



Damselflies use different movement strategies for short- and long-distance dispersal

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Abstract. 1. Dispersal is an important process for any organism, but especially for endangered species in fragmented landscapes. To enhance the dispersal of a certain species, connectivity measures are implemented, which require knowledge on the species' dispersal behaviour and habitat. It is often assumed, that the preferred reproductive habitat of a species is also used as the main dispersal habitat. Although this assumption has often been confirmed, there are also cases where it has been disproved.

2. With a combination of a mark-resight study and genetic analysis conducted in a fragmented agricultural landscape in Switzerland, the dispersal habitats of the threatened damselfly *Coenagrion mercuriale* were analysed for different distance classes. In addition, maximum dispersal distances were estimated.

3. The mark-resight study detected movement over short distances (≤ 500 m) mainly within the reproductive habitat of *C. mercuriale* (i.e. streams).

4. In contrast, the genetic study detected both short- and long-distance dispersal. Short-distance dispersal occurred along streams, and discontinuity of streams hindered dispersal. Long-distance dispersal was suggested to happen along more or less straight lines and crossing agricultural land. Genetic analysis also showed that populations were well connected and that few individuals dispersed over larger distances (≤ 4500 m).

5. Our study showed that connected reproductive habitat enhanced short-distance dispersal in *C. mercuriale*. Although short-distance dispersal occurred frequently, long-distance dispersal was rare, but important to connect more isolated populations. Therefore, it would be relevant to differentiate between these two dispersal types when planning connectivity measures.

Key words. *Coenagrion mercuriale*, conservation, dispersal, dispersal types, gene flow, landscape genetics, mark-recapture, Odonata.

Introduction

Dispersal and gene flow are important processes for a species' long-term survival, especially in fragmented landscapes. In particular, threatened and sedentary species, such as many damselflies (Rouquette & Thompson, 2007a; Allen & Thompson, 2010), suffer from the negative effects of landscape fragmentation. Studying the dispersal of such species, is therefore of importance in conservation

management, as it provides essential knowledge for the implementation of connectivity measures, such as maximum dispersal distances or the identification of landscape elements hindering or facilitating dispersal (Segelbacher *et al.*, 2010). The landscape elements used by an organism during dispersal are often referred to as dispersal habitat (e.g. Reunanen *et al.*, 2000; Revilla & Wiegand, 2008). Dispersal habitat is thus the habitat type(s) through which a species disperses. It is not necessarily the same as the reproductive habitat, that is the habitat type in which the species reproduces (e.g. Palomares *et al.*, 2000).

Dispersal can be defined as 'the active or passive attempt to move from a natal or breeding site to another

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breeding site' (Clobert *et al.*, 2009) and usually is a result of different types of movements. Most important are the following (i) routine movements among resting, mating and feeding sites, which coincidentally result in dispersal or (ii) directed intended movements to new sites (Van Dyck & Baguette, 2005; Baguette & Van Dyck, 2007; Delattre *et al.*, 2010). Previous mark-recapture studies on damselflies reported that routine movement mainly occurs across short distances and that these movements are bound to the species' reproductive habitat. In contrast, movement across larger distances does not seem to be restricted to the reproductive habitat in damselflies. In *Calopteryx splendens* and *C. virgo* (Stettmer, 1996; Ward & Mill, 2007) home-range movement was only observed within the reproductive habitat (i.e. streams), but this was not the case for long-distance movement (Stettmer, 1996). Purse *et al.* (2003) observed similar patterns in *C. mercuriale* (Charpentier 1840, Odonata: Coenagrionidae) at a site with a stream of 560 m length surrounded by several peripheral streams at distances of 60–800 m. Movements over short distances (<300 m) predominantly occurred along streams, whereas for larger distances (>300 m), along stream and across-land movements were equally likely. Also Hunger and Röske (2001) only recorded movement in *C. mercuriale* along streams whereas long-distance movement was not observed at all.

