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2 Habitat associations of the endangered damselfly, *Coenagrion*
3 *mercuriale*, in a water meadow ditch system in southern England

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8 **Abstract**

9 The damselfly *Coenagrion mercuriale* (Charpentier) (Odonata: Coenagrionidae) is threatened throughout Europe. It is listed on
10 the EC Habitats and Species Directive and is the only odonate currently given priority status in the UK Biodiversity Action Plan.
11 Information about the habitat preferences of this species is required to guide conservation and management programmes. We
12 obtained estimates of density of mature adult *C. mercuriale* during an intensive mark-release-recapture study over 7.65 km of a
13 water meadow ditch network in the Itchen Valley, Hampshire. Detailed habitat information was also collected, including a variety
14 of physical variables, and data about the in-channel and bankside vegetation. *C. mercuriale* density and movement were analysed in
15 relation to habitat variables and local population size using Generalized Linear Models. Mean adjacent population density was the
16 single most important factor determining density. However the species was also associated with a number of habitat features, the
17 most important of which were: a channel substrate consisting primarily of silt, wide underwater ledges (berms), in-channel emergent
18 dicots, and bankside monocots. The presence of trees was negatively associated with damselfly density. Mean net lifetime movement
19 was greatest from sections with low density, with smaller than average berms, and with deeper water. The causes and consequences
20 of these findings are discussed in relation to the conservation and management of this rare species.

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22 *Keywords:* *Coenagrion mercuriale*; Conservation; Generalized linear models; Habitat; Odonata

24 **1. Introduction**

25 Many dragonfly and damselfly species have shown a
26 significant decline in Europe during the last century
27 (Van Tol and Verdonk, 1988). These authors evaluated
28 the status of 164 indigenous European odonate species
29 and considered 61 to be endangered, vulnerable or rare.
30 A steady decline in diversity was reported from almost
31 everywhere in Europe, but the situation was worst in
32 the most urbanised and industrialised regions, including
33 England.

34 The Odonata are one of the most well-known and
35 well documented invertebrate groups and, along with

Lepidoptera, have been used as indicators of a more 36
widespread reduction in insect abundance and diversity. 37
Insects are declining more rapidly than vertebrates over 38
much of Europe and three reasons have been suggested 39
to account for this disparity (Thomas, 1994): many in- 40
sects occupy very narrow niches, often associated with 41
a temporary successional phase; patches may remain 42
suitable for only a short time period; and insects are of- 43
ten too sedentary to colonise new patches of suitable 44
habitat that are not extremely close to old sites. 45

All odonates are dependent upon aquatic habitats for 46
larval development. These habitats, perhaps more than 47
most, have been vulnerable to destruction or alteration 48
over the last century. Drainage, pollution, canalisation 49
of watercourses, and alteration of management prac- 50
tices, along with many other threats, have all impacted 51

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52 on the viability of aquatic biotopes. The resultant loss of
53 habitat, together with impoverishment and fragmenta-
54 tion of remaining areas, has had a critical impact on
55 many species. This paper is concerned with one such
56 declining species, the damselfly *Coenagrion mercuriale*
57 (Charpentier).

58 *Coenagrion mercuriale* (the southern damselfly) is
59 principally confined to the south and west of Europe
60 and is threatened over much of its range. The main cen-
61 tres of population are in France, Spain and Italy, where
62 its status is considered to be widespread but vulnerable
63 (Grand, 1996). Elsewhere, it is declining (Germany and
64 the UK), in danger of extinction (Austria, Belgium and
65 Switzerland), or extinct (Luxembourg, the Netherlands,
66 Poland, Romania and Slovenia) (Grand, 1996). In the
67 UK it is currently limited to 28 of the UK's 10 km grid
68 squares and has declined by 38% since 1985 (Purse,
69 2001). Its declining status has been recognised both at
70 the national and international level and it has become
71 the focus of European-wide conservation efforts. It is
72 protected under the Bern Convention and the EC Habi-
73 tats and Species Directive. In the UK it is protected un-
74 der the Wildlife and Countryside Act of 1981 and is the
75 only odonate currently given priority status in the UK
76 Biodiversity Action Plan (HMSO, 1994, 1995).

77 *Coenagrion mercuriale* is restricted to two fragmented
78 biotopes in the British Isles. These are small lowland
79 heathland streams emanating from base-rich substrates,
80 and calcareous streams and fens. Although the species is
81 found less often on the latter habitat type in the UK, this
82 is the more typical habitat in the remainder of its Euro-
83 pean range (Buchwald, 1994; Sternberg et al., 1999).
84 Within these biotopes, *C. mercuriale* is believed to re-
85 quire unshaded, permanently flowing small channels
86 with groundwater influence and abundant marginal
87 aquatic vegetation. Thus the species is highly specialised
88 in its habitat requirements and probably needs active
89 management if it is to persist in the long term. It also
90 means that it will tend to be patchily distributed and will
91 shift its occupancy of areas as habitat management
92 progresses.

93 The development of an effective conservation strat-
94 egy for *C. mercuriale* is dependent upon a detailed
95 knowledge of the species ecological requirements,
96 including its population dynamics, patterns of move-
97 ment and dispersal, and habitat requirements of all life
98 stages (Thompson et al., 2003). Appropriate manage-
99 ment can then be applied at both the local and the regio-
100 nal scale. The work described in this paper investigates
101 variation in the density of mature adult *C. mercuriale*
102 in relation to habitat variables and local population size
103 in its calcareous stream habitat. The aim is to provide
104 management guidelines on the habitat preferences of
105 *C. mercuriale* so that sites can be managed to conform
106 to these preferences. Our findings are applicable
107 throughout the European range of this species.

