

Dispersal characteristics and management of a rare damselfly

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Summary

1. *Coenagrion mercuriale* is a rare damselfly in Britain and mainland Europe and has been declining in the last 30 years. It has specialized habitat requirements and has been viewed, traditionally, as a poor disperser. Knowledge of its dispersal ability was considered in its Biodiversity Species Action Plan as essential for the formulation of appropriate conservation management strategies.

2. Mark–release–recapture (MRR) studies of *C. mercuriale* in two large UK heathland populations were undertaken. Mature adults had a low rate of movement within continuous areas of habitat (average < 25 m movement), low emigration rates (1.3–11.4%) and low colonization distances (maximum 1 km), all comparable to similarly sized coenagrionids.

3. Movements were more likely within than between patches of suitable habitat over short to medium distances (50–300 m). Between-patch movements were more likely between patches that were close together. Scrub barriers reduced dispersal.

4. The probability of dispersal between two recaptures depended on the length of the time interval between them. *Coenagrion mercuriale* performed considerable between-patch movements within a small fraction (1–2 days) of its mean mature adult life span (7–8 days).

5. Qualitative comparison of field colonization distances measured here and distances between UK sites occupied by *C. mercuriale* revealed that empty sites within large clusters of sites would probably be recolonized rapidly and dispersal events would be frequent. However, such events would occur rarely within small isolated sites or clusters of sites, leaving local populations prone to extinction.

6. *Synthesis and applications.* These data show that management effort should be directed towards maximizing the likelihood of *C. mercuriale* recolonizing sites naturally within 1–3 km of other populations (particularly within large clusters). Scrub boundaries should be removed between existing populations and empty, but suitable, sites to facilitate stepping-stone dispersal movements.

Key-words: *Coenagrion mercuriale*, heathland, landscape connectivity, metapopulation

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Introduction

Dispersal is an undirected movement away from the natal habitat patch (den Boer 1990) and is a life-history trait that has profound consequences for populations, especially in fragmented habitat (Dieckmann, O'Hara

& Weisser 1999). Dispersal plays a vital role in both local and metapopulation dynamics (Thomas & Hanski 1997), determining the probability of colonization of empty habitat and the probability of extinction, via 'rescue effects' and 'genetic rescue' (Ingvarsson & Whitlock 2000; Ingvarsson 2001). A positive relationship has been demonstrated between dispersal rate and both local population and metapopulation persistence in model (Travis & Dytham 1999) and empirical systems (Thomas & Hanski 1997 and references therein).

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The relative costs and benefits of dispersal, at the level of the individual, will be determined by the size, spacing, quantity, quality and temporal variability of habitat within particular landscapes (Thomas 2000). Increased habitat fragmentation is likely to increase the *per capita* mortality rate of dispersal such that genes associated with dispersal are likely to be lost from isolated populations (Dieckmann, O'Hara & Weisser 1999), leading to non-random extinction of populations and species characterized by different levels of dispersal (Thomas 2000). Between 15% and 35% of individuals in some butterfly metapopulations are estimated to die between patches (Thomas & Kunin 1999; Hanski, Alho & Moilanen 2000). To quantify the costs and benefits of dispersal in a fragmented landscape, empirical data are required on key parameters of landscape connectivity such as habitat-specific movement rates (Pither & Taylor 1998) and on movement behaviours in different landscape structures (amount/configuration of suitable habitat; Wiens 1997).

Odonates have inherently patchy habitats (Conrad *et al.* 1999), being restricted to water in the egg and larval stages. Most of the mature adult life span is also spent at the breeding site. Flight is multifunctional in odonates, used both within patches for location of food, mates and oviposition sites and between patches for dispersal (Van Dyck & Matthysen 1999). Temporary emigration for roosting and maturation is common in female and immature odonates, yet the process of dispersal has been poorly documented in this group (Michiels & Dhondt 1991; Corbet 1999), leading some authors to suggest that between-patch movements are uncommon (Fincke 1982; Utzeri *et al.* 1984; Banks & Thompson 1985; Michiels & Dhondt 1991). However, at a local scale, newly created biotopes, such as artificial lakes, are rapidly colonized by eurytopic (species with wide habitat preferences) and vagile odonate species (Steytler & Samways 1995). At a broader scale, expansions in species' distributions have occurred in response to processes like deforestation and global warming (Sternberg, Buchwald & Röske 1999). This suggests that many odonates are capable of between-patch movement, even if such movements have not been directly observed. In view of this, and the considerable fragmentation of wetland biotopes (Foster 1991; Thomas 1991; Thomas & Morris 1995), direct investigation of between-patch dispersal in odonates is required (cf. Conrad *et al.* 1999), particularly in specialized species that are susceptible to biotope fragmentation (Steytler & Samways 1995).

The southern damselfly *Coenagrion mercuriale* (Charpentier) has a south-west European distribution but has declined in countries in the northern and eastern boundaries of its distribution, including Britain (Grand 1996). It is highly specialized, being restricted to two fragmented biotopes in Britain. These are small lowland heathland streams and ditches on old water meadow ditch systems on chalk streams. Within these biotopes, a requirement for a thermally advantageous

microclimate (e.g. use of unshaded, permanently flowing, small watercourses with perennial herbaceous aquatic vegetation) restricts the species further to patches of early successional habitat. Thus long-term regional persistence is likely to depend on metapopulation dynamics and insects occupying a shifting habitat mosaic (Thomas & Hanski 1997). The scale and timing of rotational habitat management for such early successional species (e.g. by rotational cutting or grazing) must be appropriate to the within-patch dispersal ability of the species in question (Usher & Jefferson 1991). This is of particular relevance to watercourses occupied by *C. mercuriale* on old water meadow ditch systems where selective rotational mowing or cutting of bank-side vegetation (Röske 1995) and hand clearance of channel vegetation (Strange 1999) is often carried out.

Given the patchy nature of habitat for this species and its status in Britain (rare in the *British Red Data Book*; Shirt 1987), this paper reports on an investigation of its dispersal ability using mark–release–recapture (MRR) data from two large heathland populations of *C. mercuriale*. The current state of knowledge of the habitat requirements of *C. mercuriale* is insufficient to permit accurate habitat mapping and assessment of the relative role of habitat area, habitat quality and isolation in determining patch occupancy in Britain (cf. Hanski, Kuussaari & Nieminen 1994). However, the extent of within- and between-patch dispersal in mature adults was examined in relation to the current spatial configuration of British sites (Fig. 1) to permit estimation of the likelihood of migration, colonization and extinction events in different parts of Britain. Furthermore, how dispersal is affected by those aspects of landscape connectivity that are influenced by heathland management regimes (i.e. interpatch distances, habitat type and scrub barriers) was assessed and an appropriate management strategy proposed.