To measure dispersal and gene flow, both direct and indirect methods can be applied (Clobert, 2001). Direct methods, for instance mark-recapture/resight studies or radio tracking (Vinatier *et al.*, 2010), assess actual movement events. While mark-recapture studies reconstruct movement by assessing the presence or absence of marked individuals at different locations, radio tracking directly tracks movement paths. Yet, it remains difficult to track immature individuals, which might disperse across larger distances and it is often not known whether the observed movement also results in mating and gene flow. Furthermore, direct methods require a large number of tracked individuals to detect rare long-distance dispersal events (Allendorf & Luikart, 2007; Hassall & Thompson, 2012). But, these rare events are especially important to maintain connectivity between distant populations and for (re)colonisations of suitable sites. In contrast, most indirect genetic methods (e.g. using pairwise F_{ST} -values) represent historic or recent gene flow and only assess dispersal events that result in mating and gene flow. As genetic methods are able to detect long-distance dispersal events, they have been suggested to complement studies using direct methods (Watts *et al.*, 2004a; Keller *et al.*, 2010).

Various factors have been identified to affect long-distance dispersal in damselflies. Firstly, morphological adaptation in the form of increased forewing length can be found in long-distance dispersing individuals, as, for instance, found for males of *C. puella* (Conrad *et al.*, 2002). A study on *C. maculata* found that morphology as well as movement distance are linked to habitat configuration: compared to individuals in a continuous habitat,

individuals in a fragmented habitat, where foraging habitats were distant from the reproductive habitat, had a more mobile morphology (i.e. increased wing length and width) and moved across a larger area (Taylor & Merriam, 1995). Furthermore, parasites like mites, for instance, can increase individual movement distances (i.e. parasitised individuals move over larger distances than unparasitised), as shown for populations of *Ischnura pumilio* (Allen & Thompson, 2010) and *I. elegans* (Conrad *et al.*, 2002). But, movement behaviour in fragmented landscapes has not been studied for most damselfly species. For instance in *C. mercuriale*, most movement studies have been carried out in more or less continuous habitat (Hunger & Röske, 2001; Purse *et al.*, 2003; Rouquette & Thompson, 2007b), and few long-distance movement events up to 1790 m along streams have been recorded in this species (e.g. Rouquette & Thompson, 2007a).

This study investigated the dispersal of *C. mercuriale* in a highly fragmented agricultural landscape of the Swiss plateau. With a combination of a mark-resight study and genetic analysis we (i) examined whether dispersal mainly occurred within *C. mercuriale*'s reproductive habitat or whether it depended on other landscape elements at various distances. Furthermore, we (ii) estimated maximum dispersal distances.

Materials and methods

Study area

Our study area was located in the Oberraargau region of Switzerland around the town of Langenthal (Fig. 1). The area is dominated by intensive agriculture. Therefore, many of the remaining natural or semi-natural habitats are highly fragmented. Nevertheless, the area is part of the Swiss Smaragd network. Smaragd aims to protect threatened and rare animal and plant species as well as their habitats and is the Swiss equivalent to the Natura 2000 framework of the European Union (Delarze *et al.*, 2003; Hedinger, 2009). In the Oberraargau, many streams, ditches and their verge vegetation form habitats for numerous species, like the threatened damselfly *C. mercuriale* that inhabits slow-flowing, calcareous, summer-warm streams and ditches (Sternberg *et al.*, 1999). In Switzerland, the species is categorised as critically endangered (Gonseth & Monnerat, 2002). Within the Smaragd framework, all populations of *C. mercuriale* have been recorded in 2008 by checking all potentially suitable streams throughout the region (Hepenstrick, 2008). Since 2009, populations and nearby, unoccupied streams are monitored yearly for census population size (i.e. by counting all present individuals) and new colonisations. Census population sizes fluctuated moderately during the last few years, one population became extinct because of a dried stream, and (re-)colonisation events of unoccupied streams up to about 1.2 km have

