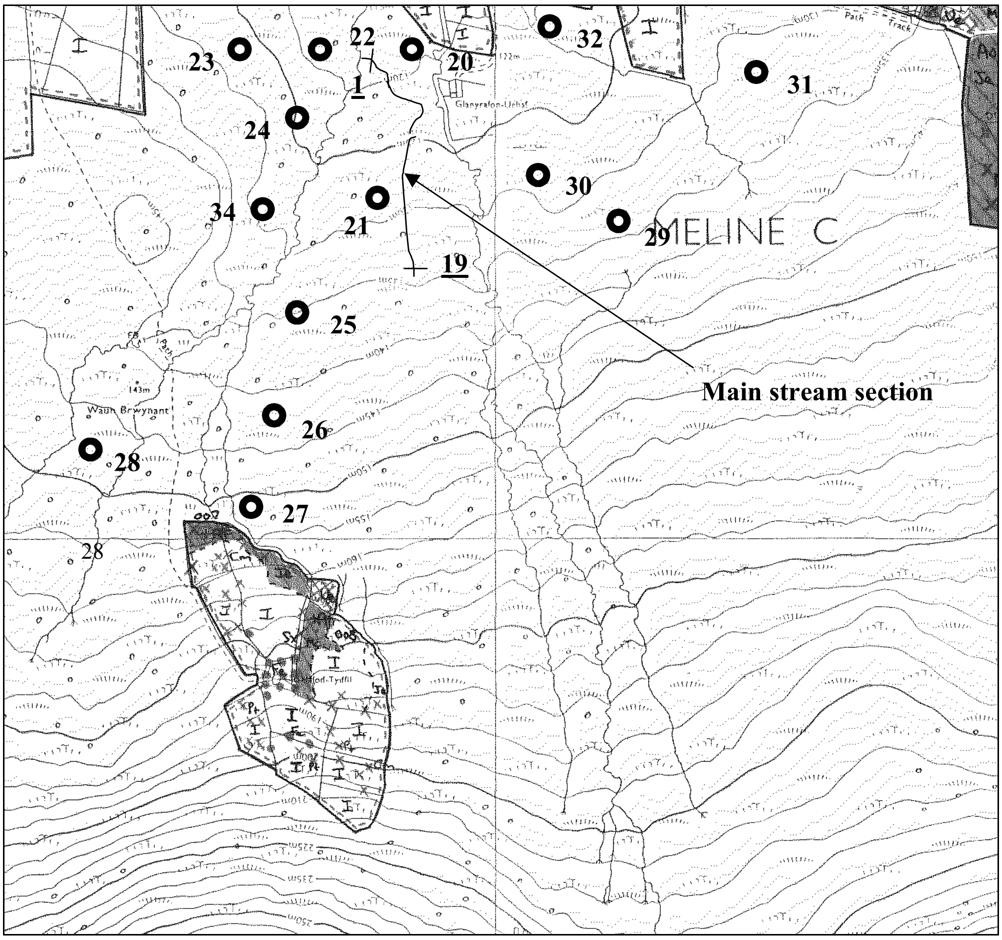


Figure 6.2 Map of Glan-yr-afon study area, Mynydd Preseli. Limits of main stream section (sections 1-19) are indicated by short lines across stream whilst centres of peripheral patches of mire are indicated by rings (20-34).

Frequency of within and between patch movements in the Southern Damselfly

Over 2000 individuals were marked in both sites, and recapture proportions ranged from 15-36% (Table 6.1). In describing the dispersal potential of an endangered species, it is important to distinguish between movements across suitable habitat and those across unsuitable habitat. Movements between two recaptures were divided into three types:

1. Non-movements
2. Within stream transfer – movement to a different part of the same stream section
3. Between stream transfer – movement to a different stream section at Crockford, or from the main stream section to one of the fourteen peripheral patches at Glan-yr-afon Uchaf.

Table 6.1 Number of males (M) and females (F) marked and recaptured, and recapture proportions (RP) in each site.

Site	Sex*	No. marked	No. recaptured	RP (%)
Crockford	M	2350	708	30.1
	F	597	116	19.4
Glan-yr-afon Uchaf	M	1474	533	36.1
	F	514	80	15.6

The frequency of each of these types of movement is shown in Table 6.2.

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%). Males and females did not differ in the proportion of individuals that performed the three types of movement in their lifetime either at Crockford (χ^2=1.59, p =0.452, 2 d.f.) or at Glan-yr-afon Uchaf (χ^2=2.76, p =0.252, 2 d.f.).

There was a significant difference in the proportion of individuals performing these three types of movements between the two sites (males and females amalgamated - χ^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 between patches was 1 in the New Forest and 2 in Mynydd Preseli.

Table 6.2 Frequency and proportion of between-stream movements, within-stream movements and non-movement for males and females from both sites.

	Crockford		Glan-yr-afon Uchaf	
Movement type	No. of males (%)	No. of females (%)	No. of males (%)	No. of females (%)
n	676	118	533	80
Between-patch transfer	9 (1.3)	0 (0)	61 (11.4)	14 (17.5)
Within-patch transfer	531 (78.6)	94 (79.7)	291 (54.6)	38 (47.5)
Non-movement	137 (20.3)	24 (20.3)	181 (34.0)	28 (35.0)

The location and direction of the nine between-patch transfers in the New Forest are shown in Figure 6.3. Three of these movements occurred across a scrub barrier and six occurred across unsuitable stream. No movements occurred between sites 3, 4 and 5 even though they are relatively close together suggesting that scrub constitutes a significant barrier between these sites.

The location and direction of the between-patch transfers in Glan-yr-afon Uchaf are shown in Figure 6.4. 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 Crockford site.

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.

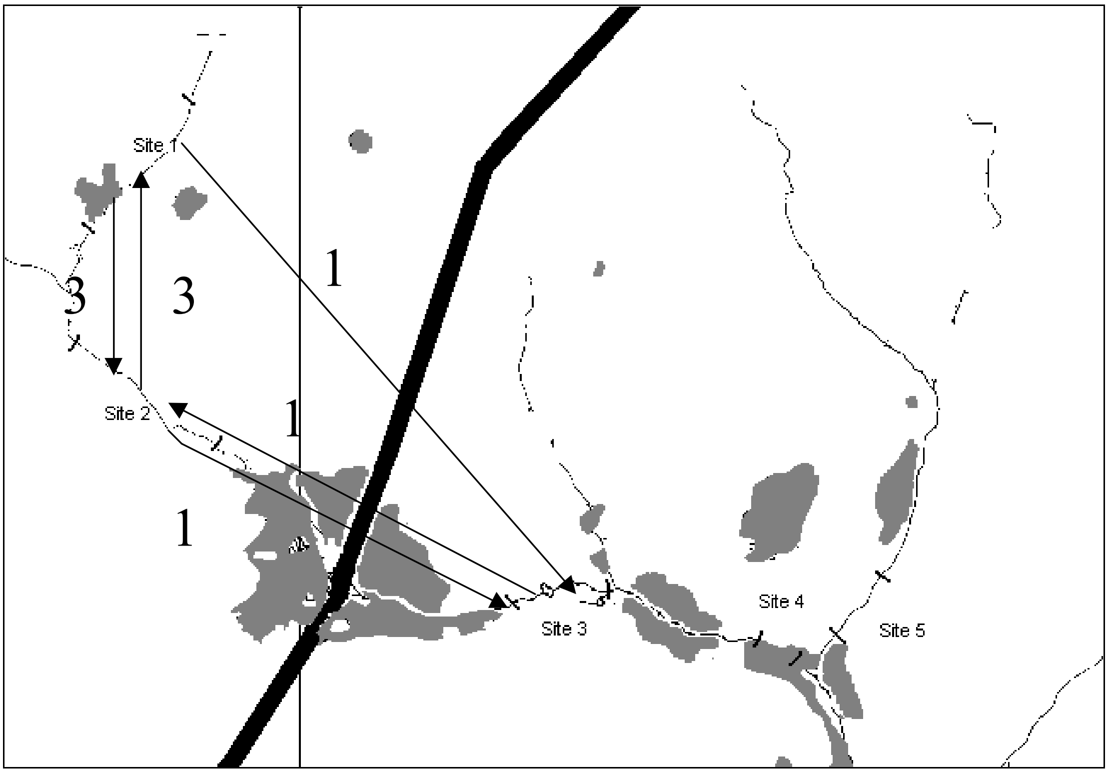


Figure 6.3 The location and direction of between-patch transfers at Crockford.