Materials and methods

STUDY SITES

MRR surveys were carried out in 1997 at two sites, Glan-yr-afon Uchaf Stream, Mynydd Preseli, Pembrokeshire, UK (SN118345–SN118346) and Crockford Stream, Beaulieu Heath, New Forest, Hampshire, UK (SU3599) (hereafter referred to as Preseli and New Forest, respectively). The division of streams into sampled and unsampled habitat permitted the observation of both within- and between-patch movements as follows. Large MAIN stream patches of continuous suitable breeding habitat were designated, divided into subsections and searched daily for individuals. Around these MAIN patches and separated by unsuitable habitat, PERIPHERAL patches were searched daily (Fig. 2). At Preseli, the MAIN patch was 560 m long, divided into 19 subsections (15–50 m in length, 47 m on average) and surrounded in various directions by 14

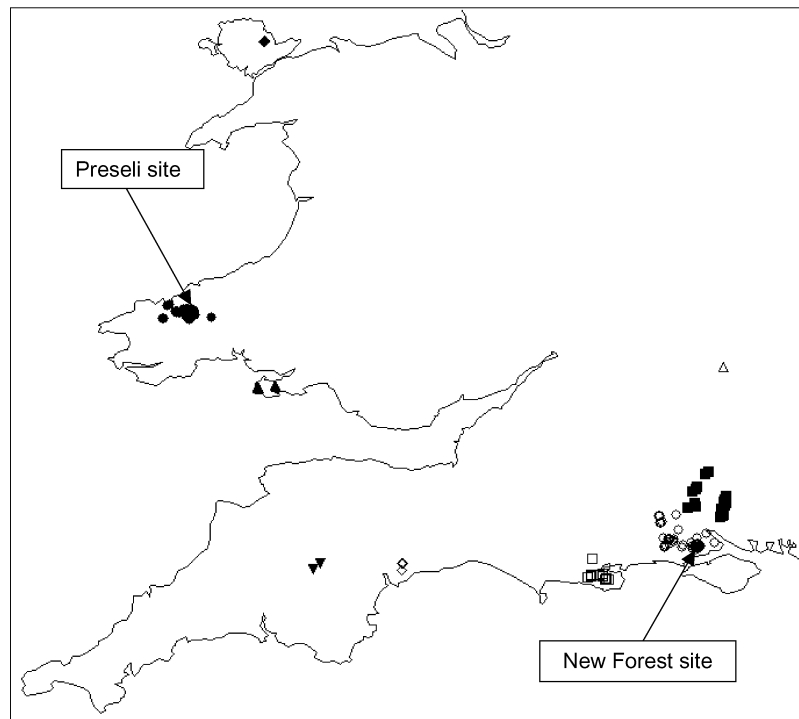


Fig. 1. Map of the UK showing sites, at a 100-m resolution, in which the southern damselfly has been recorded between 1990 and 2000. Arrows indicate the approximate location of the Preseli and New Forest study sites. Key to site clusters: closed circles, Pembrokeshire; open circles, New Forest Hampshire; closed squares, Itchen and Test Valley, Hampshire; open squares, Dorset; closed triangles, Gower; open triangles, Oxford; closed diamonds, Anglesey; open diamonds, Devon; inverted closed triangles, Dartmoor.

PERIPHERAL patches at distances of 60–800 m (Fig. 2a). At New Forest, there were two short MAIN patches (sites 1 and 2, each 300 m in length, divided into 12 × 25-m subsections and separated by a 220-m stretch of unsuitable stream) (Fig. 2b). Three PERIPHERAL patches were designated downstream on the same stream system. These were sites 3 (620 m from site 2, 1060 m from site 1), 4 (1090 m from site 2, 1470 m from site 1) and 5 (1190 m from site 2, 1560 m from site 1). At Preseli, habitat between MAIN and PERIPHERAL patches consisted of a mixture of valley mire and wet heath. At New Forest, intervening habitat consisted mainly of valley mire and wet heath, with some humid and dry heath. Extensive lengths of tall scrub boundaries separated all patches except 1 and 2. In sites occupied by *C. mercuriale*, scrub consists of small, stunted trees and shrubs and, on these heathlands, a mixture of bog myrtle *Myrica gale* L., gorse *Ulex gallii* Planchon and tree species (willow, birch, alder and oak).

MRR PROTOCOL

At the New Forest site, between 6 June and 31 July (flight period is late May to early August at this site), a 6-h mark–recapture exercise was performed daily in sites 1 and 2. Each subsection was searched (for both unmarked and marked individuals) for 15 min by walking along the stream. Unmarked *C. mercuriale* were captured using a standard insect net and marked individually by a combination of a number written on the

forewing (with indelible pen) and a dot of paint on the thorax. Sex, age (immature or mature adult) and subsection were noted and the individual was released in the middle of the subsection in which it had been found. Upon recapture, date and identity, location (including subsection) and age of individuals were noted. Mature adults seen for the first time were scored as being 1 day old (cf. Fincke 1982). Age was not calculated for mature adults marked on the first and second day of the study as they were unlikely to have been seen on the first day of their mature adult life span. Sites 3, 4 and 5 were searched intermittently for marked individuals throughout the season when field assistants were available.

At the Preseli site, between 10 June and 9 August, a 3-h mark–recapture exercise was performed daily, as described above, on the main study stream beginning at midday. The order in which the sections were searched was varied randomly. Most peripheral patches were searched every day for individuals although patches further away were searched less frequently.