2. Study sites

The distribution of *C. mercuriale* in the Itchen Val-
ley was taken from survey work carried out in 1998
(Stevens and Thurner, 1999) and 1999 (Strange,
1999). The species occurs principally on old water
meadow carriers and ditches in three main areas along
the Itchen flood plain between Southampton and Win-
chester (Fig. 1). From north to south these are, Mar-
iner's Meadow, Highbridge, and the lower Itchen
Complex, with the three areas separated by two gaps
of approximately 3 km of largely sub-optimal habitat.
The lower Itchen Complex is a large area of near-con-
tinuous habitat, so to ensure comparable sampling
intensity we divided this area into five sub-sites of
approximately equal length. These divisions also corre-
sponded to changes in management practices and
hence potential differences in habitat. From north to
south these are West Horton, Allington Manor, and
three sub-sites (upper, middle and lower) within the
Itchen Valley Country Park (IVCP). In total, 7.65
km of ditch was surveyed at the seven sites and sub-
sites.

The IVCP is owned and managed by the local
council as a public amenity, with recreation and con-
servation the principal management objectives. The
other sites are all privately owned farmland. All of
the areas investigated in this study are managed as
grazing pastures, although practices vary between sites.
The IVCP, Mariner's Meadow and Highbridge are cat-
tle grazed, West Horton is sheep grazed, whilst Alling-
ton Manor is grazed by a combination of cattle and
horses. Stocking intensity is lowest at the IVCP, at
around 1.1 grazing units per hectare, and is highest
at Allington Manor. The ditches and their banks are
fenced in West Horton, but are open to grazing in
Mariner's Meadow, Highbridge and Allington Manor.
The upper section of the IVCP is also open to grazing,
but most of the middle and lower sections are fenced
on one side to encourage habitat suitable for the water
vole (*Arvicola terrestris*) and otter (*Lutra lutra*). Final-
ly, the channel and bank profiles varied both within
and between sites. The channels at West Horton, for
example, were u-shaped with almost vertical banks
and little marginal vegetation, the channels at Mari-
ner's Meadow were generally shallow and wide, whilst
a wide range was present at the IVCP. In several loca-
tions, underwater ledges or platforms were present at
the edges of the main channel. These berms are
formed either by dredging at two different levels dur-
ing management works, or by the action of livestock
trampling the soft banks, and provide ideal habitat
for marginal aquatic vegetation. Thus we were able
to investigate the association of *C. mercuriale* with a
variety of different habitats and management regimes
during the course of this study.

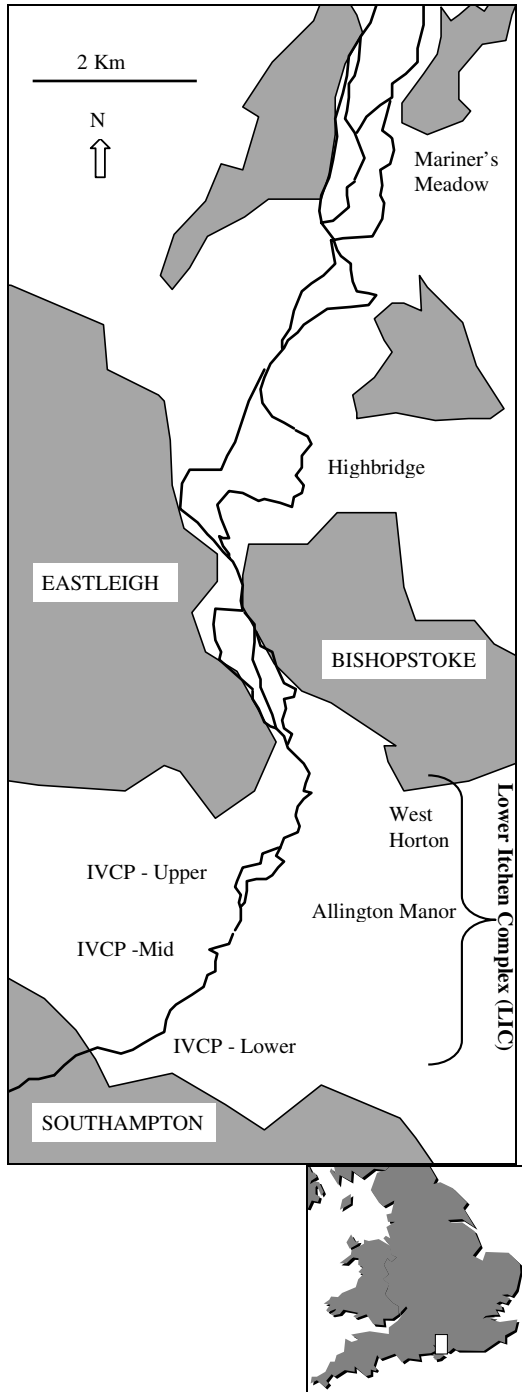


Fig. 1. Location of the seven sites and sub-sites in the Itchen Valley, Hampshire. The main channels of the River Itchen are represented by the thick black line, and urban areas are shown in grey. The inset map shows the approximate location of the Itchen Valley in the UK.

163 **3. Methods**

164 *3.1. Coenagrion mercuriale survey*

165 Density of *C. mercuriale* was derived from a large
 166 mark-release-recapture (MRR) experiment that we per-
 167 formed in all seven areas in the summer of 2001. At each

site or sub-site a pair of research assistants captured 168
 damselflies with a kite net and recorded the location 169
 using a Global Positioning System (GPS) calibrated to 170
 the Ordnance Survey. Animals were marked by writing 171
 a unique alphanumeric code on the left forewing in 172
 waterproof ink and by putting a small dab of paint from 173
 a paint marker pen on the thorax. We sampled every day 174
 for 5 weeks from 12th June, except during bad weather 175
 when adult damselflies are not active. This coincided 176
 with the peak flight period in this area. 177

We divided each site into 50 m × 50 m sections and the 178
 damselflies marked or recaptured within each section 179
 were tabulated. We chose sections of this size as the med- 180
 ian net lifetime movement recorded in this study was 31.9 181
 m, and 65.7% of individuals moved less than 50 m in 182
 their lifetime (J.R. Rouquette, unpublished). Thus the 183
 scale of each section reflects the approximate scale of life- 184
 time movement for the majority of damselflies. Density 185
 was then calculated as the average number of *C. mercur-* 186
iale seen in that section per day of recording. 187