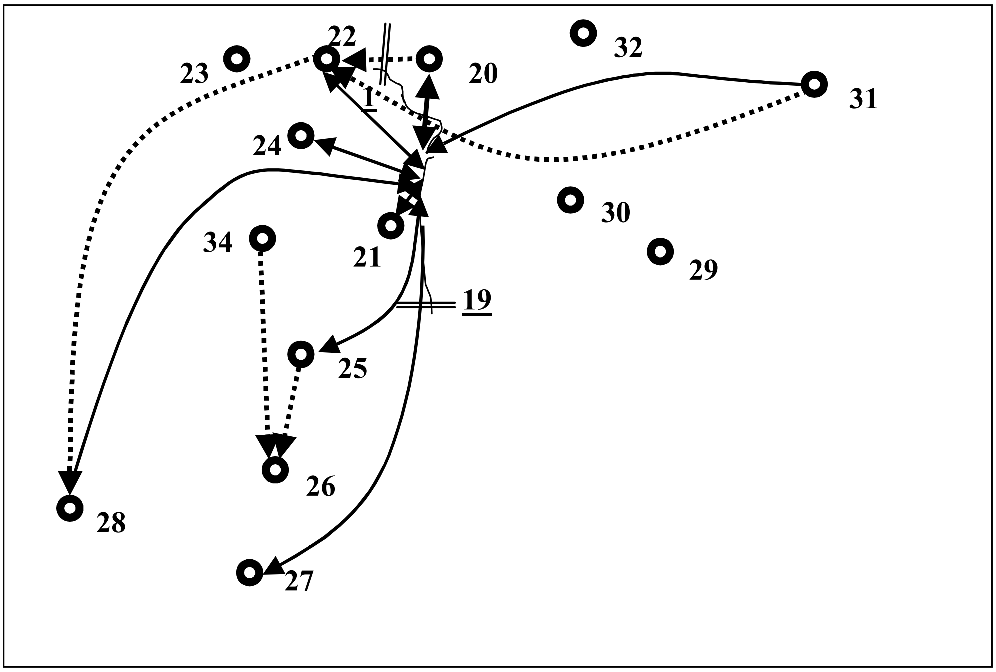


Figure 6.4 The location and direction of the between-patch transfers at Glan-yr-afon Uchaf. Solid arrows indicate movements between the main patch and peripheral patches whilst broken arrows indicate movements between peripheral patches. Within-patch movements are not shown here.

For each pair of subsections in sites 1 to 2 at Crockford, the number of transfers between them were scored and the pairs were divided into distance categories depending on the distance between them. Similarly, for Glan-yr-afon Uchaf, outward movements from the subsections in the main patch either to other sections in the main patch (within-stream movement) or to peripheral patches (between patch movements) were considered.

In both sites, 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 (Crockford, transfers between sites 1 and 2 - Spearman's r_s=-0.835, $p < 0.001$, n=16; Glan-yr-afon Uchaf, 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). This means that transfers were more likely to occur between pairs of sites that were close together (Figures 6.5 & 6.6).

At Glan-yr afon Uchaf, 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 *df*) were more likely to occur within the main stream patch than between patches. There was no such difference for long distance transfers in Glan-yr-afon Uchaf (distance categories between 300-599m - χ^2=1.74, p=0.181, 1 d.f.).

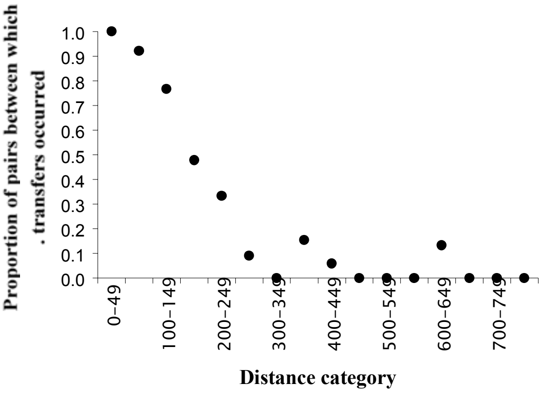


Figure 6.5 Proportion of pairs between which transfers were observed for each distance category for individuals from sites 1 and 2 – Crockford.

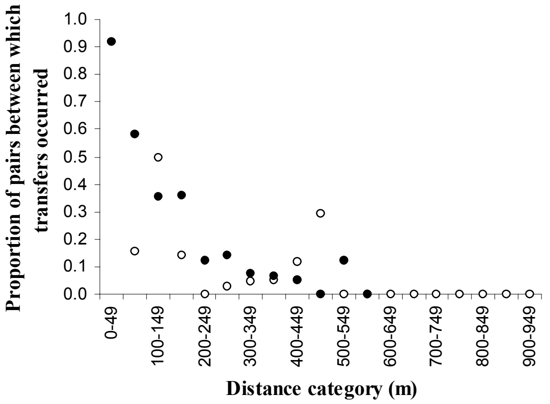


Figure 6.6 Proportion of pairs of sites between which transfers were observed for each distance category for individuals from the main stream section – Glan-yr-afon Uchaf. Transfers within the main stream section – closed circles; transfers from the main stream section to peripheral sites – open circles.

The effect of phenotype and time taken for movements on dispersal

Movements were investigated by the calculation of dispersal parameters for each individual as defined in Table 6.3. Figure 6.7 shows how they are calculated for a hypothetical individual that moved four times in its lifetime. *L* 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 travelled in one movement.

Table 6.3 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/t_n

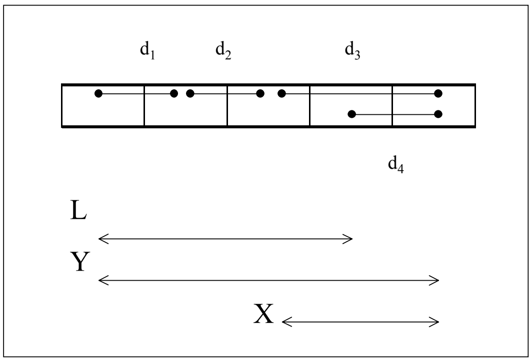


Figure 6.7 Diagram of four movements between five stream sections with corresponding dispersal parameters.

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 at Crockford and those marked on the main stream section at Glan-yr-afon Uchaf. The percentage distributions of *L* (regardless of whether movements were between or within-stream transfers) for males and females from both sites are shown in Figure 6.8.

In both sites, most recaptured individuals dispersed over short distances but a few moved up to 1km.

At Crockford, 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.

At Glan-yr-afon Uchaf, 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 (Glan-yr-afon Uchaf male), and that achieved in 2 days was 610m (Crockford male).

There was no difference between males and females in any of the dispersal parameters for Crockford or Glan-yr-afon Uchaf (Table 6.4). 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 Glan-yr-afon Uchaf probably due to the greater availability of habitat at these distances there.

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 (Crockford females – median_t=17.85, median_r=17.90, Mann Whitney W =1088.5, p=0.67; Glan-yr-afon Uchaf females - median_t=19.38, median_r=19.58, W=1517.5, p=0.59) or, in Crockford males (median_t=16.20, median_r=16.10, W =42852.5, p=0.95). For Glan-yr-afon Uchaf males, residents were significantly larger than transfers (median_t=17.20, median_r=17.40, W=46274.0, p=0.0072).

There was no correlation between body size and any of the three dispersal parameters for males and females in either the Crockford (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 Glan-yr-afon Uchaf (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).

Thus no consistent sex or size bias in dispersal during an individual's lifetime was found. For movements 1 to 5 of males from both sites, stepwise regression models were performed to see if the following factors affected the probability of moving more than 0m, at least 50m and at least 200m:

- age of the individual during the movement
- day of season
- the length of the time interval between the two recaptures
- order of the movement by that individual (i.e. 1st, 2nd, …5th)

The length of the time interval had a significant positive affect on the distance moved in an interval in all models. (Appendix 10 of W1-021/PR).

Table 6.4 Medians and Komolgorov-Smirnov Tests comparing dispersal parameters between males and females in each site.

	Crockford				Glan-yr-afon Uchaf			
Parameter	μ_{males} ±. s.e	$\mu_{females}$ ± s.e	Z	p	μ_{males}± $s.e.$	$\mu_{females}$ ± $s.e.$	Z	p
L	48.1 ± 3.0	46.2 ± 6.2	0.470	0.639	69.6 ± 4.9	98.6 ± 18.3	0.948	0.187
X	50.7 ± 3.0	49.2 ± 6.3	0.959	0.094	72.5 ± 4.9	100.2 ± 18.2	0.948	0.206
Y	52.2 ± 3.0	48.4 ± 6.4	0.818	0.202	74.6 ± 5.0	101.7 ± 18.2	0.958	0.199
d_l(m)	38.2 ± 2.0	43.8 ± 5.4	-	-	4.5 ± 0.2	5.6 ± 0.5	-	-
t_l (days)	3.7 ± 0.1	4.4 ± 0.3	-	-	18.2 ± 1.4	21.2 ± 3.9	-	-
v_l (m/day)	14.9 ± 0.7	16.3 ± 2.9	-	-				

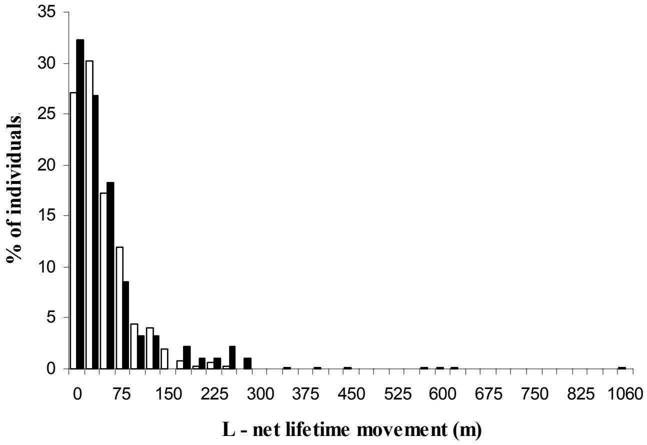


Figure 6.8a Percentage distribution of net lifetime movements (L) for males (open bars) and females (closed bars) from Crockford.