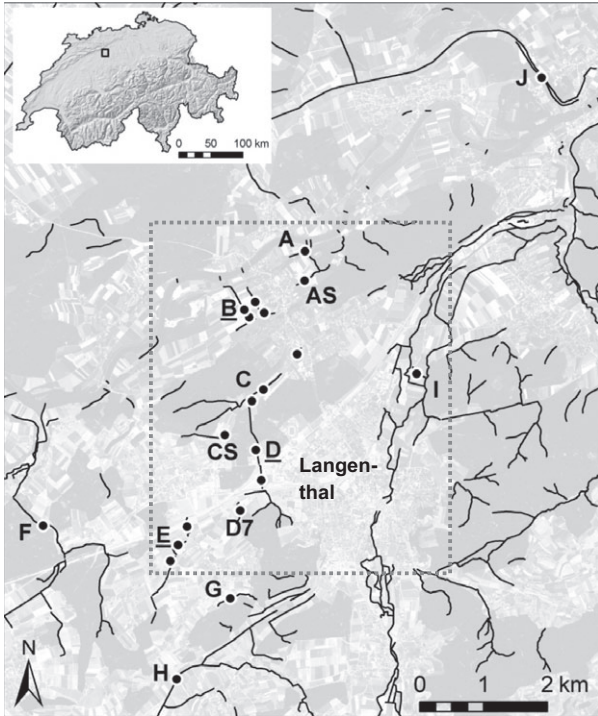


Fig. 1. Populations of *Coenagrion mercuriale* (A–J) in the Oberargau region in Switzerland (square in the inset). Solid lines represent above-ground streams. The dashed line shows the area surveyed in the mark-resight study, and underlined letters represent marking sites. Genetic samples were collected in all populations.

been observed (C. Forrer, Büro. Kappeler, unpubl. data). In 2009, when we conducted this study, *C. mercuriale* was found at 13 sites (Fig. 1). Eight central streams (sites A, B, C, CS, D, E, I) harboured at least 30 counted males. We counted males by walking (max. 1 h) along each section of uninterrupted stream of maximally 250 m length at peak-flying season. Five peripheral or even newly colonised streams had smaller populations with <30 counted males (sites AS, F, G, H, J). Distances between adjacent sites ranged from 400 m to 4500 m. Within the Smaragd project, several conservation measures, in addition to basic maintenance of streams, were implemented to preserve the populations of *C. mercuriale*. The corresponding management concept recommends extensively managed meadow strips (min. 6 m in width) on either side of streams and adaptation of mowing regimes, including weed control in stream beds using basket mowers.

Mark-resight study

A mark-resight study was conducted at peak-flying season of *C. mercuriale* (mid-June to end of July 2009) in the central part of the study area (dashed square in Fig. 1). This area of about 30 km² included nine stream

systems, which were at least 500 m apart from each other. Maximum length of more or less uninterrupted stream habitat was about 700 m. Individuals flying within an uninterrupted habitat stretch were defined as a local population. Damselflies were caught with an insect net. We only marked male damselflies, because numbers of females at streams were generally low. Individuals were marked on front wings with coloured points on four different wing positions (left-right, basal-apical) at three sites with large populations (sites B, D, E; Fig. 1). In total, 455 males were individually marked on their wings with coloured dots applied with Edding 4000 deco marker pens. Every day with suitable weather for damselfly flight was used to either mark or resight individuals. Marking was done during three periods: June 13–14, June 21–24 and July 9–10. All other days were used for resighting marked individuals using close-focussing binoculars in the following way: all inhabited stream sections in the central part of the study area (Fig. 1; dashed square) were searched for marked individuals once every third day with good weather conditions. Stream sections where individuals were marked, as well as direct neighbouring sections, were visited more frequently, that is 12 (site B), 17 (site D) and 16 times (site E), and the first resighting was mostly done at the first or second day after marking. As markings were well visible from a distance, individuals were not caught again. We calculated resighting rates, as well as dispersal rates and distances for each stream section. Furthermore, the data allowed the calculation of a minimum estimate of individual longevity for *C. mercuriale*.