STATISTICAL ANALYSES

Dispersal parameters were calculated (modified from Scott 1973) for all individuals marked in sites 1 and 2 at New Forest and those marked on the main stream section at Preseli as follows; net, unidirectional movement of an individual during its lifetime (L); distance between recapture n and recapture $n + 1$ of an individual

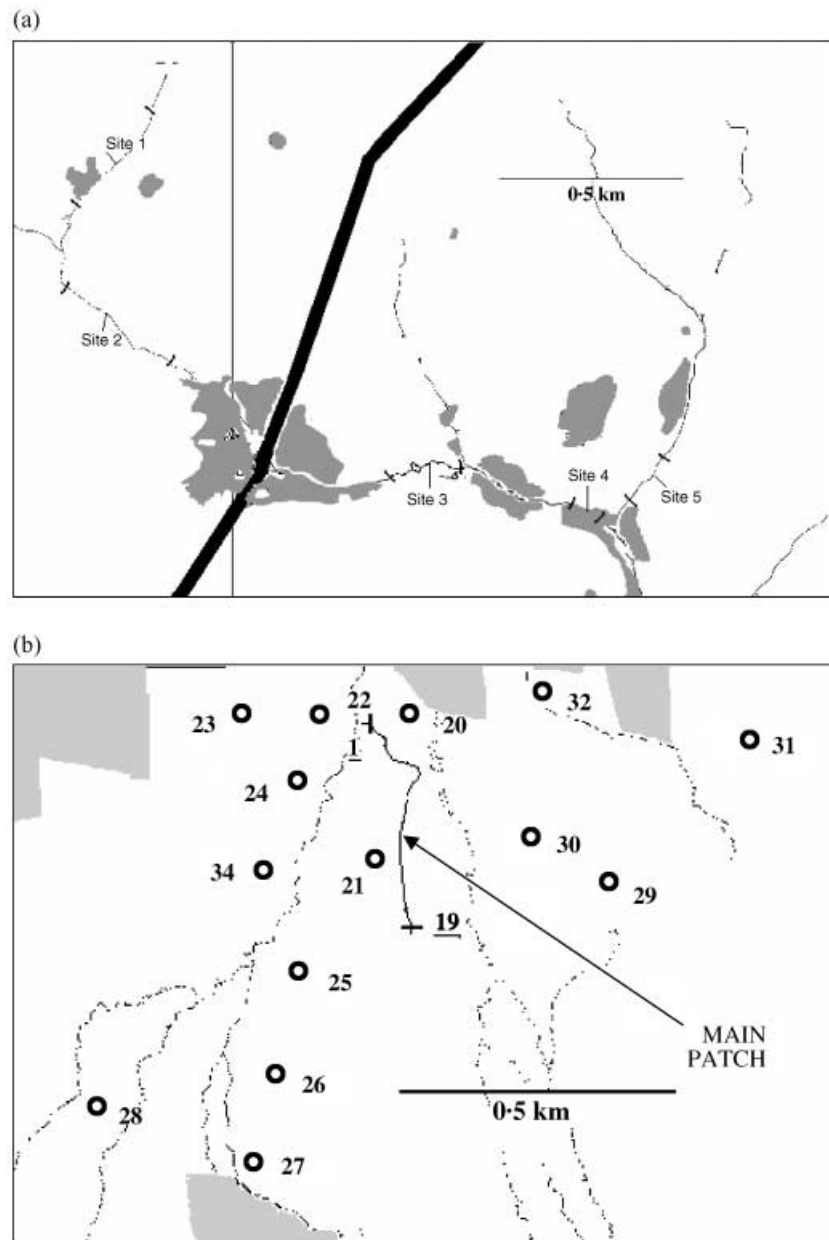


Fig. 2. Map of study stream systems at (a) the New Forest site, showing the extent of sampled sites 1–5 (limits indicated by short black lines across stream), scrub (grey shaded areas) and a road (black shaded area), and (b) the Preseli site, showing the extent of the MAIN patch (limits indicated by short black lines across stream, subsections 1–19), the PERIPHERAL patches (indicated by black rings 20–34) and farmland (grey shaded areas).

(d_n); time between recapture n and recapture $n + 1$ of an individual (t_n); velocity between recapture n and recapture $n + 1$ of an individual, i.e. d_n/v_n (v_n). The mean parameter values were calculated. The frequency of three types of movement, non-movements, within-patch movements (i.e. between subsections in a MAIN patch) and between-patch movements, were scored.

Conditional logistic stepwise regressions (Trexler & Travis 1993) were used to investigate the relationship between distance dispersed between two consecutive recaptures and the following independent variables: mid-point age during movement (AGE), mid-point day of season during movement (DAY), length of the interval in days (TIME) and order of movement (i.e.

first to fifth movement made by an individual; ORDER). A binary dispersal variable, $DIST_0$ was constructed where individuals were scored as 0 if they moved 0 m during the interval between two consecutive recaptures and 1 if they moved further than 0 m. Two more variables, $DIST_{50}$ and $DIST_{200}$, were constructed in the same way, with individuals scored depending on whether they moved at least 50 m or at least 200 m, respectively. Logistic regression analyses were performed with $DIST_0$, $DIST_{50}$ and $DIST_{200}$ as the dependent variables in turn and with AGE, DAY, TIME and ORDER as the independent variables. All movements (first to fifth) of all males from Preseli and New Forest were used.

The effect of the distance between pairs of sites on the probability that individuals will transfer between them was analysed as follows. In the New Forest, in MAIN sites 1 and 2, there were 276 possible pairwise combinations of subsections that could be distributed between 50-m distance categories. The presence or absence of transfers was scored for all possible combinations of subsections without distinguishing between the two possible directions of the transfers (from MRR results; data for males and females were combined). For each distance category, the proportion of pairs in the category in which transfers took place was calculated. This analysis was repeated at Preseli, on outward movements from the MAIN patch, distinguishing between transfers within the main stream patch (361 pairs) and transfers (247 pairs) from the main stream to peripheral sites. This facilitated investigation of whether transfers of a given distance were less likely to occur across unsuitable habitat.

Because habitat is divided into sampled and unsampled areas in MRR studies, short-distance movements will tend to stay within sampled habitat but longer distance movements are more likely to fall into unsampled areas (Stettmer 1996; R. Wilson, personal communication). We therefore performed a correction for this sampling bias on observed dispersal distances for New Forest. At New Forest, where sections of suitable habitat were well defined and approximately linear, observed frequencies of dispersal distances (for all recapture intervals of all individuals) were corrected by the theoretical probability of recapture (p_r) at each distance interval, i.e. the ratio of sampled vs. unsampled stream at each distance. In sites 1 and 2, there were 48 possible displacements from sites 1 and 2, 24 (number of stream sections) \times 2 (number of possible directions). Thus, p_r is the number of possible displacements that were recaptured in sampled habitat divided by the total number of possible displacements. For example, 16 of the 48 possible movements of 610 m from the 24 subsections in sites 1 and 2 resulted in an individual remaining in the sampled area, giving a p_r of 0.33 at 610 m. The corrected number of movements at each distance was found by dividing the observed actual number of movements by p_r .