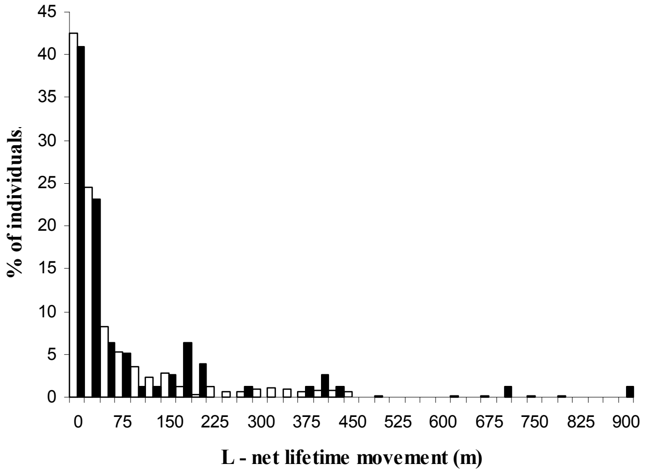


Figure 6.8b Percentage distribution of net lifetime movements (L) for males (open bars) and females (closed bars) from Glan-yr-afon Uchaf.

The effect of correcting for bias against observing long distance dispersal in field studies

In both sites, there were stretches of unsuitable stream divided by unsampled sections. This introduces a spatial bias into the observed dispersal distribution. 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. This is shown in Figure 6.9, 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.

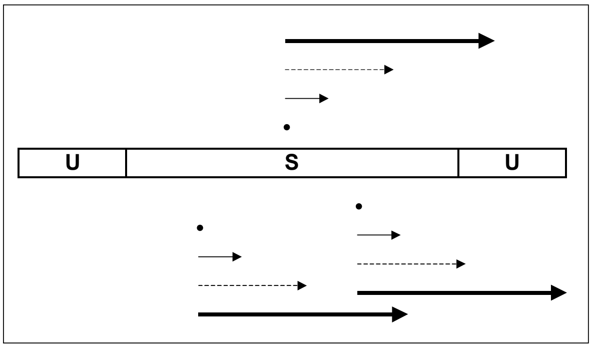


Figure 6.9 Diagram of short (thin, unbroken arrows), medium (thin, broken arrows) and long distance (thick, unbroken arrows) movements from three release points (black dots) along a sampled (S) and unsampled (U) stretch of stream habitat.

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. However, at Crockford, sections of suitable habitat could be well defined and were approximately linear (Figure 6.1). 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. At Glan-yr-afon Uchaf, due to the patchy, ill-defined nature of suitable habitat for the Southern Damselfly, 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.

The effect of this correction on the distribution of distances for all movements between two recaptures ($d_n s$) is shown in Figure 6.10. The mean of observed movements was 38.4 ± 2.0m whilst the mean of corrected movements was 57.9 ± 2.7. 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.

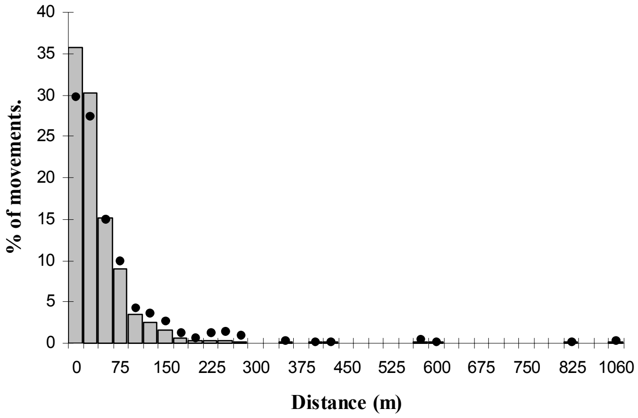


Figure 6.10 Percentage distribution of movements of different distances for observed data (grey bars) and data corrected for the theoretical probability of recapture (closed circles).

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).

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

It is pertinent to compare these field observed colonisation distances and emigrations rates to the distances found between local populations in different regions of Britain. The aim of this section is to make qualitative comparison between the dispersal ability of the Southern Damselfly and the distances between its British sites in different regions. Distances between sites was quantified using six-figure grid references from the most recent surveys in each region (1998 & 1999 surveys for Hampshire, 1996-1999 surveys for Pembrokeshire). These point data are at a low resolution (100m apart) compared to the size of habitat patches occupied by the Southern Damselfly (Chapter 2), and thus 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.

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, and the Gower, and six sites in Dorset (with two sub-populations on Povingdon Heath). Four larger clusters were considered i.e. the rest of Pembrokeshire (Mynydd Preseli), the Itchen and Test Valleys, the New Forest, and Dorset.

Isolation was described in two ways. Firstly, the distance between each grid reference and the first neighbour further than 250m away (points within 250m were assumed to be from the same population as the focal grid reference) was calculated regardless of whether the neighbour was in the same or a different cluster or site. Secondly, to describe isolation within clusters, grid references from large and small clusters were treated differently.

In the ‘two site’ clusters, the distance between the two populations and the distance to the nearest other cluster was measured.

For the four largest clusters, 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.

In Devon, Dartmoor and Gower, the distance separating the two populations in each cluster exceeds the maximum dispersal distance observed for the Southern Damselfly, whilst the distance between populations in the Oxford cluster (and probably also in the Anglesey cluster) does not (Table 6.5). Given that the field observations may underestimate maximum dispersal distance exchange of individuals between populations may occur in Devon, and Dartmoor as well as in Oxford and Anglesey given a sufficient number of generations. Distances between clusters would not permit exchange of individuals between clusters.

Table 6.5 Distance between populations in ‘two site’ clusters, and distance to and identity of the nearest neighbouring cluster.

Cluster	Distance between two sites (km)	Distance to nearest cluster (km)	Name of nearest cluster
Oxford	0.92	60	New Forest
Anglesey	2.00	152	Preseli
Devon	3.87	36-38	Dartmoor
Dartmoor	4.10	36-38	Devon
Gower	7.10-8.00	42-47	Preseli

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 Preseli clusters in Figures 6.11-6.14. Given the low number of points for the Dorset cluster, a raw frequency distribution is shown in Figure 6.14. In the New Forest, 60% of grid references are situated 1km or less away from their nearest neighbour (Figure 6.11) 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 (Figure 6.12). In Preseli, 90% of grid references are situated 1km or less away with only 5% situated further than 3km away from their nearest neighbour (Figure 6.13). In Dorset, 3 of the 8 sites are within 1km of their neighbours but all sites are within 3km of their nearest neighbours (Figure 6.14). Thus in these large clusters a high level of exchange between populations is possible.

Comparison of mean isolation indices across each region (Table 6.6) suggests that grid references in Preseli 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 due to a much higher density of grid references in this region.

The differences between clusters in both mean isolation index ($\text{median}_{NF}=3.18$, $\text{median}_{IT}=1.48$, $\text{median}_{P}=0.29$, Kruskal-Wallis $H=123.12$, 2 d.f., $p < 0.001$) and distance to nearest neighbour ($\text{median}_{NF}=0.83$, $\text{median}_{IT}=0.40$, $\text{median}_{P}=0.32$, Kruskal-Wallis $H=41.68$, 2 d.f., $p < 0.001$) are significant.

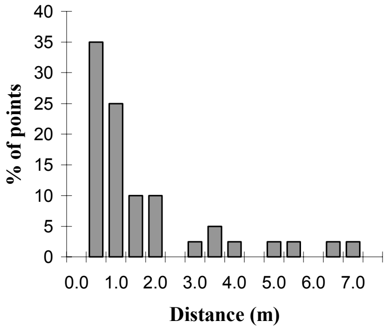


Figure 6.11 Percentage frequency distribution of distances between each point (grid reference) and its nearest neighbour (> 250m away) for New Forest sites (*n*=41).

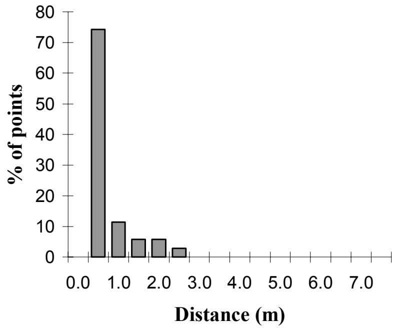


Figure 6.12 Percentage frequency distribution of distances between each point (grid Figure reference) and its nearest neighbour (< 250m away) for Itchen & Test sites (*n*=35).