Genetic analysis

For genetic analysis, 450 unmarked individuals were caught with an insect net at 19 stream sections across the study area (120 km²; Fig. 1) towards the end of the mating season. Streams were split up into sections if they were interrupted by roads, settlements or when they were partly tunnelled. We collected tibiae of mid-legs of up to 30 males per stream section and stored them in 100% ethanol at –20 °C in the dark. DNA was extracted with the DNeasy Blood and Tissue Kit (Qiagen, Germany), amplified at 12 microsatellite loci (LIST4-002, LIST4-023, LIST4-024, LIST4-031, LIST4-034, LIST4-035, LIST4-037, LIST4-042, LIST4-060, LIST4-062, LIST4-063, LIST4-066) developed by Watts *et al.* (2004b) and analysed on an ABI 3700xl sequencer (Applied Biosystems, Carlsbad, CA, USA). Lab procedures and genetic diversity measures are given in detail in Keller *et al.* (2012). All loci were unlinked and Hardy-Weinberg equilibrium conditions were met in all populations. Pairwise genetic distances (F_{ST} ; Weir & Cockerham, 1984), a measure of historical gene flow (Whitlock & McCauley, 1999), were calculated for all pairs of stream sections using the program GENEPOP 4.0.10 (global F_{ST} = 0.043; Raymond & Rousset, 1995). Slightly negative F_{ST} -values were set to 0.

Dispersal paths

To analyse the most likely dispersal routes of *C. mercuriale*, we created potential dispersal paths between stream sections. To minimise the risk of inaccurate genetic differentiation measures due to small sample size, stream sections with <10 individuals were excluded from the analysis. The resulting dataset consisted of 15 stream sections. We focussed on two different dispersal types which were reported in earlier studies on *C. mercuriale* (Hunger & Röske, 2001; Purse *et al.*, 2003). Model A assumed dispersal along a straight line between each pair of stream sections ($N = 105$ pairwise comparisons), estimated by Euclidian distance (Fig. 2). Model B represented the hypothesis of dispersal along preferred habitat, i.e. streams. Paths along streams were estimated in ARCGIS 9.3.1 (ESRI, Redlands, CA, USA) with the cost path tool (Adriaensen *et al.*, 2003). For that, above-ground streams were derived from a vectorised land-cover map (vector 25, resolution = 10 m; Swisstopo, Wabern, Switzerland), buffered with 20 m and then converted to a grid/raster (cell size = 5 m). Cells that covered matrix, that is every landscape element other than stream, were arbitrarily given a high cost value of 50, 100, 500 or 1000, and cells representing streams were assigned a low value of 1. Hence, the higher the cost value of the matrix, the more costly and less likely were paths through matrix and resulting paths were mostly bound to habitat (here: along streams). For model A, path lengths, that is Euclidian distances in [m], were calculated for each pair of stream sections (variable d_{straight}). For model B, path lengths, that is distances along streams, (d_{stream} ; in [m]), as well as distances over matrix, (d_{gap} ; in [m]), were calculated. The data set was split into three Euclidian distance classes to test for distance-dependent dispersal behaviour: (i) 0–1.5 km, (ii) 1.5–3 km, and (iii) >3 km between pairs of populations

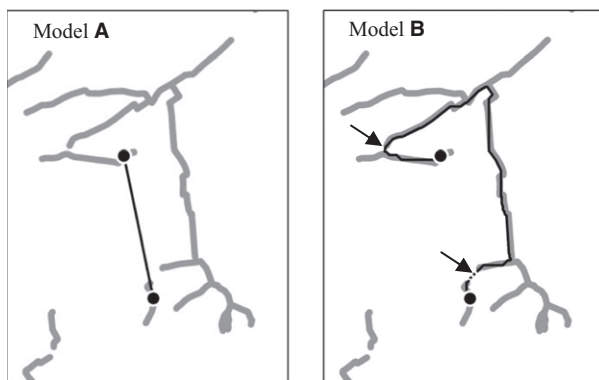


Fig. 2. Dispersal paths (black lines) for two dispersal models of *Coenagrion mercuriale*, drawn for two example populations (circles). Grey lines depict the reproductive habitat of *C. mercuriale* (i.e. above-ground streams). Model A assumes dispersal along a straight line and Model B stands for dispersal along streams. Arrows show gaps within habitat along dispersal path B.