188 *3.2. Habitat survey*

Immediately following the end of the MRR work, we 189
 recorded a suite of environmental variables (Table 1). 190
 We measured eight variables describing the physical 191
 characteristics of the channel and banksides, including 192
 one that recorded the management regime. The width 193
 of berms was recorded where present. We collected 194
 information on whether a section was fenced on one 195
 or both sides, but this variable was dropped from the 196
 analysis as it was highly correlated with our grazing 197
 variable. 198

We recorded the percentage cover of vegetation in 199
 two 1 m² quadrats, one on each bank, and averaged 200
 the results. The percentage cover of in-channel vegeta- 201
 tion in a strip between the two bankside quadrats was 202
 also assessed. Due to the enormous number of potential 203
 variables, vegetation was recorded in terms of functional 204
 groups rather than individual species (Table 1). Bank- 205
 side vegetation height was measured on both sides at 206
 0, 0.25, 0.5, 1, 2, 5 and 10 m from the water's edge. This 207
 was converted into two variables, the mean vegetation 208
 height from 0 to 1 m and the mean vegetation height 209
 from 2 to 10 m from the water's edge. 210

Only channels with flowing water were surveyed, as it 211
 is known that year-round flow is a pre-requisite for this 212
 species (Buchwald, 1994; Winsland, 1997; Jenkins et al., 213
 1998; Thompson et al., 2003). We collected habitat data 214
 from 82 sections, which represented 54% of the ditch 215
 network. 216

217 *3.3. Statistical analysis*

We used generalized linear models (GLM; McCull- 218
 lagh and Nelder, 1983; Dobson, 2002) to assess which 219

Table 1
Habitat variables measured in each section and used as potential predictors of *C. mercuriale* density

Variable	Description
<i>Physical variables</i>	
Water depth	Mean of three measurements (cm) taken at 1/4, 1/2 and 1/3 across channel
Water width	Width of channel (cm)
Bank height	Height of bank (cm) from water's edge to bankfull level
Bank width	Width of bank (cm) from water's edge to bankfull level
Bank gradient	Gradient of bank (°) where $\tan \theta = \text{width/height}$
Substrate	Composition of bed substrate. Scale: 1, predominantly silt; 2, silt and gravel; 3, predominantly gravel.
Berm width	Width of underwater ledge/platform (see text). Scale: 0, no berm; 1, 1st quartile of widths; 2, 2nd quartile; 3, 3rd quartile; 4, 4th quartile
Grazing	Grazing animals have access to bankside. Scale: 0, no grazing on either bank; 1, grazing on one bank only; 2, grazing on both banks.
<i>In-channel vegetation</i>	
Emergent dicots	% Cover of emergent dicots, principally <i>Apium nodiflorum</i> , <i>Rorippa nasturtium-aquaticum</i> , <i>Veronica</i> spp., <i>Myosotis scorpioides</i> , and <i>Mentha aquatica</i>
Emergent monocots	% Cover of emergent monocots, principally <i>Glyceria maxima</i> , <i>Phalaris arundinacea</i> , <i>Sparganium erectum</i> , <i>Iris pseudacorus</i> and <i>Carex</i> spp.
Submerged	% Cover of submerged plants, <i>Ranunculus</i> spp., <i>Callitriche</i> spp. and others
Floating	% Cover of floating plants, principally <i>Lemna minor</i>
Open water	% Open water
<i>Bankside vegetation</i>	
Helophyte dicots	% Cover of dicots typically associated with water's edge habitat, principally <i>Apium nodiflorum</i> , <i>Rorippa nasturtium-aquaticum</i> , <i>Veronica</i> spp., <i>Myosotis scorpioides</i> , <i>Mentha aquatica</i> , <i>Rumex hydrolaphthum</i> , and <i>Epilobium</i> spp.
Helophyte monocots	% Cover of monocots typically associated with water's edge habitat, principally <i>Glyceria maxima</i> , <i>Phalaris arundinacea</i> , <i>Sparganium erectum</i> , <i>Iris pseudacorus</i> , <i>Carex</i> spp., and <i>Juncus</i> spp.
Forbs	% Cover of terrestrial dicots, including <i>Urtica dioica</i> , <i>Montia sibirica</i> , <i>Solanum dulcamara</i> , <i>Rumex acetosa</i> , <i>Cirsium</i> spp. and others
Terrestrial monocots	% Cover of terrestrial monocots, including terrestrial Gramineae, Juncaceae and Cyperaceae
Bare ground	% Cover of bare ground
Trees	Presence (1) or absence (0) of trees rooted in-channel or on the bankside.
Vegetation height 0–1 m	Direct measurement of vegetation height. Mean of four readings taken at water's edge, 0.25, 0.5 and 1 m from edge on both banks.
Vegetation height 2–10 m	Direct measurement of vegetation height. Mean of three readings taken at 2, 5 and 10 m from water's edge on both banks.

220 variables explained a significant proportion of variation
 221 in *C. mercuriale* density. GLMs are able to handle distri-
 222 butions other than the normal, including the binomial
 223 distribution, which can be used to model presence/ab-
 224 sence data, and the Poisson distribution, which is used
 225 to model count data. These distributions have proved
 226 particularly useful in modelling species distributions
 227 with respect to habitat variables and have been used in
 228 a large number of studies in recent years (Guisan and
 229 Zimmermann, 2000; Pearce and Ferrier, 2001; Guisan
 230 et al., 2002, and references therein; Rushton et al., 2004).