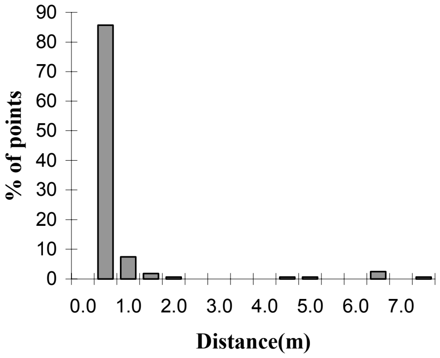


Figure 6.13 Percentage frequency distribution of distances between each point (grid reference) and its nearest neighbour (< 250m away) for Preseli sites (*n*=160).

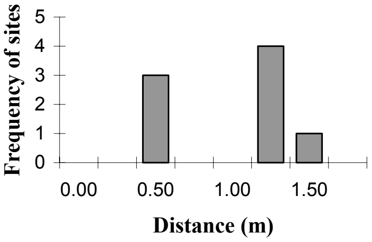


Figure 6.14 Frequency distribution of distances between each point (grid reference) and its nearest neighbour (< 250m away) for Dorset sites (*n*=8).

Table 6.6 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
Preseli	0.52 ± 0.06	160	0.16 – 7.89

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 the Southern Damselfly 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.

Mobility of the Southern Damselfly compared to other British and European studies

The mobility of the Southern Damselfly in the two British sites studied here was greater than that observed in previous studies. Hunger & Röske (2001) found that 96% of individuals in a population in south-western Germany remained within 25m of the site in which they were marked. In this study, the proportion was much lower. The maximum within-patch and between-patch movements were greater in this study, being 610m and 1060m respectively versus 170m and 300m reported by Hunger & Röske (2001). In Britain, although within-patch movements of up to 500m (away from the breeding stream) have been observed (Hold, 1997; Hopkins and 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. 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 and Roske, 2001). In addition this current study covered much of the flight period of the Southern Damselfly in each site 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.

Mobility of the Southern Damselfly compared to that of other odonates

Since Southern Damselflies fly weakly and close to the vegetation in comparison to other blue damselflies, previous authors have suggested that this species has poorer dispersal ability. However, a between-patch migration rate of 11.4% by the Southern Damselfly at Glan-yr-afon Uchaf is comparable with that of other similarly sized odonates found in a pond system with similar interpatch distances (Conrad et al., 1999) i.e. 11% for both the Blue-tailed Damselfly (*Ischnura elegans*) and the Common Blue Damselfly (*Enallagma cyathigerum)* and 16% for the Azure Damselfly (*Coenagrion puella*).

Time required for dispersal relative to lifespan of the Southern Damselfly

It is significant that the Southern Damselfly was capable of moving considerable distances between patches in periods of time (1-2 days) that are a fraction of the mean mature adult lifespan of individuals (7-8 days). Indeed, several individuals at Glan-yr-afon Uchaf performed two such movements within their lifetime. 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. 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.

Effects of some aspects of landscape connectivity on dispersal in the Southern Damselfly

With regards to landscape connectivity, this study provides some evidence that the probability of dispersal in the Southern Damselfly may depend on aspects of landscape structure such as the distance between patches and the type of intervening habitat. Dispersal was more likely between pairs of sites that were closer together 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 their study system. Thus, it is expected that for the Southern Damselfly, as with many species of butterflies, isolation will negatively affect both the colonisation of empty habitat and population persistence (due to the rescue effect and genetic rescue). Indeed, Röske (1995) found that, in the Upper Rhein region, a high proportion of population extinctions occurred in regions that were isolated from other Southern Damselfly populations and suggested that reintroduction may be unsuccessful in such areas.

The habitat type between locations seemed to influence dispersal at short to medium distances since, in Glan-yr-afon Uchaf, 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. For example, *Calopteryx maculata* moves more rapidly (from breeding streams) through neutral pasture habitat than through forest habitat which is used for foraging (Taylor and Merriam, 1995).

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. Further work is required on habitat specific movement rates and on resource use in the Southern Damselfly to determine what type of management will facilitate movement between resource patches in both heathland and chalkstream populations of this species.

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. The availability of numerous patches close to the natal patch and in a range of directions seemed to favour between-patch movement in Glan-yr-afon Uchaf. Within some species, more extensive dispersal has been found in patches linked by linear landscape features or corridors of suitable habitat probably because per capita mortality of dispersers is reduced. This may occur by chance when corridors of suitable habitat link patches.

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. There is anecdotal evidence for dispersal within a habitat patch by the Southern Damselfly 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.

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. The Southern Damselfly is similar in mobility to butterflies at the sedentary end of this spectrum such as *Plebejus argus* (Thomas and Hanski, 1997) in that it has low rate of movement within continuous areas of habitat (average movement > 25m), low emigration rates (1.3-11.4%) and low colonisation distances (approximately 1km). Thus for the Southern Damselfly, within and between-patch dispersal traits are correlated as expected in species in which flight is multifunctional. Are these dispersal traits sufficient for colonisation events to occur?

Actual colonisation distances measured by indirect methods have been found to be greater than field observed maximum dispersal distances in several butterflies (Guttierez et al., 1999; Hill et al., 1996; Lewis et al., 1997). 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 and 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).

In the Southern Damselfly, too there is some evidence that actual colonisation distances are probably greater than field observed maximum dispersal distances. The same maximum dispersal distance observed at Crockford for the Southern Damselfly in this study was observed again in a 1998 study that covered only a small proportion of the flight period (Thompson and Purse, 1999). Individuals have also been found in Europe up to 3km away from the closest known reproductive habitat in Germany (by Jentzsch & Norgall (1988) cited in Hunger and Röske, 2001). In addition 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.

Within large clusters of sites (such as the New Forest, Itchen and Test valleys, and Preseli) 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. 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 which may only be provided by dispersal. Thus small isolated clusters of populations of the Southern Damselfly in Britain 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 the Southern Damselfly 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 the Southern Damselfly, 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; Kindvall, 1999; Sutcliffe et al., 1997). 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 the Southern Damselfly 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.

Buchwald (1989) suggested that the Southern Damselfly 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 in the alpine range. There are no empirical data on mobility in populations across the range of the Southern Damselfly. However survival, general activity and breeding activity are negatively affected by adverse weather conditions on the British range edges of this species (Chapter 5). 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.

Phenotypic correlates of dispersal

There was no sex bias in dispersal in the Southern Damselfly as expected for a non-territorial, scrambling species (scrambling species are those in which competitors for a given resource (e.g. mates) are assumed to be approximately equal in competitiveness). 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 and 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 less likely to be the proximate cause for dispersal than foraging or inbreeding avoidance. No age bias in dispersal has been found in mature adult Southern Damselflies. The recapture rate of tenerals was too low to assess dispersal during the maturation phase in the Southern Damselfly.

A size bias in dispersal was not found consistently here in the Southern Damselfly. 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).

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 the Southern Damselfly. Phenotypic studies on butterflies (discussed in Van Dyck and Matthysen, 1999) have suggested that less mobile phenotypes are found in isolated habitats.

Management to facilitate dispersal in the Southern Damselfly

Detailed management recommendations for the Southern Damselfly are given in Chapter 7. However, there are specific recommendations that arise from this study of dispersal:

- 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 (Lewis et al., 1997; Thomas et al., 1992).

- 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.

Re-introduction

An early version of the species action plan for the Southern Damselfly (HMSO, 1994) discusses the possibility of re-introduction of the Southern Damselfly to empty habitat patches in Britain. Sites suggested subsequently included 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 the largest and highest quality and least isolated patches should be targeted. 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.

7. DISCUSSION – MAIN FINDINGS, HABITAT ATTRIBUTES, MANAGEMENT AND MONITORING FOR THE SOUTHERN DAMSELFLY IN BRITAIN

This chapter discusses some of the main findings of this report, outlines appropriate monitoring of the species and its habitat and recommends management regimes for the Southern Damselfly in Britain.

Ecology of the Southern Damselfly

The Southern Damselfly was found to be worthy of individual species protection since it fulfilled several of the criteria used to assess rarity. Chapter 2 revealed that the Southern Damselfly 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 (at the 1km grid square resolution). The Southern Damselfly is a stenotopic odonate 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 the Southern Damselfly 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 4). For example, both Southern Damselfly 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 revealed that British edge-of-range populations of the Southern Damselfly differ from core populations in aspects of development, presumably due to differing climatic factors (see conclusion for Chapter 3). Climatic variables influenced the Southern Damselfly in other ways - affecting mature adult survival, whether individuals were present at the breeding site and whether they engaged in reproductive activity given that they were present (Chapter 5). At Aylesbeare, adult Southern Damselflies 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). The Southern Damselfly was found to be relatively sedentary in field experiments (Chapter 6). 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 later).