Results

EXTENT OF WITHIN- AND BETWEEN-PATCH MOVEMENT, SHAPE OF THE DISPERSAL DISTRIBUTION

Mature adults marked numbered 2947 at New Forest and 1988 at Preseli. Of these individuals, 29.0% and 30.9% were recaptured at each site, respectively. Of the individuals at New Forest, nine (1.1%) moved between patches, 625 (78.6%) moved within patches and 161 (20.3%) did not change section. Of the individuals at Preseli, 75 (12.2%) moved between patches, 329 (53.7%) moved within patches and 209 (34.1%) remained in the

same patch. Thus in both sites the majority of individuals moved within the MAIN patch and the proportion of individuals not moving at all was substantial (20–47%). In both sites, most recaptured individuals dispersed over short distances but a few moved up to 1 km (maximum 1060 m at New Forest and 900 m at Preseli; Fig. 3). At New Forest, 57% of males and 59% of females were recaptured within 25 m of their marking site and only 2% of males and 4% of females moved further than 200 m. At Preseli, 43% of males and 39% of females were recaptured within 25 m of their original capture site and 9% of males and 14% of females moved further than 200 m. Individuals were capable of large movements in short time periods, e.g. 444 m in 1 day (Preseli male) and 610 m in 2 days (New Forest male).

AGE, SEASON AND TIME EFFECTS ON DISPERSAL

In movements 1–5 of males from both sites, length of time interval between recaptures (TIME) had a significant positive effect on the probability of detecting movements greater than 0 m, the probability of moving at least 50 m and the probability of moving at least 200 m in an interval (DIST₀, DIST₅₀, and DIST₂₀₀, respectively) in all stepwise logistic regression models. (In all models DIST = $1/1 + e^{-Z}$. Preseli: $Z_{\text{DIST}_{10}} = 0.052 \times \text{TIME} - 0.161$, model $\chi^2 = 5.5$, $P = 0.019$, 1 d.f., $n_0 = 312$, $n_1 = 355$; $Z_{\text{DIST}_{50}} = 0.101 \times \text{TIME} - 1.183$, model $\chi^2 = 15.6$, $P < 0.001$, 1 d.f., $n_0 = 511$, $n_1 = 126$; $Z_{\text{DIST}_{200}} = 0.150 \times \text{TIME} - 3.952$, model $\chi^2 = 11.9$, $P < 0.001$, 1 d.f., $n_0 = 612$, $n_1 = 25$. New Forest: $Z_{\text{DIST}_{10}} = 0.149 \times \text{TIME} - 0.092$, model $\chi^2 = 46.7$, $P < 0.001$, 1 d.f., $n_0 = 388$, $n_1 = 694$; $Z_{\text{DIST}_{50}} = 0.140 \times \text{TIME} - 1.194$, model $\chi^2 = 56.7$, $P < 0.001$, 1 d.f., $n_0 = 716$, $n_1 = 366$; $Z_{\text{DIST}_{200}} = 0.222 \times \text{TIME} - 5.352$, model $\chi^2 = 26.6$, $P < 0.001$, 1 d.f., $n_0 = 1064$, $n_1 = 18$.) AGE, DAY of season and ORDER did not have a significant effect on distance moved in an interval.

EFFECTS OF LANDSCAPE STRUCTURE ON DISPERSAL

A significantly greater proportion of individuals moved between patches at Preseli in comparison with within patches and non-movements (males and females combined; $\chi^2 = 128.5$, $P < 0.001$, 2 d.f.; Fig. 4). At New Forest, three out of nine between-patch movements occurred across a scrub barrier and six occurred across an unsuitable stream. No movements occurred through scrub between sites 3, 4 and 5 even though they are relatively close together. At Preseli, between-patch movements occurred in several different directions and the majority of transfers involved movement from a peripheral patch to the main stream section (45/71). More dispersal of an intermediate distance occurred at Preseli (Fig. 3 and Table 1; males $Z = 2.50$, $P < 0.001$; females $Z = 1.25$, $P = 0.045$).

There was a negative correlation between the distance category (mid-point) and the proportion of pairs

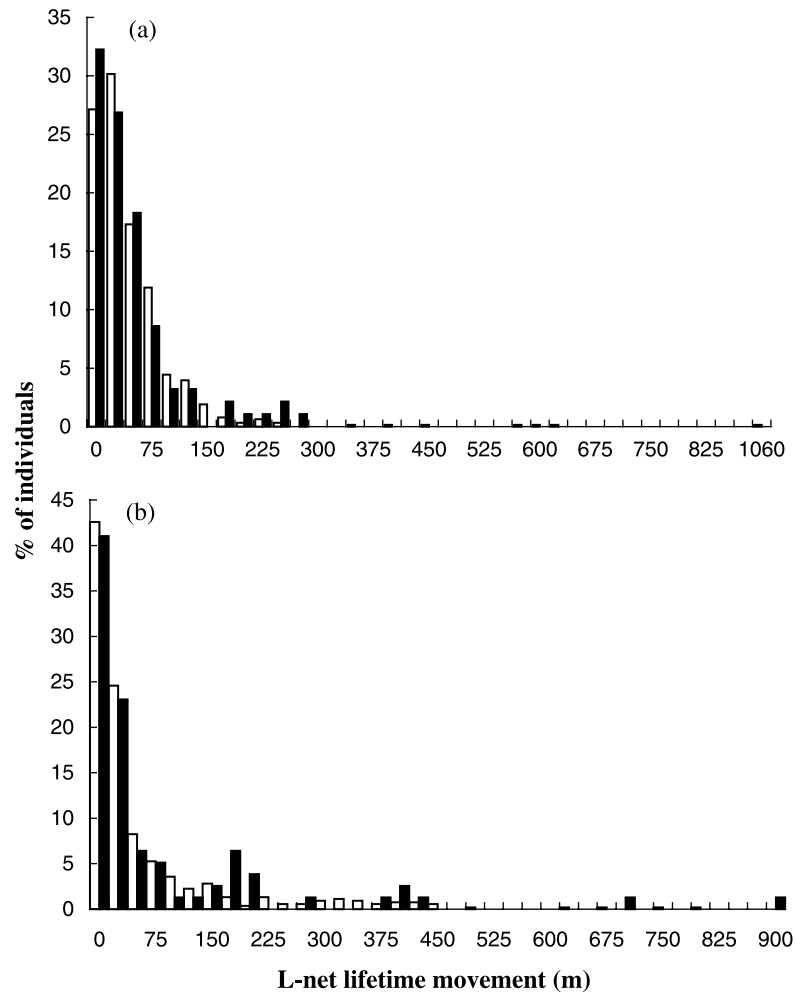


Fig. 3. Percentage distribution of net lifetime movements (L) for males (open bars) and females (closed bars) at (a) New Forest and (b) Preseli. In both sites, most recaptured individuals dispersed over short distances but a few moved up to 1 km.