231 In our study, mean density of *C. mercuriale* was used
 232 as the dependent variable. As this is based on count
 233 data, a Poisson error structure was the most appropri-
 234 ate, and it was related to the set of predictors using a
 235 logarithmic link function (Crawley, 1993; Dobson,
 236 2002). However, the distribution of *C. mercuriale*
 237 was aggregated, showing marked overdispersion and so a
 238 quasi-likelihood function was used (SAS Institute Inc.,
 239 1999; Crawley, 2002). In effect this adjusts the scale
 240 parameter of the model (using Pearson's $\chi^2/\text{d.f.}$) so that
 241 the variance in *C. mercuriale* density is proportional to,

rather than equal to, the mean. Poisson regression has
 been used widely on a variety of different taxa, including
 birds (Chamberlain et al., 1999; Bradbury et al., 2000;
 Robinson et al., 2001; Henderson et al., 2004), mammals
 (Laurance, 1997; Jaberg and Guisan, 2001), insects
 (Maggini et al., 2002; Mac Nally et al., 2003; Meggs et
 al., 2004), and the species richness of plants (Heikkinen
 and Neuvonen, 1997).

A backwards selection procedure was used starting
 from the maximal model with all variables included
 (Crawley, 2002). The least significant variables were re-
 moved sequentially until all remaining variables were
 significant at $p \leq 0.05$. All removed variables were then
 refitted to check whether they explained additional varia-
 nce. Where categorical variables remained in the min-
 imal adequate model, simplified categories were also
 tested (Crawley, 1993). D^2 and adjusted D^2 (the equiva-
 lents of R^2 and adjusted R^2) were calculated according
 to standard formulae (Guisan and Zimmermann, 2000).

All variables that were not normally distributed were
 subjected to an appropriate transformation before mod-
 el building. Water width, bank gradient and both vege-

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264 tation height variables were log₁₀ transformed, bank
 265 height was square root transformed, and all plant per-
 266 centage cover variables were arcsine transformed. Qua-
 267adratic terms were included to test for possible non-
 268linear effects of the continuous variables. Due to the
 269large number of potential explanatory variables, model
 270building followed a two-stage process. In the first stage,
 271the 8 physical variables and their quadratic terms, where
 272appropriate, were fitted. In the second stage the in-chan-
 273nel and bankside vegetation variables and their qua-
 274dratic terms were added to the minimal adequate
 275model from the first stage.

276 One potential problem with our study design was
 277that sections were not spatially independent because
 278they were clustered within sites. It is possible that sec-
 279tions within one site or sub-site are more similar than
 280those from a different site, particularly if unmeasured
 281variables acting at the site/sub-site level were present.
 282This potential problem was dealt with by adding a series
 283of dummy variables representing each site or sub-
 284site into the best model from stage two. Two factors
 285were tested; a “sites” factor with three levels, corre-
 286sponding to the three principal areas (Mariner’s Mea-
 287dow, Highbridge, and the lower Itchen Complex), and
 288a “sub-sites” factor, corresponding to the seven sub-
 289sites. This is the “raw data approach” suggested by
 290Legendre (1993) to deal with broadscale spatial
 291autocorrelation.

292 We also examined whether patterns of *C. mercuriale*
 293density were related to local population size. This could
 294result as sections were not spatially independent from
 295their neighbours and damselflies may aggregate in areas
 296where large populations are already present. To investi-
 297gate this possibility we calculated variables representing
 298the mean density and the maximum density of *C. mercu-*
 299*riale* in all adjacent sections. These variables were added
 300to the minimum adequate habitat model. All analyses
 301were performed in SAS release 8 (SAS Institute Inc.,
 3021999).

303 3.4. Movement in relation to habitat features and density

304 If habitat is sub-optimal, individuals may move fur-
 305ther in search of more suitable areas. There may,
 306therefore, be a link between movement and certain
 307habitat features. We investigated this possibility by
 308calculating the mean net lifetime movement for all
 309damselflies first marked in each section. This was then
 310used as the dependent variable in a new GLM, with
 311the habitat variables and density as predictors. This
 312time the response variable was normally distributed,
 313so a normal error structure was assumed and was re-
 314lated to the predictors using an identity link function
 315(Crawley, 1993). This is analogous to least-squares lin-
 316ear regression. Model building followed the same pro-
 317cedure as above.

4. Results

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4.1. *Coenagrion mercuriale* density

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320 During the 5 weeks of the MRR experiment, 7816 *C.*
 321*mercuriale* were marked, and there were 3325 recapture
 322events. A breakdown of the numbers at each site and
 323sub-site is given in Table 2. As each site contained
 324roughly equal lengths of potential ditch habitat, these
 325figures give a crude indication of the strength of the col-
 326onies. The damselfly was present in reasonable numbers
 327at all sites, but the upper and middle sections of IVCP
 328contained particularly strong populations. The site with
 329the lowest population was West Horton, where it was
 330found in good numbers on one short stretch of stream,
 331but was almost absent from the rest of the site.

332 Fig. 2 shows the frequency distribution of mean
 333*C. mercuriale* densities for each of the 82 sections for
 334which we collected habitat data. *C. mercuriale* was
 335recorded in 77 of these sections and the modal density
 336was less than 1 damselfly per section per day. However,
 337the data deviated from a Poisson distribution as there
 338were more high density sections than expected, indicat-
 339ing that *C. mercuriale* was from an aggregated or over-
 340dispersed distribution. The highest recorded was an
 341average of 35.7 damselflies per day, from a section in
 342IVCP – upper.

4.2. Habitat associations

343

344 The single best predictor of high *C. mercuriale* density
 345was the presence of wide berms (Table 3 – Habitat mod-
 346el), and this factor alone explained 31.2% of the total
 347variance. Initially, both the 3rd and 4th width quartiles
 348were fitted to the model, but this was replaced by a sin-
 349gle variable describing the wider half of berm widths
 350(Berm width *B*) without a significant fall in deviance
 351and leading to a slightly improved fit.

352 Moderately wide banks were also favoured, which to-
 353gether with berms underneath the water, provide habitat
 354for bankside and in-channel vegetation. Channel sub-
 355strates consisting primarily of silt were also preferred.