Mortality was investigated at several stages in the life cycle of the Southern Damselfly. At the egg stage, mortality during the hatch period was found to average 14% (but was highly variable - Chapter 3) 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 or dispersal may be substantial during this period whilst, in the mature adult stage, it was consistently low (Chapter 5). 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 and Germany, examination of other habitat features used by this stage (and by the egg stage) is essential, Given that the Southern Damselfly 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 the Southern Damselfly.

In addition, it would then be possible to map habitat (or resource) patches for this species and investigate the effects of habitat area, quality and isolation on patch occupancy. The effect of aspects of landscape connectivity on a range of behaviours including dispersal could also be investigated.

Monitoring of the Southern Damselfly

The UK Biodiversity Action Plan for the Southern Damselfly (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 for the Southern Damselfly 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 SSSI's, as part of the Natura 2000 series (SPA's, SAC's) or as Ramsar sites, 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. For example, for a species this may be population 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 feature falls outside either threshold with respect to a particular attribute. This report not only provides some information on how best to observe population size or structure of the Southern Damselfly, it also provides information on the habitat attributes required by the species.

Counting the Southern Damselfly on monitoring visits

First, it is necessary to consider which life stage of the Southern Damselfly to count. Although, habitat use by larvae will more accurately reflect the requirements of the majority of the life cycle and larval sampling can be carried out at any time of year, they are notoriously difficult to sample and time-consuming to identify. Exuviae of the Southern Damselfly 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 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 indicates that peak emergence lies outside this period. In Chapter 5 it was revealed that both general and reproductive activity peak at mid-day and that the presence of the Southern Damselfly 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 (Figure 4.12) 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. For monitoring, consideration for each site should be given to the maximum count of individuals normally supported on a site (or part of a site) as a species attribute to be met or passed.

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 the Southern Damselfly, standardising counts by fixing the time taken for counts may be inappropriate given that 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 the Southern Damselfly may be spent roosting, feeding or sheltering in surrounding vegetation. 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. Point data in the form of grid references have their limitations for biological recording. Monitoring visits could simply record that a particular threshold count has been passed at a particular grid reference. If 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) overlaying a map containing polygons that represent the area covered by waterbody and the area utilised on previous monitoring visits by the Southern Damselfly. This will facilitate detection of change in counts in response to alteration in particular habitat attributes and allow comparison in densities of the Southern Damselfly across sites.

Habitat attributes that indicate favourable habitat condition for the Southern Damselfly in Britain

In Chapter 2, the main threats to the condition of habitat for the Southern Damselfly 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 agriculture. Thus, those habitat attributes that relate to vegetation structure and physical features of watercourses are likely to constitute key attributes for the Southern Damselfly. It is also important to focus observational effort on those features (from Table 2.11) 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 7.1 and 7.2 present key and subsidiary habitat attributes that generally indicate favourable condition of sites for the Southern Damselfly 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 the Southern Damselfly is an interest feature. The upper and lower limits given in Tables 7.1-7.2. for favourable condition are similarly non-specific. The number of attributes that indicate favourable condition for the Southern Damselfly may be greater than that for other rare species in Britain and thus this species may be more costly to monitor. Since, the Southern Damselfly uses a wide range of resource types (as do other odonates) and is highly stenotopic, it is difficult to provide a shorter list of attributes that adequately describe favourable habitat 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 4). In this regard, small sites especially may warrant more regular surveillance.

Table 7.1 Key and subsidiary habitat attributes (with suggested upper and lower limits) that indicate favourable condition for the Southern Damselfly 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*	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 7.2 Key and subsidiary habitat attributes (with suggested upper and lower limits) that indicate favourable condition for the Southern Damselfly 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 watercourse/mire
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, Filipendula 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 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

Management recommendations for the Southern Damselfly

This section describes management practices that are recommended for maintenance of favourable condition of habitat for the Southern Damselfly 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. Since a number of the proximate habitat features (Chapter 2) and habitat attributes (Table 7.1) for the Southern Damselfl*y* are influenced by each management practice, they are not discussed individually here.

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 in order to produce poaching of watercourse margins and diversity of tussock structure favoured by the Southern Damselfly. 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 and fences could be employed to concentrate stock on areas of watercourse containing the Southern Damselfly (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.

The time of year in which stock are grazed will depend on the accessibility of the site, the biotope and the number and type of animals used. On most sites cattle are usually grazed for some period between April and October, whilst horses and stock on unenclosed commons (regardless of type) are grazed all year round.

Vegetation clearance

Clearance of bankside vegetation

Bankside plant species which commonly shade or choke watercourses occupied by the Southern Damselfly include *Myrica gale, Juncus* sp., *Molinia caerulea*, *Schoenus nigricans* and *Sparganium erectum*. Whilst some of these plant species will be prevented from attaining excessive cover or height by grazing, some clearance of vegetation may also be required. On heathland sites, hand clearance of *Myrica gale* may be required since it 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 5m of a ditch edge on chalkstream sites. In addition, scrub may be left in place on short sections of stream. In some sites, where trees or scrub pose a risk to water availability, 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, abundance of adult populations was observed in areas of watercourse 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 the Southern Damselfly (Röske, 1995). Surveillance should be carried out to investigate the effect of cutting in British Chalkstream sites before this management practice is employed more broadly.

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 the Southern Damselfly in particular (Winsland, 1994). Mechanical excavation of the channel on meadow brooks and ditches in south-west Germany produced dramatic reductions in population of the Southern Damselfly 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 the 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 and chalkstream sites. Cutting by hand implement (such as a sythe) is recommended whilst mechanical cutting of any kind is not. 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. Cut vegetation 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*.

Burning

Burning has been employed in winter on 13 (one illegally) of the heathland sites considered in Chapter 2. Controlled burning has long been used to enhance the quality of grazing on heathland (Tubbs, 1974). An example of the use of burning on a Southern Damselfly site in conjunction with grazing has already been described above. 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 the Southern Damselfly habitat and was associated with a lack of aquatic vegetation (Stevens and Thurner, 1999). Cordrey (1997) states that burning may damage *Sphagnum* and pollute watercourses. Many heathland sites occupied by the Southern Damselfly 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.

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 the loss of larval population that 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. 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 excavated alongside existing ditches) 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 the Southern Damselfly, the growth of such vegetation will slow water flow and may help prevent headward erosion and siltation.

Water quality

Nutrient run-off from farmland should be minimised in catchments of watercourses containing the Southern Damselfly populations. This can be achieved through negotiation with landowners and farming interest groups to minimise the use of artificial fertilisers and to deploy mitigation measures such as buffer strips (see below) and other environmentally-friendly land management techniques. 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 toxic to all 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. 2000).

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 Chapter 2, the maintenance of a protection strip, a minimum of 10m wide of extensive grassland around watercourses has been recommended (Buchwald et al., 1989). It is recommended that agricultural land, adjacent to sites in Britain, are also used extensively. If the conversion of the entire adjacent field to extensive use is inappropriate, the maintenance of a strip of extensive use of at least 20m of land, on either side of the watercourse, is suggested.

The sympathetic management of existing and potential adjacent sites may be grant-aided by English Nature (Special Sites of Scientific Interest (SSSIs) only) or the Department for Environment, Food and Rural Affairs in England, or the Countryside Council for Wales. Contact the individual organisations for further information. Such action may encourage this species to extend its range.

Dispersal and re-introduction

Management recommendations to facilitate dispersal between sites are described in detail in Chapter 6. Generally, the management practices described above should be employed, where possible, in empty sites within 1-3 km of extant populations and 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.

For some of these activities, especially near watercourses and wetlands, the prior permission is required from the Environment Agency before undertaking such operations. Furthermore, within, or close to, statutory conservation sites, (SSSIs or candidate Special Areas of Conservation (SACs)) – the prior consent of Countryside Council for Wales or English Nature may be required.