Table 1. Mean \pm SE of net lifetime movement (L), distance (d_i), time (t_i) and velocity (v_i) of movement between the first two recaptures for males and females at both sites

Parameter	New Forest		Preseli	
	Males	Females	Males	Females
L	48.1 \pm 3.0	46.2 \pm 6.2	69.6 \pm 4.9	98.6 \pm 18.3
d_i (m)	38.2 \pm 2.0	43.8 \pm 5.4	–	–
t_i (days)	3.7 \pm 0.1	4.4 \pm 0.3	4.5 \pm 0.2	5.6 \pm 0.5
v_i (m day ⁻¹)	14.9 \pm 0.7	16.3 \pm 2.9	18.2 \pm 1.4	21.2 \pm 3.9

in the category between which transfers occurred (Fig. 5), suggesting that transfers were more likely between pairs of sites that were close together (New Forest, transfers between sites 1 and 2, Spearman's $r_s = -0.835$, $P < 0.001$, $n = 16$; Preseli, transfers to other main stream sections, $r_s = -0.865$, $P < 0.001$, $n = 11$, transfers to peripheral sites, $r_s = -0.748$, $P < 0.001$, $n = 18$).

Transfers were not more likely within the main stream patch than between patches to peripheral sites at long distances (distance categories between 300 and 599 m) at Preseli ($\chi^2 = 1.74$, $P = 0.181$, 1 d.f.). However, transfers at short (50–149 m; $\chi^2 = 5.10$, $P = 0.024$,

1 d.f.) and medium (150–299 m; $\chi^2 = 10.31$, $P = 0.001$, 1 d.f.) distances were more likely to occur within the main stream patch than between patches. At Preseli, transfers from the main patch to peripheral patches were more likely than transfers in the opposite direction ($\chi^2 = 5.92$, $P = 0.023$, 1 d.f.).

EFFECT OF A CORRECTION FOR SAMPLING BIAS ON DISPERSAL DISTANCES

The mean of observed movements was 38.5 \pm 2.0 m while the mean of movements corrected for bias was 57.9 \pm 2.7 m. The percentage of movements of 0–50 m was decreased by this correction but the percentage of movements at all other distance categories was increased (Fig. 6). The percentage of movements of 1 km or more increased from 0.09% to 0.25%, suggesting that three such movements, not one, would have occurred in this study population in 1997. There was a substantial increase in the mean net lifetime movement for both males ($\mu_{\text{observed}} = 41.2 \text{ m} \pm 3.4$; $\mu_{\text{corrected}} = 61.8 \text{ m} \pm 4.6$) and females ($\mu_{\text{observed}} = 41.2 \text{ m} \pm 6.6$; $\mu_{\text{corrected}} = 69.9 \text{ m} \pm 8.8$) that were only recaptured once, when corrected in the same way.