Table 2
 Total numbers of *C. mercuriale* marked and recaptured at each site or sub-site in the Itchen valley, Hampshire, over a 5-week period in June and July 2001

Site or sub-site	Individuals marked	Recapture events	Total number
Mariner’s meadow	1071	773	1844
Highbridge	779	460	1239
West Horton	351	182	533
Allington Manor	558	324	882
IVCP – upper	2152	764	2916
IVCP – mid	1874	427	2301
IVCP – lower	1031	395	1426

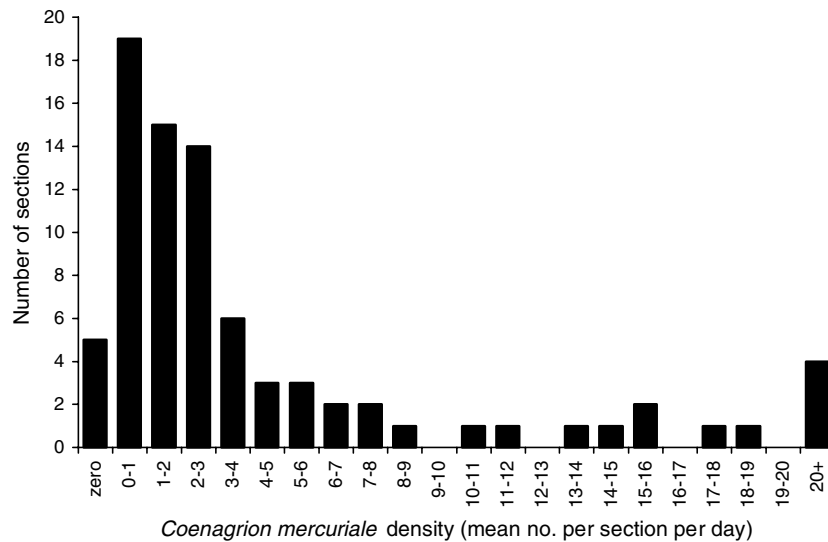


Fig. 2. Frequency distribution of mean *C. mercuriale* densities in 82 sections in the Itchen Valley, Hampshire.

Table 3
Significant predictors of *C. mercuriale* density derived from two Poisson regression models

Model	Variable	χ^2	<i>p</i>	Parameter estimates	Standard error
Habitat model Deviance = 158.49 d.f. = 68 Dev./d.f. = 2.33 $D^2 = 0.725$ Adj. $D^2 = 0.672$	Berm width <i>B</i>	44.73	***	1.336	0.200
	Vegetation height 2–10 m	15.91	***	−1.310	0.329
	Emergent dicots	12.12	***	0.0344	0.0099
	Bank width	11.97	***	0.0332	0.0096
	Vegetation height 0–1 m	11.82	***	1.420	0.413
	Helophyte monocots	11.00	***	0.0349	0.0105
	Bank width ²	10.18	**	−0.0001	0.0000
	Bare ground	8.61	**	0.0266	0.0091
	Open water	8.11	**	0.0253	0.0089
	Submerged	8.00	**	0.0235	0.0083
	Floating	7.53	**	0.0529	0.0193
	Substrate 1	5.32	*	0.436	0.189
	Terrestrial monocots	4.64	*	0.0250	0.0116
	Intercept	30.78	***	−6.510	1.174
	Final model Deviance = 98.58 d.f. = 71 Dev./d.f. = 1.39 $D^2 = 0.829$ Adj. $D^2 = 0.805$	Adjacent mean density (log ₁₀)	63.27	***	1.827
Terrestrial monocots		27.85	***	0.0377	0.0071
Substrate 1		16.67	***	0.562	0.138
Helophyte monocots		13.84	***	0.0188	0.0050
Berm width <i>B</i>		5.84	*	0.406	0.168
Emergent dicots		5.54	*	0.0212	0.0090
Trees		5.05	*	−0.820	0.365
Site IVCP-lower		4.78	*	−0.564	0.258
Helophyte dicots		4.69	*	0.0467	0.0216
Helophyte dicots ²		4.00	*	−0.0009	0.0004
Intercept		27.99	***	−2.524	0.477

Deviance, degrees of freedom, deviance/d.f., D^2 , and adjusted D^2 are shown for both models. For each variable retained in the model, the *p*-value derived from χ^2 tests, parameter estimates and standard errors are shown (**p* < 0.05, ***p* < 0.01, ****p* < 0.001). “Habitat model” is derived using habitat variables only; “Final model” incorporates a variable for the density of *C. mercuriale* in adjacent sections and a “sub-sites” variable. For a fuller explanation of variables see Table 1 and text.

356 *C. mercuriale* was significantly associated with three of
 357 the four types of in-channel vegetation – emergent dicots,
 358 submerged, and floating vegetation. However, it
 359 was also associated with open water and was not found
 360 in large numbers where the channel was substantially
 361 choked. On the bankside, both helophyte and terrestrial

monocots were favoured but there was no preference for
 other groups. Taller vegetation was preferred in the first
 metre, but shorter vegetation from 2 to 10 m from the
 water’s edge. Finally, an element of bare ground, usually
 caused by grazing livestock, was associated with higher
 densities.

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Table 4

The fit of Poisson regression models to explain *C. mercuriale* density, incorporating: (a) habitat variables only; (b) habitat variables and variables representing each site or sub-site; (c) habitat variables, sub-sites variables and variables describing local population size; (d) removal of non-significant variables and addition of significant ones to derive the final model described in Table 3

	Deviance	d.f.	Dev./d.f.	D^2	Adj. D^2
(a) Habitat model	158.49	68	2.33	0.725	0.672
(b) +sites	147.14	66	2.23	0.744	0.686
+sub-sites	123.24	62	1.99	0.786	0.720
(c) +maximum adjacent density	116.04	61	1.90	0.798	0.732
+mean adjacent density	111.27	61	1.82	0.807	0.743
+Log ₁₀ (mean adj. density)	100.49	61	1.65	0.825	0.768
(d) Non-significant variables removed	113.47	74	1.53	0.803	0.784
Significant variables added – final model	98.58	71	1.39	0.829	0.805

The habitat model from Table 3 is used as the base habitat model. The best model from (b) is used as the base model for (c) and the best model from (c) is used as the base model in (d). The deviance, degrees of freedom, deviance/d.f., D^2 , and adjusted D^2 are shown for each model.