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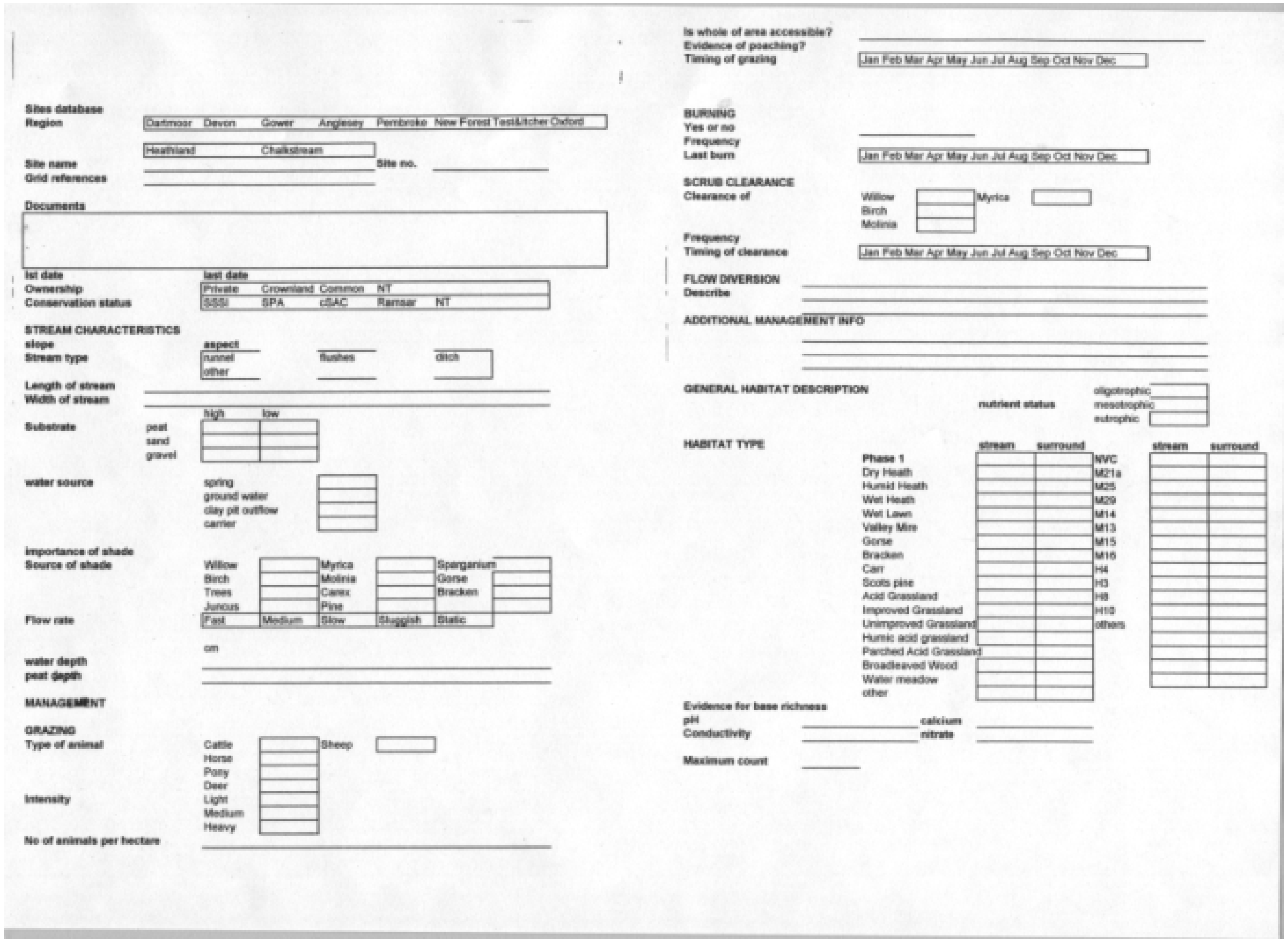
APPENDICES

Appendix 1- Sample questionnaire



Sites database

Region Dartmoor Devon Gower Anglesey Pembroke New Forest Test&Itchen Oxford

Heathland Chalkstream

Site name ____________ **Site no.** ____________

Grid references ____________

Documents

Ist 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

	stream	surround		stream	surround
Phase 1			NVC		
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					

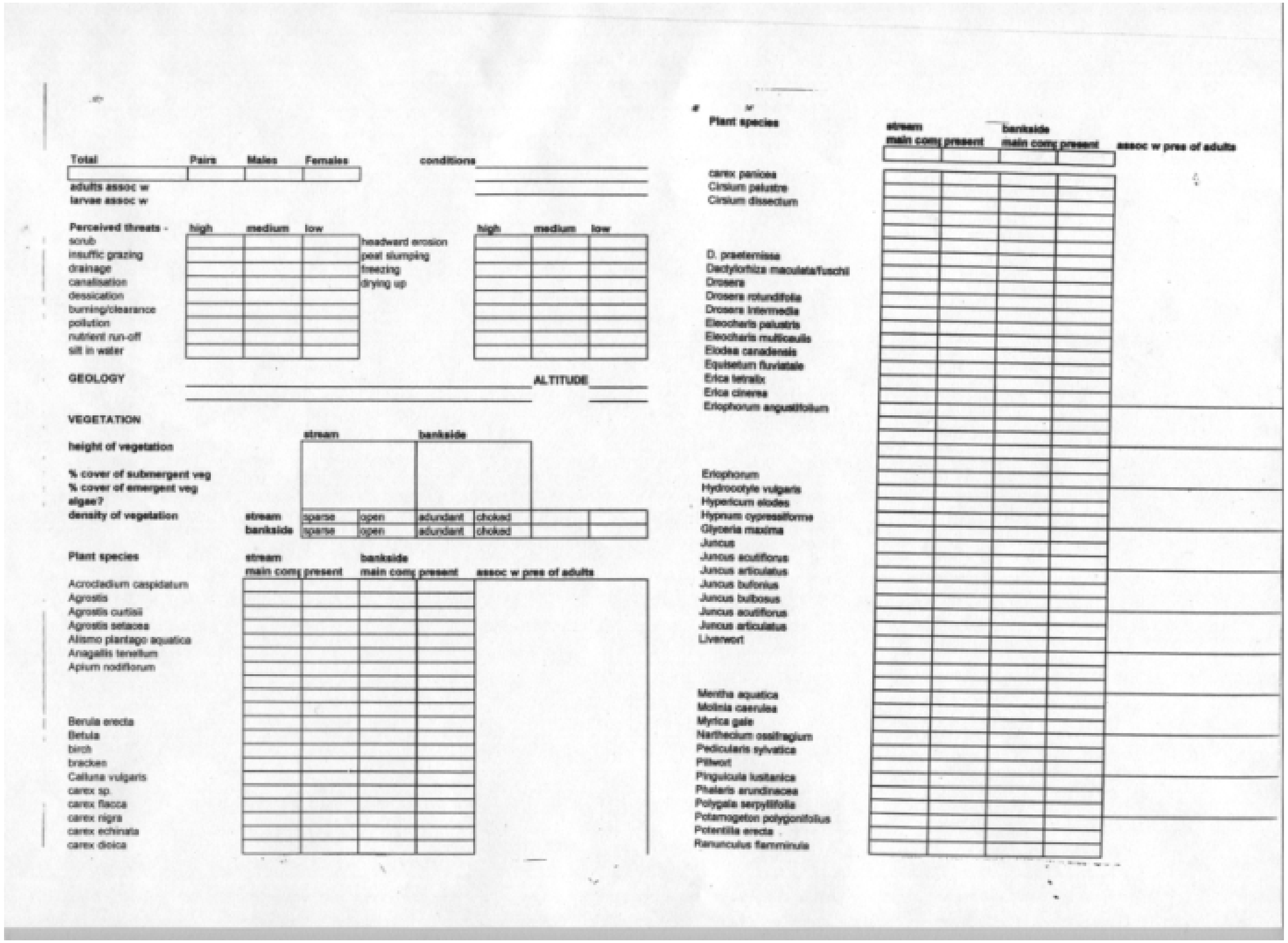
Evidence for base richness

pH ____________ **calcium** ____________

Conductivity ____________ **nitrate** ____________

Maximum count ____________

Appendix 1 continued.



Total	Pairs	Males	Females

adults assoc w

larvae assoc w

conditions ______

Perceived threats -	high	medium	low		high	medium	low
scrub				headward erosion			
insuffic grazing				peat slumping			
drainage				freezing			
canalisation				drying up			
dessication							
burning/clearance							
pollution							
nutrient run-off							
silt in water							

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 comp	stream present	bankside main comp	bankside present	assoc w pres of adults
Acrocladium caspidatum					
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 comp	stream present	bankside main comp	bankside present	assoc w pres of adults
carex panicea					
Cirsium palustre					
Cirsium dissectum					
D. praetermissa					
Dactylorhiza maculata/fuschi					
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 – Table of site names, numbers, altitudes, slopes, grid references (for centre of population), sources, maximum recent adult Southern Damselfly count and habitat type for 72 sites covered in documents.