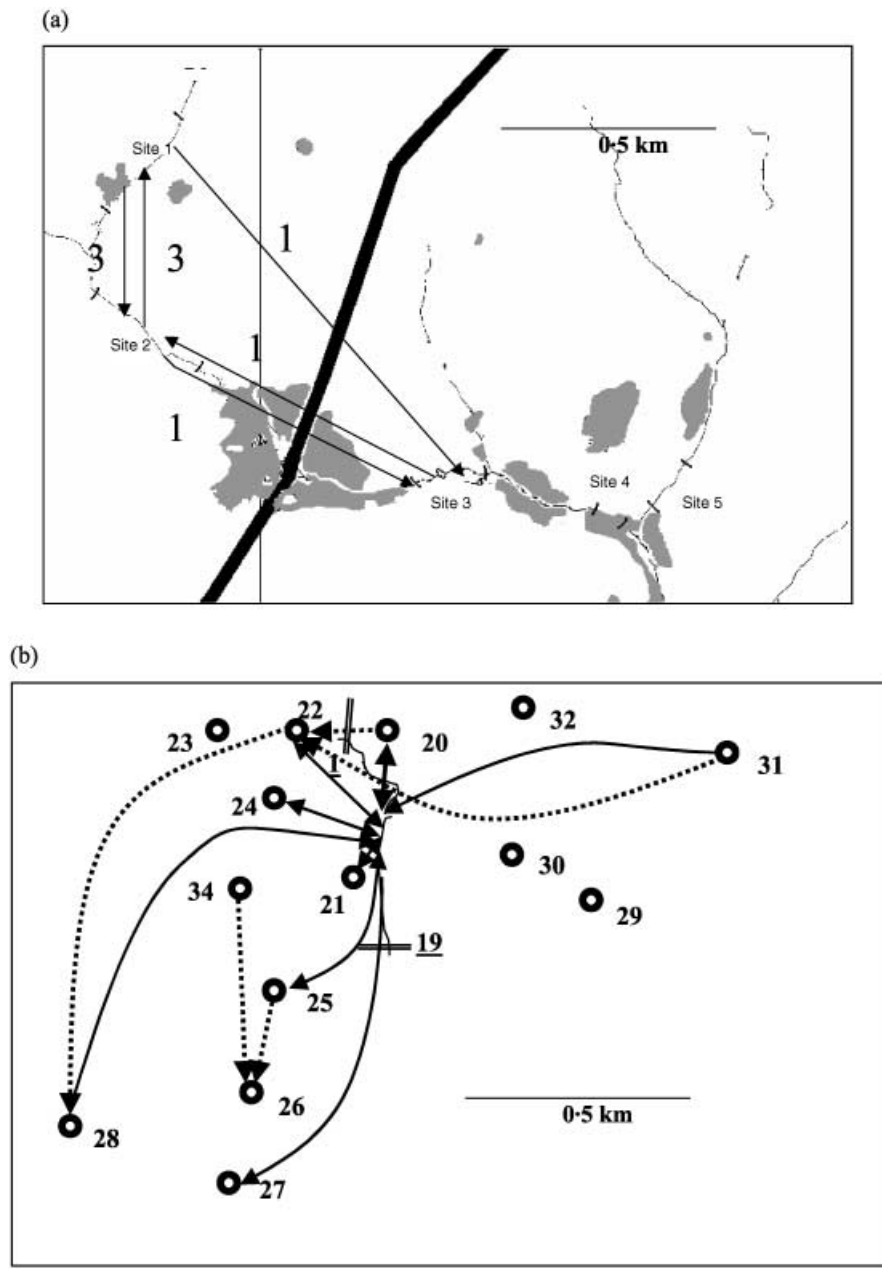


Fig. 4. Map of study stream systems showing the location and direction of the between-patch movements at (a) New Forest and (b) Preseli; solid arrows indicate movements between the MAIN patch and PERIPHERAL patches whilst broken arrows indicate movements between PERIPHERAL patches. At Preseli, there were more between-patch movements, more intermediate distance dispersal and movements occurred in more different directions than in the New Forest.

Discussion

WITHIN- AND BETWEEN-PATCH MOVEMENT AND SHAPE OF DISPERSAL DISTRIBUTION

The *C. mercuriale* populations examined here showed more extensive dispersal than in previous studies. In a south-west German population, 96% of individuals remained within 25 m of their original location (vs. 20–47% found here); maximum within- and between-patch dispersal distances were 170 m and 300 m, respectively (Hunger & Röske 2001), vs. 610 m and 1060 m in the New Forest. If the scale over which dispersal is measured is smaller than that at which organ-

isms move, then dispersal distances are underestimated (W. Koenig cited in Dieckmann, O’Hara & Weisser 1999). The maximum distance between sampled patches in the German population was only approximately 600 m (Hunger & Röske 2001), vs. 800 m (Preseli) and 1560 m (New Forest) in our study populations. The disparity in observed mobility between this study and the German one probably arises due to our larger sample size of individuals, longer duration and larger distances between and within sampled patches.

Because *C. mercuriale* flies weakly and close to the vegetation in comparison to other blue damselflies, previous authors have suggested that this species has poorer dispersal ability (Winsland 1997). However, a

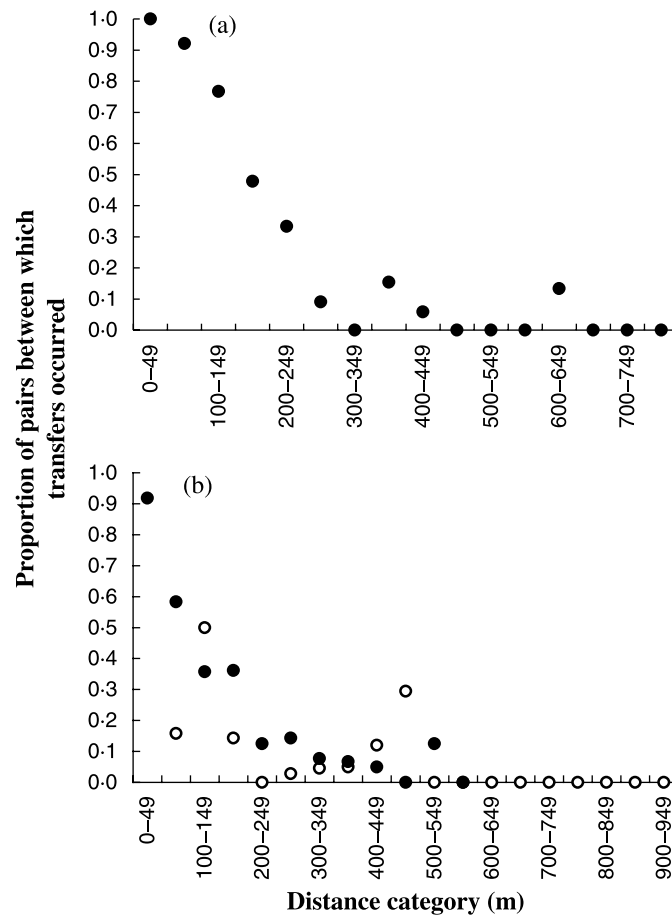


Fig. 5. Proportion of pairs of patches between which transfers were observed for each distance category at (a) New Forest for individuals from sites 1 and 2, and (b) Preseli for individuals from the main stream section; closed circles indicate transfers within the main patch, open circles indicate transfers from the main patch to peripheral sites. Dispersal was more likely between patches that were closer together at New Forest (a) and within rather than between patches at Preseli (b).

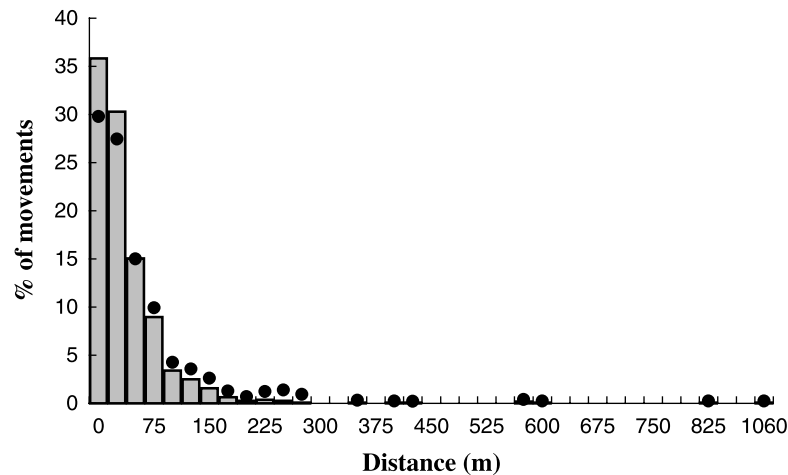


Fig. 6. Percentage distribution of movements of different distances for observed data from New Forest (grey bars) and data corrected for the theoretical probability of recapture at that site (closed circles).

between-patch movement rate of 11.4% in males of *C. mercuriale* at Preseli was comparable to that of similarly sized odonates such as *Ischnura elegans* (11%), *Enallagma cyathigerum* (11%) and *Coenagrion puella* (16%) derived in a pond system with similar interpatch distances (Conrad *et al.* 1999).