368 There was a significant improvement to the habitat
369 model on fitting a “sites” factor with three levels, but
370 a much greater improvement on fitting a “sub-sites” fac-
371 tor (Table 4). However, only one level was significant
372 and this corresponded to the IVCP – lower sub-site. This
373 implies that there was some factor acting on this sub-site
374 that was unmeasured but could explain additional vari-
375 ance. The factor was negative, indicating that there were
376 lower than expected densities throughout the sub-site.
377 This factor level was retained in the final model.

378 4.3. Effects of local population density

379 Density of *C. mercuriale* could be better explained by
380 incorporating information on local population size. In-
381 deed, mean adjacent population density was the single
382 most important factor determining density in the final
383 model, and could explain 56.0% of the total variance.
384 To investigate whether the relationship was exponential,
385 linear or asymptotic, three different versions of this fac-
386 tor were fitted (Telfer et al., 2001). These were the max-
387 imum density in adjacent sections, the mean density, and
388 Log₁₀ transformed mean density respectively. Log₁₀
389 mean density provided the best fit to the data, with the
390 worst fit provided by the maximum density (Table 4).
391 An asymptotic response was, therefore, implied.

392 4.4. Final model

393 Log₁₀ mean density was the single best predictor in
394 the final model (Table 3). However, even accounting
395 for this spatial autocorrelation and including the “sub-
396 sites” factor relating to IVCP – lower, five of the habitat
397 variables from the best habitat model continued to sig-
398 nificantly improve the fit of the model. These were; a
399 channel substrate consisting primarily of silt, wide
400 berms, in-channel emergent dicots, and bankside mono-
401 cots, both those associated with water’s edge habitat
402 (helophyte monocots) and those of a more terrestrial
403 nature (terrestrial monocots). All were positively associ-
404 ated with *C. mercuriale* density. In addition, three fur-

ther variables significantly improved the fit of the
model when refitted in the final step of the model build-
ing process. The presence of trees was negatively associ-
ated with damselfly density, whilst bankside helophyte
dicots showed a quadratic response, with greatest dam-
selfly densities at intermediate percentage cover of this
vegetation type.

405 4.5. Effect of habitat and density on movement 412

413 We were able to calculate movement data for 68 of
414 the 82 sections for which we had collected habitat data.
415 This represents a subset of the movement data. The
416 mean net lifetime movement for damselflies first marked
417 in these 68 sections ranged from 10.1 to 144.2 m with a
418 median of 33.8 m.

419 Three habitat variables had a significant effect on *C.*
420 *mercuriale* movement (Table 5 – habitat model). Move-
421 ment was increased from sections with smaller than
422 average berms (Berm width *A*), and from sections with
423 deeper water. There was a quadratic effect of bank
424 height, with greatest movement occurring from sections
425 with either low or high banks.

426 There was no improvement to the model on fitting a
427 “site” or “sub-site” factor. However, the addition of *C.*
428 *mercuriale* density did significantly improve the model,
429 with greatest movement occurring in sections with low
430 densities of damselflies. Log₁₀ mean density provided a
431 slightly better fit than the untransformed variable. Nar-
432 row berm width and water depth remained significant,
433 although bank height was no longer significant and
434 was deleted from the final model. Density in neighboring
435 sections did not improve the fit of the model.

436 5. Discussion

437 5.1. Habitat associations

438 Mature adult *C. mercuriale* are strongly associated
439 with certain physical and vegetation characteristics of

Table 5

Significant predictors of mean *C. mercuriale* movement derived from two GLM regression models

Model	Variable	<i>t</i>	<i>p</i>	Parameter estimates	Standard error
Habitat model <i>F</i> = 6.81*** d.f. = 4,63 <i>R</i> ² = 0.302 Adj. <i>R</i> ² = 0.258	Berm width <i>A</i>	4.04	***	0.235	0.058
	Water depth	2.82	**	0.0028	0.0010
	Bank height	−2.01	*	−0.238	0.119
	Bank height ²	2.01	*	0.0150	0.0074
	Intercept	4.80	***	2.264	0.472
Final model <i>F</i> = 11.23*** d.f. = 3,64 <i>R</i> ² = 0.345 Adj. <i>R</i> ² = 0.314	Berm width <i>A</i>	3.50	***	0.201	0.057
	<i>C. mercuriale</i> density (log ₁₀)	−2.93	**	−0.220	0.075
	Water depth	2.39	*	0.0022	0.0009
	Intercept	17.17	***	1.529	0.089

The *F*-value and the associated *p*-value, degrees of freedom, *R*², and adjusted *R*² are shown for both models (**p* < 0.05, ***p* < 0.01, ****p* < 0.001). For each variable retained in the model, the *p*-value derived from *t*-tests, parameter estimates and standard errors are shown. “Habitat model” is derived using habitat variables only; “Final model” incorporates a variable for the density of *C. mercuriale*. For a fuller explanation of variables see Table 1 and text.

440 the water meadows ditches in the Itchen Valley. The
441 most important physical features were the presence of
442 wide underwater berms and a substrate consisting pri-
443 marily of silt. Wide berms provide suitable habitat for
444 emergent vegetation and warm shallow areas with slow
445 flow for larvae. Indeed, the percentage cover of emer-
446 gent dicots was positively correlated with wide berms
447 (Spearman’s correlation with Berm width *B*, *r*_s = 0.319,
448 *p* < 0.01). Similarly, silt deposits occur in areas of slow
449 flow and around the roots of aquatic vegetation.
450 *C. mercuriale* larvae are most often found in shallow,
451 slow-flowing channels or in the silty margins of larger
452 channels, on or around the roots of emergent vegetation
453 (Hold, 1998; Purse, 2001; J.R. Rouquette, unpublished).
454 Thus, adults are likely to be associated with channels
455 that provide such habitats.