Site name	site no.	Region	Altitude (in m a.s.l.)	Maximum Slope (%)	100m Grid references	Sources	Maximum SD count (year of count)	habitat type
Cothill Fen, Parsonage Moor	1	Oxf	69-70	4.0	41/ -	Paul (1998), Thurner (2000)		valley fen
Dry Sandford Pit	2	Oxf	75-80	2.0	41/ -	Paul (1998), Thurner (2000)		calcareous fen (flooded sandpit)
Aylesbeare Common	3	Dev	110-115	13.3	30 / 055907	Kerry (1989, 1994, 1999), Knight (1983), Smallshire (1995)	120 (1999)	Acid H with base rich mire
Colaton Raleigh	4	Dev	85-90	2.4	30 / 050868	Kerry (1994), Knight (1983), Smallshire (1995)	100 (1986)	Acid H with base rich mire
Tor View Moor	5	Dar	245	5.3	20 / 690918	Smallshire (1995, 1998)	43 (2000)	Rhos pasture mire (acidic VM)
Moortown Bottom, Gidleigh Common	6	Dar	285	3.2	20 / 662888	Smallshire (1995, 1998)	24 (1998)	Rhos pasture mire (acidic VM)
Creech Heath	7	Dor	50	1.7	30 / 927835	Sutcliffe (1998), Winsland (1994)	254 (1995)	Lowland wet H
Norden Heath	8	Dor	40	<1	30 / 940830	Sutcliffe (1998), Winsland (1994)	53 (1994)	H
Corfe Common West	9	Dor	25-29	4	30/ 956814	Sutcliffe (1998), Winsland (1994)	42 (2000)	H
Corfe Common East	10	Dor	35	<1	30 / 967811	Sutcliffe (1998), Winsland (1994)	12 (1994)	H/unimproved grassland
Hartland Moor	11	Dor	20	4	30 / 943842	Sutcliffe (1998), Winsland (1994)	19 (1994)	H/fen arm
Povingdon - Orchard Cottage mire Outflow Mire	12	Dor	30-35	3.1	30 / 892831 30 / 892829	Edwards (2000), James & Wiggers (2000), Sutcliffe (1998), Winsland (1994)	405 (1993), 101 (2000) 16 (2000) 12 (2000)	H/poor fen
Houghton, King's Sombourne	13	Tes	30	<1	41 / 347316	Stevens & Thurner (1998)	15-58 (1998)	WMDS (improved grassland)
South of Clarendon Way	14	Tes	10	<1	41 / 348312	Stevens & Thurner (1998)	67-350 (1998)	WMDS (improved grassland)
Itchen Valley Country Park South	15	Itc	10-20	1.1	41 / 455160	Hold (1998), Stevens & Thurner (1998), Strange (1998)	160 (1999)	WMDS
Itchen Valley Country Park North	16	Itc	10	<1	41 / 460169	Hold (1998), Stevens & Thurner (1998), Strange (1998)	192(1999)	WMDS
West of Willow Farms South	17	Itc	10	<1	41 / 463167	Stevens & Thurner (1998)	3-7 (1998)	WMDS (improved grassland)
West of Willow Farms North	18	Itc	10	<1	41 / 465172	Stevens & Thurner (1998)	11-16 (1998)	WMDS (improved grassland)
South of Highbridge Farm	19	Itc	10-15	1.8	41 / 465208	Stevens & Thurner (1998)	medium	WMDS (semi -improved grassland)
Otterbourne, Twyford Moors S	20	Itc	20-25	3.6	41 / 475234-41 / 475235	Stevens & Thurner (1998), Strange (1999)	6-35 (1998)	WMDS
Otterbourne, Twyford Moors N	21	Itc	20-25	1.6	41 / 475236	Stevens & Thurner (1998), Strange (1999)	8-58 (1998)	WMDS (improved grassland)
Mariner's meadow south, Twyford	22	Itc	25	0.7	41 / 476241	Stevens & Thurner (1998)	6-16 (1998)	WMDS (semi -improved grassland)
Applemore	23	NF	15	3.5	41 / 394071	Stevens & Thurner (1998)	3 (1998)	Acid dry H
Rowbarrow	24	NF	15	2.4	41 / 357045	Stevens & Thurner (1998)	2 (1998)	Acid dry H

Appendix 2 continued.

Site name	site no.	Region	Altitude (in m a.s.l.)	Maximum Slope (%)	100m Grid references	Sources	Maximum SD count (year of count)	habitat type
Blackwell Common	25	NF	10-15	1.7	41 / 434017	Stevens & Thurner (1998)	1 (1998)	Acid dry H
Hill Top	26	NF	-	-	41 / 404032	Stevens & Thurner (1998)	nil (1998)	H
Upper Crockford West	27	NF	35	1.6	40 / 343997	Stevens & Thurner (1998)	strong (1998)	H
Upper Crockford East	28	NF	30	1.4	40 / 347997	Hopkins & Day (1998), Stevens & Thurner (1998)	strong (1998)	H
Lower Crockford	29	NF	20	2.1	40 / 355989-40/355988	Stevens & Thurner (1998)	strong (1998)	H
Upper Peaked Hill	30	NF	20	2.0	40 / 359995-40 / 360995	Stevens & Thurner (1998)	strong (1998)	H
Lower Peaked Hill	31	NF	20	<1%	40 / 361990-40 / 361991	Stevens & Thurner (1998)	strong (1998)	H
Horsebush Bottom	32	NF	25-30	2.0	40 / 367993	Stevens & Thurner (1998)	5 (1998)	Acid dry H
Bagshot Moor	33	NF	-	-	40 / 369001	Stevens & Thurner (1998), questionnaire	14 (1998)	H & acid/SI grassland
Greenmoor Stream North	34	NF	30	<1	40 / 335995	Stevens & Thurner (1998)	21 (1998)	acid/I grassland
Greenmoor Stream South	35	NF	30	<1	40 / 337987	Stevens & Thurner (1998)	10-14 (1998)	acid/I grassland
Frogmoor	36	NF	20	4.1	40 / 349979	Stevens & Thurner (1998)	1-4 (1998)	H/VM
Round Hill	37	NF	25-30	2.3	41 / 329020	Stevens & Thurner (1998)	126 (1998)	H through mixed woodland
Hatchet Moor	38	NF	35	0.7	41 / 355013	Stevens & Thurner (1998)	12-42 (1998)	wet H/VM
Hatchet Pond and Stream	39	NF	40	0.7	41 / 360013	Stevens & Thurner (1998)	9-49 (1998)	wet H/VM
Three Beech Bottom	40	NF	-	-	41 / 293004	Stevens & Thurner (1998)	9-16 (1998)	VM/acid grassland
Setley Plain	41	NF	30-35	<1	41 / 296002	Stevens & Thurner (1998)	strong (1998)	VM/acid grassland
Widden Bottom	42	NF	35-40	3.5	40 / 289994	Stevens & Thurner (1998)	29 (1998)	VM/acid grassland
Stoney Moor	43	NF	55-60	1.8	40 / 213995	Stevens & Thurner (1998)	18-46 (1998)	
Holmsley Station	44	NF	40	<1	40 / 232008	Stevens & Thurner (1998)	0-55 (1998)	
Common Moor	45	NF	55	1.6	41 / 204045	Stevens & Thurner (1998)	9-17 (1998)	
Mill Lawn	46	NF	40-45	3.1	41 / 227034	Stevens & Thurner (1998)	21-86 (1998)	H/ VM/acid grassland
Burley Lawn, West of Rooks Bridge	47	NF	35-40	2.3	41 / 234036	Stevens & Thurner (1998)	78-228 (1998)	H/ VM/acid grassland
Burley Lawn, East of Rooks Bridge	48	NF	35-40	2.9	41 / 236036	Stevens & Thurner (1998)	92-299 (1998)	H/ VM/acid grassland
Rock Hills, Creek Bottom	49	NF	40-45	4.2	41 / 238034	Stevens & Thurner (1998)	25-56 (1998)	Acid dry H/acid grassland
Stagbrake Bog	50	NF	-	-	41 / 246029	Stevens & Thurner (1998)	2-31 (1998)	Acid dry H/acid grassland

Appendix 2 continued.

Site name	site no.	Region	Altitude (in m a.s.l.)	Maximum Slope (%)	100m Grid references	Sources	Maximum SD count (year of count)	habitat type
Duckhole Bog	51	NF	45-50	4.9	41 / 252022	Stevens & Thurner (1998)	0-8 (1998)	Acid dry H
Oberwater	52	NF	-	-	41 / 260034 – 41 / 262032	Stevens & Thurner (1998)	nil (1998)	Acid dry H/VM
Acres Down	53	NF	50-55	9.1	41 / 271086	Stevens & Thurner (1998)	7-21 (1998)	H/VM
Nomansland	54	NF	45	-	41 / 263174	Stevens & Thurner (1998)	nil (1998)	Acid dry H/VM
Gypsie Hollies	55	NF	50	2.5	41 / 194128	Stevens & Thurner (1998)	strong (1998)	wet H/VM
Lay Gutter Valley	56	NF	50-55	<1	41 / 191128	Stevens & Thurner (1998)	200+ (1998)	acid/wet heath
Millersford Bottom West	57	NF	65-60	4.6	41 / 184164	Stevens & Thurner (1998)	10-63 (1998)	VM
Millersford Bottom East	58	NF	65-70	10.1	41 / 187168	Stevens & Thurner (1998)	10-35 (1998)	H
Russell's Meadow	59	Itc	10-15	1.6	41 / 468208	Strange (1999)	moderate (1998)	H
Highbridge, Russell's Meadow	60	Itc	20	<1	41 / 468212	Strange (1999)		wet H/VM
Rosemary Leet	61	Itc	20-25	2.1	41 / 476223	Strange (1999)	weak (1998)	VM/acid grassland
Twyford moor	62	Itc	20-25	1.2	41 / 472232	Strange (1999)	weak (1998)	WMDS/semi-improved grassland
Mariners Meadow North	63	Itc	20-25	2.4	41 / 479236	Strange (1999)		WMDS
Waun Fawr, Casmael SSSI	64	Pem	150-165	3.4	22 / 016303- 22 / 017303- 22 / 019304	Evans (1989), 1999 site visit report	174 (1999)	Wet pasture
Rhos Fach, Gors Fawr	65	Pem	180-185	1.5	22 / 132293	Evans (1989), site proforma – Fowles (2000), Skidmore (1996)	strong (1989)	Mire/semi-improved grassland
Rhossili Down and Sluxton Farm	66	Gow	65-75	6.7	22 / 554290	site proforma – Fowles (2000),Jenkins (1997), Pawson (1996), Woodman (1997), Wright (1996)	130 (1995) small nos 1996. 1997	Heathland and wet pasture
Cefn Bryn	67	Gow	70-75	2.9	22 / 555090	site proforma – Painter (2000), Jenkins (1997), Pawson (1996), Woodman (1997), Wright (1996)	261 (1997)	wet H/soligenous VM
Ffynnon Clegy Boia	68	Pem	35	<1	12 / 742251	Evans (1989), site proforma – Fowles (2000),	12 max 2 in 1996	Wet pasture
Pont Clegyr	69	Pem	40	1.5	12 / 769251	Evans (1989), site proforma – Fowles (2000),		wet H + boggy pasture
Cors Erddreiniog (Nant isaf)	70	Ang	80	3.3	23 / 477823	Colley (1983, 1993), Colley & Howe (1998, 1999), Howe (1997), Evans (1989), site proforma – Fowles (2000),	75 in 1999	*Molinia* grassland/VM/calcareous flushes
Cors Tewgyll	71	Pem	270	10	22 / 134313	Skidmore (1996)		wet unimproved pasture/fen
Glan-yr-afon Uchaf	72	Pem	125-135	3.8	22 / 118345	Hopkins & Day (1997), Skidmore (1996)		wet H/VM