AGE, SEASON AND TIME EFFECTS ON DISPERSAL

Coenagrion mercuriale was capable of moving considerable distances between patches in short periods of time (1–2 days) that constituted a small fraction of the

mean mature adult life span of individuals (7–8 days). While *C. mercuriale* moved about 0.5 km in 1 or 2 days, larger zygoptera such as *Calopteryx splendens* and *Calopteryx virgo* (Stettmer 1996) move around 1 km in the same time period. Due to sparse recapture data for particular individuals, the time interval between recaptures did not explicitly reflect the time taken for a movement. However, despite this, the time interval rather than date or age of individual was a significant predictor of the probability of moving more than 0, 50 or 200 m. As both sexes reproduce throughout their mature adult life spans and dispersal occurs in a relatively short time, individuals should be able to reproduce during and after dispersal. Therefore, they may make a genetic contribution to patches other than the natal patch during their life span.

No age bias in dispersal has been found in mature adult *C. mercuriale*. However, it has been suggested that odonate dispersal occurs in the immature adult stage that temporarily emigrates away from the breeding site during maturation and often performs a 'maiden flight' immediately after emergence (Parr 1976; Henderson & Herman 1984; Utzeri *et al.* 1984). Recapture rate of immatures was too low to assess dispersal during this stage in *C. mercuriale*, but Conrad *et al.* (1999) found no difference in dispersal between immature and mature adults in 11 pond-dwelling odonates. Larval dispersal has been observed in some stream-dwelling invertebrates (Bilton, Freeland & Okamura 2001) although the highly sparse distribution of suitable habitat for *C. mercuriale* along stream systems (B.V. Purse, personal observation) makes such a mechanism unlikely in this species.

LANDSCAPE EFFECTS ON DISPERSAL AND THE EFFECT OF A CORRECTION FOR SAMPLING BIAS

At both sites, there was a significant correlation between the probability of dispersal and distance between pairs of sites for both within- and between-patch movements. Similarly, Conrad *et al.* (1999) found that the greatest number of dispersal events occurred between the two ponds that were closest together in their study system. Thus, it is expected that for *C. mercuriale*, as with many species of butterflies (Thomas & Hanski 1997; Baguette, Petit & Queva 2000), isolation will negatively affect patch occupancy (with regards to both colonization of empty habitat and population persistence). Indeed, Röske (1995) found that, in the Upper Rhein region, a high proportion of population extinctions of *C. mercuriale* occurred in regions that were isolated from other populations and suggested that reintroduction may be unsuccessful in such areas.

The habitat between locations seemed to influence dispersal at short to medium distances as, at Preseli, movements within the stream were more likely than between-patch movements at a particular distance

category. This suggests that the valley mire habitat between patches constituted a greater barrier to dispersal than continuous stream habitat. Habitat-specific movement rates have been found in other odonates. Pither & Taylor (1998) found that *Calopteryx maculata* moved more rapidly from breeding streams through neutral, pasture habitat than through forest habitat that was used for foraging. The medium-scale, habitat-specific movement behaviour of this, and a sympatric species, *Calopteryx aequabilis* has been used to predict its broader scale distribution patterns across heterogeneous landscapes (Jonsen & Taylor 2000).

Scrub boundaries seemed to prevent dispersal, with only a small number of between-patch movements occurring across them at the New Forest. Emigration rate should be examined experimentally in a range of patches or streams differing in their proportion of boundary covered by scrub or tall vegetation (cf. Kuusaari, Nieminen & Hanski 1996).

When the New Forest data were corrected for the theoretical probability of recapture at each distance, the probability of movements of more than 1 km increased from 0.09% to 0.25% of movements and the mean movement increased from 39 to 58 m. Stettmer (1996) similarly found that such a correction increased estimates of mean movement in two calopterygid species, from 135 to 189 m. Thus the configuration of sampled and unsampled habitat influences the detectability of dispersal, and differences in the rate of dispersal observed between the two sites in this study could arise either from differences in landscape connectivity between sites or in the configuration of sampled and unsampled habitat.

COENAGRION MERCURIALE IN BRITAIN AND COLONIZATION DISTANCES

Coenagrion mercuriale has a low rate of movement within continuous areas of habitat (average < 25 m), low emigration rates (1.3–11.4%) and low colonization distances (approximately 1 km). Actual colonization distances in *C. mercuriale* are probably greater than field-observed maximum dispersal distances due to the bias against observing long-distance dispersal events. A mismatch is often found between field estimates of long-distance dispersal and indirect evidence from colonization events in butterflies (Hill, Thomas & Lewis 1996; Lewis *et al.* 1997; Gutierrez, Thomas & Leon-Cortes 1999). Indeed, individuals of *C. mercuriale* have been found up to 3 km away from the closest known reproductive habitat in Germany (Hunger & Röske 2001) and colonization events are suspected to have occurred at two sites in Hampshire, UK, Horsebush Bottom (Jenkins 2001) and Roundhill (B.V. Purse, personal observation), that were 0.5 km and 2.7 km, respectively, away from source populations.

Extant British *C. mercuriale* sites fall into nine clusters separated by distances of 25–152 km (Purse 2001; Fig. 1). In the five smallest clusters of extant British *C.*

Table 2. Number of 100-m grid reference points, percentage of points with a neighbouring point within 1 km and 3 km and mean of isolation indices across the points within each large cluster of *C. mercuriale* sites. Up-to-date six-figure grid reference biological records of *C. mercuriale* presence were taken to indicate population extent in each cluster. The isolation index for a grid reference point is the mean of the distances between it and each of its 10 nearest neighbours (from Purse 2001)