456 The plant groups that were associated with the high-
457 est densities of *C. mercuriale* were in-channel emergent
458 dicots, bankside monocots, and bankside helophyte di-
459 cots. Trees were actively avoided. The roots of in-chan-
460 nel emergent dicots form the preferred habitat for
461 developing larvae. Adults also preferentially choose
462 such plants for oviposition, as eggs are laid directly into
463 the stems of submerged and emergent plants. In a study
464 in the New Forest, Purse (2001) found that females
465 showed a marked preference for plants with soft stems
466 and thin cuticles, containing spongy parenchyma cells
467 rather than thicker collenchyma cells. Strange (1999)
468 reported that species favoured for oviposition in the Itch-
469 en Valley included *Apium nodiflorum*, *Rorippa*
470 *nasturtium-aquaticum* and *Veronica beccabunga*, and
471 that grasses were not favoured. Similarly, Sternberg et
472 al. (1999) reported that a wide variety of plant species
473 are used for oviposition in Baden-Württemberg, Ger-
474 many, but plants with hard parts are avoided.

475 Bankside monocots are used by adult *C. mercuriale*
476 for a variety of purposes. They provide suitable perching
477 sites close to the water’s edge for basking, foraging, for

478 males waiting for females, and for copulating pairs. 478
479 They provide shelter during periods of inclement weath- 479
480 er and to escape from predators. They may also increase 480
481 the availability of prey items, although greatest prey 481
482 abundance is likely to occur in areas with a diverse 482
483 and heterogeneous vegetation structure (Drake, 1995). 483
484 Finally, they could provide suitable night-time roosting 484
485 sites, although adults will usually roost away from the 485
486 water’s-edge in the Itchen Valley (J.R. Rouquette, 486
487 unpublished). 487

488 Bankside helophyte dicots are also able to provide 488
489 shelter and potential perching sites. However, the spe- 489
490 cies in this group are largely the same as the species in 490
491 the in-channel dicots group (Table 1), differing only in 491
492 whether the plants are rooted in the channel or on the 492
493 bankside. They are probably, therefore, assessed in the 493
494 same way by *C. mercuriale* and could be used as a cue 494
495 to indicate suitable oviposition and larval habitat. 495

496 Trees are avoided in the Itchen Valley, probably be- 496
497 cause they cast shade onto the watercourse, reducing 497
498 temperature and hence flight manoeuvrability. In 117 498
499 sites investigated in Germany, 70% were completely un- 499
500 shaded, and no site was more than 20% shaded (Buch- 500
501 wald, 1994). The vast majority of sites in the UK are 501
502 also unshaded (Winsland, 1997; Purse, 2001). The tree 502
503 variable that we measured during this study only in- 503
504 cluded trees that were rooted in the channel or bankside 504
505 quadrats, and so will have underestimated the effect of 505
506 shading. Unfortunately, we did not include a direct mea- 506
507 surement of shade, although it has been collected for a 507
508 related research project (J.R. Rouquette, unpublished). 508
509 Most sections were completely unshaded, or at most 509
510 shaded for a small part of the day. However, larger areas 510
511 of the IVCP – lower sub-site were overgrown by bank- 511
512 side trees and shrubs. It is likely that this unmeasured 512
513 factor resulted in the lower than expected densities 513
514 throughout this sub-site that was evident in the final 514
515 model. 515

516 It is worth noting that although the density of
 517 *C. mercuriale* was higher in areas with ample emergent
 518 dicots, high percentage cover of vegetation per se was
 519 not favoured, and open water was positively associated
 520 with density in the earlier habitat model. In this study
 521 emergent vegetation cover ranged from 0% to 100% with
 522 a mean of 32%. Typically this was made up of 14%
 523 emergent dicots and 18% emergent monocots. Other
 524 authors have previously noted that *C. mercuriale* did
 525 not occur on sites that were overgrown with emergent
 526 vegetation in the Itchen Valley (Hold, 1998; Strange,
 527 1999) and in other parts of the UK (Evans, 1989; Wins-
 528 land, 1997; Stevens and Thurner, 1999). In Germany,
 529 *C. mercuriale* occupied habitats with emergent vegeta-
 530 tion cover ranging from 3% to 100%, and submerged
 531 vegetation of at least 1%, but appears to prefer sections
 532 of water with 30–60% emergent vegetation (Buchwald,
 533 1994). Other studies have indicated that the species pre-
 534 ferred lower vegetation densities, and that there are
 535 regional differences. Sternberg et al. (1999) reported a
 536 preferred density of 1–20% in the upper Rhine Valley,
 537 but 10–40% in the Alpine region, and 50–90% in calcar-
 538 eous marsh habitat.

539 5.2. Local population size and habitat selection

540 Local population size has a major effect on *C. mercuriale*
 541 density, implying a degree of spatial autocorrela-
 542 tion. That is to say, individuals are attracted to areas
 543 that already contain high densities of conspecifics. There
 544 are a number of reasons that could explain this pattern.
 545 Firstly, there is strong selection pressure for females to
 546 choose oviposition sites with habitat features that max-
 547 imise the growth and survival of offspring. Secondly,
 548 individuals may be using the presence of conspecifics
 549 as a cue for habitat quality. For example, in a small
 550 experiment in Brittany, France, Martens (2000) showed
 551 that tandem pairs of *C. mercuriale* landed preferentially
 552 on leaves where a single motionless male in the typical
 553 vertical position of a tandem male was present. Finally,
 554 this pattern may be driven by the need to find mates and
 555 avoid inbreeding in this non-territorial species.

556 It is believed that odonates select habitat in a hierar-
 557 chical manner (Corbet, 1999). Selection follows a se-
 558 quence of decreasing scale from biotope to larval
 559 habitat to oviposition site, using different selection cues
 560 at each stage. At the larger scales it is likely that odo-
 561 nates use mostly visual cues and are, for example, at-
 562 tracted by light reflecting from water bodies. Given a
 563 range of artificial materials, *Aeshna juncea* was most at-
 564 tracted to black plastic foil, which gave a coarse pattern
 565 of reflection on a dark background (Wildermuth, 1993).
 566 This may go some way to explain why *C. mercuriale* is
 567 not common in sites that are overgrown with emergent
 568 vegetation. At finer scales it is likely that they use a com-
 569 bination of visual, tactile and thermosensory cues (Cor-

bet, 1999). At all stages, damselflies may be assessing
 habitat directly or using presence of conspecifics as a
 cue, or a combination of these factors.