Appendix 2 continued.

Site name	site no.	Region	Altitude (in m a.s.l.)	Maximum Slope (%)	100m Grid references	Sources	Maximum SD count (year of count)	habitat type
Mirianog ganol, Afon Clun Maen	73	Pem	175-190	7.3	22 / 138340- 22 / 141340- 22 / 144340	Skidmore (1996)		wet H/VM
Brynberian	74	Pem	145-245	5.7	22 / 087333- 22 / 090333- 22 / 097336	Skidmore (1996), questionnaire		wet H/VM
Glynsaithmaen	75	Pem	220-225	5.0	22 / 118307	Skidmore (1996), questionnaire		wet H/soligenous VM
Waun Isaf	76	Pem	185-190	2.4	22 / 141300- 22 / 142300	Evans (1989), Skidmore (1996)	1985 extinct	wet H/soligenous VM

Key to regions – Oxf=Oxford, Dev = Devon, Dar = Dartmoor, Dor=Dorset, Itch=Itchen valley, Hampshire, Tes=Test valley, Hampshire, NF= New Forest, Hampshire, Ang = Anglesey, Gow = Gower, Pem = Pembrokeshire.

Key to habitat type – H=heathland, VM = valley mire, WMDS = water meadow ditch system on a chalk stream, I=improved.

Appendix 3. 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 3. 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 3. 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 3. 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 Fach	May-98	H	Pem	22/139305	6.7	60	0.000	0.013	0.013	0.015	0.002	0.000	0.000
Tewgyll Fach	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 4a - Range (1st line) and mean ± s.e. (2nd line) of pH, conductivity, nitrate and ammonia in samples from extant sites in each region. * on 3rd line is range or single values from stream sources, only shown where data were available.

	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, 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)

Appendix 4b - Range (1st line) and mean ± s.e. (in parentheses on 2nd line) of different types of phosphate in samples from extant sites in each region. * on 3rd line is range or single values from stream sources, only shown where data were available.

	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	0-0.041	0.018-0.026	0-0.062	0.005-0.050
	(0.010 ± 0.001)	(0.018 ± 0.005)	(0.017 ± 0.004)	(0.030 ± 0.007)	(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	0-0.111	0-0.055	0-0.478	0-0.401
	(0.047 ± 0.017)	(0.080 ± 0.034)	(0.064 ± 0.032)	(0.054 ± 0.023)	(0.019 ± 0.037)
	*0.012	*0-0.048	*0.035	-	-
Anglesey	0-0.021	0-0.028	0.007-0.015	-	-
	(0.010 ± 0.005)	(0.010 ± 0.007)	(0.005 ± 0.007)	-	-
	*0.015	*0.000	*0.000	-	-
Pembrokeshire (except St David's)	0-0.2	0-0.2	-	0-0.308	0-0.019
	(0.019 ± 0.010)	(0.025 ± 0.012)	-	(0.037 ± 0.017)	(0.012 ± 0.021)
	*0.003-0.015	*0-0.026	-	*0.019-0.021	-
St David's	0-0.067	0.014-0.031	-	0.022-0.074	0-0.046
	(0.035 ± 0.015)	(0.025 ± 0.004)	-	(0.041 ± 0.012)	(0.016 ± 0.010)
Gower	0.008-0.122	0.009-0.053	-	0.019-0.117	0.010-0.107
	(0.058 ± 0.024)	(0.024 ± 0.010)	-	(0.056 ± 0.022)	(0.043 ± 0.028)
Itchen Valley Country Park	0.306-0.320	0.437-0.816	0.132-0.499	-	-
	(0.314 ± 0.004)	(0.607 ± 0.111)	(0.293 ± 0.108)	-	-
Test Valley	0.049-0.072	0.113-0.127	0.041-0.078	-	-
	(0.060 ± 0.012)	(0.120 ± 0.007)	(0.060 ± 0.018)	-	-

Appendix 5 Mean (± s.e.) head width, tibia length and wingbud length for instar groups of the Southern Damselfly.

Instar Group	*n*	Mean head width ± s.e. (mm)	Mean tibia length ± s.e. (mm)	Mean wing bud length ± s.e. (mm)
A	71	0.65 ± 0.01	0.60 ± 0.01	-
B	199	1.18 ± 0.01	0.96 ± 0.01	0.13 ± 0.03
C	351	1.78 ± 0.01	1.37 ± 0.01	0.56 ± 0.02
D	273	2.47 ±0.01	1.81 ± 0.01	1.25 ± 0.01
E	214	2.99 ± 0.01	2.16 ± 0.01	2.09 ± 0.02
F	83	3.47 ± 0.02	2.48 ± 0.02	3.93 ± 0.05

Appendix 6 Mean, range and median of head width, tibia length and wingbud length for instars for *P. nymphula*.

Instar	*n*	Mean head width ± s.e. (mm)	Mean tibia length ± s.e. (mm)	Mean wing bud length ± s.e. (mm)
2	3	0.53 ± 0.00	0.54 ± 0.00	-
4	2	0.86 ± 0.13	0.81 ± 0.02	-
5	6	1.19 ± 0.03	1.25 ± 0.02	0.26 ± 0.15
6	3	1.33 ± 0.04	1.44 ± 0.02	0.28 ± 0.05
7	15	1.61 ± 0.02	1.66 ±0.02	0.38 ± 0.02
8	16	1.91 ± 0.02	1.92 ± 0.03	0.68 ± 0.03
9	5	2.14 ± 0.03	2.11 ± 0.02	0.81 ± 0.10
10	27	2.40 ± 0.02	2.43 ± 0.03	1.26 ± 0.04
11	17	2.96 ± 0.03	2.99 ± 0.04	2.24 ± 0.03
12	4	3.60 ± 0.03	3.55 ± 0.03	4.16 ± 0.46
13	2	4.11 ± 0.34	4.23 ± 0.23	5.07

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 in order of the percentage of the total abundance made up of each taxa. Total frequency across samples is also given.

	Position and sample number											
Taxa	B1	B2	M1	M2	M3	M4	T1	T2	T3	T4	Total	% of total
Chironomidae	3	8	8	1	2	5	3	12	18	2	62	31.6
Gammaridae	4	3		1			1	5	2	2	18	9.2
Anisoptera (mainly Libellulidae)	3	2	2	4		2		1	1		15	7.7
Hydrophillidae			5	1			3	2	2	1	14	7.1
Hydroptilidae		5	3				1	2	2		13	6.6
Gerridae		1	2	6		1	1			2	13	6.6
Corixidae	1		3	2	1		1		1		9	4.6
Hydrobidiae			4			1	1	1	2		9	4.6
Limnephlidae	2	3			1c	2	1	1	1		9	4.6
Hydrometridae			1	2					2		5	2.6
Lymnaeidae		1						1	1	2	5	2.6
Oligochate							3		1		4	2.0
Ephemerellidae	1	1	1			1					4	2.0
Zygoptera (mainly Calyopterygidae)	2	1						1			4	2.0
Simulidae		2						1			3	1.5
Dytiscidae									1	1	2	1.0
Baetidae			1					1			2	1.0
Hydracarinidae								1			1	0.5
Tipulidae		1									1	0.5
Elmidae				1							1	0.5
Leuctridae								1			1	0.5
Sphaeridae										1	1	0.5
								Total abundance			196	

Key: c=case, all other numbers refer to frequencies of larval stages.

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