Cluster	No. of points	% of points that have a neighbouring point		Mean (\pm SE) isolation index of points (km)
		Within 1 km	Within 3 km	
Dorset	7	43	100	3.97 \pm 0.25
New Forest	41	60	80	4.59 \pm 0.52
Itchen and Test Valley	35	85	100	2.24 \pm 0.44
Pembrokeshire	160	90	95	0.52 \pm 0.06

mercuriale, two populations are generally separated by distances that exceed the maximum field colonization distances observed in this study. In the four largest clusters of *C. mercuriale* sites, most populations have neighbouring populations within 3 km (Table 2), and between 43% and 100% of populations had neighbouring populations within 1 km. Thus populations in large clusters are much less isolated due to a high density of populations. There is a high probability that sites that became empty in these large clusters would be rapidly recolonized and dispersal events would be frequent, even though field-observed colonization distances are only 1 km. In the five small isolated clusters, dispersal and colonization events would occur rarely (and only if actual colonization distances are larger than field-observed distances) and the *per capita* mortality of dispersers would be high. Thus in the latter, the risk of population extinction would be increased because several dispersal events may be required to 'rescue' populations from stochastic or genetic extinction. Wide variation in population numbers and bottlenecks increase the extinction risk due to inbreeding depression in small populations unless alleviated by very high population numbers, which may only be provided by an influx of dispersers (Dunham *et al.* 1999). Indeed, in butterfly systems, Thomas & Hanski (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. Between-population variation in dispersal rates may be observed within a species due to variation in landscape connectivity but also because the local populations densities determine the absolute number of migrants (Lewis *et al.* 1997; Gutierrez, Thomas & Leon-Cortes 1999). In some parts of the UK there are small clusters of small populations of *C. mercuriale*, and in these clusters the frequency of dispersal events may be more limited due to a lower absolute number of migrants.

MANAGEMENT TO FACILITATE DISPERSAL IN *C. MERCURIALE*

Many of the species action plans for rare British invertebrates, including that for *C. mercuriale*, contain the following two actions relating to colonization events: the encouragement of the natural spread of a species

through appropriate management of former sites or sites adjacent to extant sites, and reintroduction of a species to such sites (HMSO 1994; <http://www.ukbap.org.uk/>).

The relative effectiveness of these two strategies for conservation for a focal species will depend on the life-history characteristics, including dispersal ability (Néve *et al.* 1996; Schultz 2001), on the degree to which particular metapopulations are fragmented and on whether sufficient information is available about such characteristics. For example, in butterflies Oates & Warren (1990) found that reintroductions rarely succeed in the long term particularly in single or small groups of habitat patches. The success of reintroduction attempts depends on metapopulation structure (Néve *et al.* 1996; Thomas & Hanski 1997). It is least successful for butterflies with an open population structure because the limited number of released individuals tends to disperse and suffer high *per capita* mortality before reaching a suitable habitat patch. If the focal species is sedentary, the reintroduction would lead to the establishment of very few colonies (Thomas, Thomas & Warren 1992). Specialist species with intermediate dispersal tendencies, like *Procllossiana eunomia* (Néve *et al.* 1996) and *C. mercuriale*, may suffer a lower *per capita* mortality due to dispersal from an introduced population and colonization events may be more frequent. However, small sites should be protected, in addition to large core sites, to facilitate stepping-stone processes and recolonization. Such stepping-stone movements have allowed some butterfly species to colonize sites at greater distances than their maximum single dispersal distances (Thomas, Thomas & Warren 1992; Lewis *et al.* 1997). Indeed, in most cases the largest and highest quality and least isolated patches should be targeted for reintroduction or management (Thomas & Hanski 1997).

To maximize the chances of successful reintroduction, species-specific empirical data are required on the relative fitness of individuals of differing provenance in the empty habitat (Webb & Pullin 1996; Nicholls & Pullin 2000; Hamilton 2001; Wilkinson 2001). For example, we need to know how many individuals should be released to compensate for high dispersal mortality, to enable females to be multiply mated to increase fecundity (Reinhardt & Kohler 2000) or to

facilitate the 'rescue effect' and 'genetic rescue' (Ingvarsson & Whitlock 2000; Ingvarsson 2001).

Such information is not currently available for *C. mercuriale* and limited numbers of individuals are available for release attempts. In small site clusters suitable habitat is so fragmented that reintroduction will not lead to the establishment of stable populations. It is recommended that current management effort be directed instead towards maximizing the likelihood of natural colonization events within larger, less fragmented site clusters. This could be achieved by active management of empty habitat patches within 1–3 km of other populations (particularly within large clusters of sites) in as many different directions and distances from source populations as possible. Scrub should be removed (with the retention of some shelter) between populations and also between resource patches (e.g. roosting and breeding areas) within a patch. As well as removing barriers to dispersal, scrub removal has led to dramatic increases in population size on several British *C. mercuriale* sites (Purse 2001). Increases in population abundance act as a buffer against extinction through stochastic events or inbreeding depression, and increase the absolute number of potential dispersers within a system.

Such active management should not generally conflict with the requirements of other species on heathlands. The creation of increased areas of sunlit streams generally favours stenotopic odonate species (Steytler & Samways 1995). In lowland heathland restoration, scrub and bracken removal are commonly used to maintain an early seral stage in heathland succession, increasing habitat for a range of vertebrates and invertebrates including common lizard *Lacerta vivipara*, nightjar *Caprimulgus europaeus*, woodlark *Lullula arborea* and Dartford warbler *Sylvia undata* (Bacon 1998; Kirby 1992), although a mosaic of seral stages should ideally be maintained (Usher & Jefferson 1991).

Where possible, the habitat between populations and resource patches within sites should be managed as valley mire or wet heath because these may be more conducive to stepping-stone dispersal than grassland or dry heath found between many sites. Control of vegetation growth and water levels on all sites will maximize the area of suitable habitat and maintain the temporal stability of the habitat (Purse 2001). This study provides evidence of the impact on dispersal estimates of the scale over which dispersal is measured and illustrates the importance of correcting for theoretical probability of recapture within particular patch configurations when comparing dispersal estimates between studies. Further empirical data are required on habitat-specific movement rates and resource use in *C. mercuriale* to determine what type of management will facilitate movement between resource patches in both heathland and chalk stream populations. When a detailed habitat definition has been obtained for *C. mercuriale* in Britain, spatially explicit modelling of

habitat occupancy in relation to habitat area (and quality) and isolation would be beneficial. Maximum likelihood methods devised by Hanski, Alho & Moilanen (2000) for use with capture histories from multisite mark–recapture studies should be applied to estimate mortality within a patch and mortality during dispersal separately. The use of population-specific molecular markers has proved essential in determining the actual frequency of dispersal between populations of a range of freshwater invertebrates (Bilton, Freeland & Okamura 2001) and would be applicable to dispersal in *C. mercuriale*.

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