573 5.3. *Coenagrion mercuriale* movement

574 As further confirmation of the tendency of this spe-
 575 cies to aggregate, we found that movement was inverse
 576 density dependent. In other words, the greater the den-
 577 sity of *C. mercuriale*, the shorter the average distance
 578 moved. This is the opposite effect to that found in most
 579 other species. It is beyond the scope of this paper to dis-
 580 cuss this feature in detail; the factors affecting movement
 581 and dispersal are described elsewhere (J.R. Rouquette,
 582 in preparation). However, the most plausible explana-
 583 tions are likely to be once again, access to high quality
 584 habitat and to conspecifics in a species utilizing scramble
 585 competition (Thompson et al., 2003).

586 The only habitat features that significantly affected
 587 movement in the final model were the presence of nar-
 588 row berms and deep water, both of which resulted in
 589 greater movements. It would seem that *C. mercuriale*
 590 is moving away from areas where these two features
 591 are present. This ties in well with the habitat model,
 592 where larger than average berms were favoured. If dam-
 593 selflies are associated with wide berms, which provide
 594 large areas of suitable habitat then it seems reasonable
 595 that they should move away from areas providing less
 596 suitable habitat, particularly if better is available nearby.
 597 The response to water depth is probably similar. Chan-
 598 nels that are deep provide less of the preferred shallow
 599 margins with abundant emergent vegetation and so
 600 damselflies are likely to move away.

601 5.4. Methodological considerations

602 Although our regression models uncovered statisti-
 603 cally significant relationships between the predictor vari-
 604 ables and *C. mercuriale* density that appear to fit with
 605 the known ecology of the species (Thompson et al.,
 606 2003), the results are subject to a number of assumptions
 607 and limitations. Ideally, we would have validated our
 608 findings using an independently collected data set. How-
 609 ever, this was not logistically feasible and our data set
 610 was too small to be able to divide it into a training sub-
 611 set and a validation subset. This makes it harder to
 612 ascertain the general usefulness and application of our
 613 models. Indeed, lack of field validation has been identi-
 614 fied as a serious issue limiting the validity of this type of
 615 study (e.g. Guisan et al., 2002). Linked with this, models
 616 developed for one part of a species range often have only
 617 limited success when applied to a separate area. It would
 618 be interesting to test our model in the neighbouring Test
 619 Valley, where the species occurs in a similar habitat to
 620 the Itchen Valley, or to other parts of the UK where
 621 *C. mercuriale* occurs on different habitats.

622 There is always the potential problem of overfitting
623 when performing a regression with a large number of
624 predictor variables. Crawley (1993) suggests that there
625 should be no more than about $n/3$ parameters in the ini-
626 tial model and we achieved this by fitting the model in
627 stages. Again, however, field validation would have im-
628 proved our confidence in the final model.

629 We chose to amalgamate plant species into functional
630 groups, which we felt was justified on both statistical
631 and ecological grounds. This radically reduced the num-
632 ber of potential predictor variables, thereby reducing the
633 chance of overfitting and of spurious correlations. Many
634 of the plant species were sparsely distributed and could
635 not have been normalized before analysis. Although *C.*
636 *mercuriale* has been associated with particular plant
637 communities and functional types, it has never been
638 associated with individual species. For example, Purse
639 (2001) found that *C. mercuriale* selected a variety of
640 soft-stemmed emergent dicots for oviposition but used
641 a variety of hard stemmed emergent monocots for emer-
642 gence. Therefore, we did not think that there would be
643 any loss of information by grouping plant species into
644 these structural and functional groups.

645 5.5. Conservation implications

646 The results of this study have revealed a number of
647 habitat features with which *C. mercuriale* is associated.
648 It is encouraging that these results have confirmed no-
649 tions of habitat preferences that have until now been
650 based on a combination of survey work and anecdotal
651 evidence (e.g. Winsland, 1997; Hold, 1998; Jenkins et
652 al., 1998; Stevens and Thurner, 1999; Strange, 1999).
653 Management, therefore, should be undertaken that
654 encourages the key habitat attributes identified. Chan-
655 nels with wide shallow margins and abundant emergent
656 herbaceous vegetation are the primary goal and can best
657 be achieved by a combination of mechanical re-profiling
658 and light grazing. Periodic dredging is required to stop
659 the channels from silting up completely and to remove
660 excess vegetation. During dredging operations, berms
661 should be created. Cattle can also help to create a com-
662 plex bank profile by poaching the channel edges. Cattle
663 are also extremely important for maintaining the correct
664 vegetation structure on both the banksides and in the
665 margins of the channels. Water level management is
666 an important prerequisite in some areas and could be
667 achieved by the installation and maintenance of sluice
668 gates and other control features. Year-round flowing
669 water is essential for the survival of the species, but rea-
670 sonably constant water levels would further enhance
671 stability.

672 Movement patterns and the population structure of
673 *C. mercuriale* should have an important bearing on the
674 spatial scale of any planned management works. The
675 majority of individuals move considerably less than 50

m in their lifetimes. It is therefore essential that habitat
enhancement is carried out on short sections at a time
and that these are close to strong centres of population.
On a landscape scale, movements over 500 m are rare
and the longest recorded lifetime movement is less than
2 km (J.R. Rouquette, unpublished). This ecological dis-
tance corresponds very closely with genetic distance and
we have discovered that the populations at Mariner's
Meadow and Highbridge are genetically isolated from
those in the lower Itchen Complex (Watts et al., 2004).
Long-term persistence of the species in the Itchen Valley
and elsewhere will depend upon creation of new sites be-
tween existing locations, to re-connect populations and
enable gene flow over large distances.

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