respectively. For all three distance classes, multiple linear regression models were calculated in R (R Development Core Team, 2011), where pairwise F_{ST} between sites was used as response variable and the corresponding distance measures (d_{straight} , d_{stream} , d_{gap}) as predictor variables. As the variables d_{straight} and d_{stream} as well as d_{straight} and d_{gap} were highly correlated (Spearman's rank correlation coefficient $P > 0.8$ in both cases), two separate models were built, each including the distance measures of one of the two suggested dispersal models (Fig. 2): model (A) $F_{\text{ST}} \sim d_{\text{straight}}$, model (B) $F_{\text{ST}} \sim d_{\text{stream}} + d_{\text{gap}}$. For each distance class, the better fitting model (i.e. model A or B) was determined by model fit (R^2). Permutation testing was performed with the 'lmargin' function from the R-package 'ape' (Paradis *et al.*, 2004). 'lmargin' permutes the response variable to test for significance of regression coefficients and R^2 -values. As R^2 generally favours models with more predictor variables (Johnson & Omland, 2004), we additionally performed model selection based on Akaike's information criterion (AIC) and Akaike weights (w_i ; Burnham & Andersson, 2002). AIC measures were calculated using the R-package 'AICcmodavg' (Mazerolle, 2010).

Results

Mark-resight study

From the 455 individuals marked, 48% were resighted at least once (63% in D, 54% in B and 30% in E). Some marked individuals were resighted up to eight times. Movement was only observed within single streams, no individual changed between stream systems. A total of 22 individuals (4.8%) changed between stream sections, covering distances of 100–500 m. Hence, we only recorded movement along connected reproductive habitat, commonly believed to be suitable dispersal habitat. Longevity was on average 9 days over all sites, and individuals were maximally observed until 36 days after marking (i.e. two individuals).

Dispersal paths

Multiple linear regression models showed different results for each of the three distance classes (matrix cost = 1000; Table 1). For distance class 0–1.5 km, model B, which represented paths along streams, was highly supported according to Akaike weights ($w_i = 0.92$) and model fit ($R^2 = 0.42$). Furthermore, both variables (d_{stream} and d_{gap}) were significantly and positively correlated with pairwise genetic distances (F_{ST}). Models for distance class 1.5–3 km showed a similar, but less pronounced pattern. But, d_{stream} was not significant in the most supported model B ($w_i = 0.85$; Table 1). For distances >3 km, R^2 -values were generally lower, but only model A, presuming straight-line movement was significant ($R^2 = 0.13$;

Table 1. Multiple regression results of two dispersal models (A and B) for three distance classes among populations of *Coenagrion mercuriale* from Switzerland. Significance and sign (in brackets) of each regression coefficient, model fit (R^2) and Akaike weights (AICw_i) are given for each model. *P*-values: *** ≤ 0.001 , ** ≤ 0.01 , * ≤ 0.05

Distance class	(A) $F_{ST} \sim d_{\text{straight}}$			(B) $F_{ST} \sim d_{\text{stream}} + d_{\text{gap}}$			
	d_{straight}	R^2	AICw _i	d_{stream}	d_{gap}	R^2	AICw _i
0–1.5 km	(+)*	0.24*	0.08	(+)*	(+)**	0.42**	0.92
1.5–3 km	(+)*	0.18*	0.15	–	(+)**	0.31**	0.85
>3 km	(+)*	0.13*	0.96	–	–	0.05	0.04

Table 1). It showed a significant correlation of straight-line distance with genetic distance. Models on least cost paths based on different matrix cost values (i.e. 50, 100 and 500) showed essentially the same results (Table S1).

Discussion

Dispersal distances and longevity

We found a high resighting rate of marked individuals (i.e. 48%) compared to other studies on *C. mercuriale* that were performed in southern England. Rouquette and Thompson (2007a), for instance, recaptured 31% of 8708 marked mature males, surveying 7.65 km of ditches during 42 days in a study area with three sites occupied by *C. mercuriale*, separated from each other by 3 km. Purse *et al.* (2003) achieved recapture rates of 29% and 31% for totally 4935 marked males and females at two different sites during an observation period of at least 50 days. The mean minimum (9 days) and the maximum life span (36 days; i.e. the maximum number of days between marking and last resight) detected in this study exceeded those recorded in studies from southern England. Purse *et al.* (2003) found a mean life span of 7–8 days, and Rouquette and Thompson (2007a) recaptured marked individuals after a maximum of 29 days. Yet, compared to the results from studies from southern England, our estimates might be less accurate as we did not visit the sites every day. For instance, newly marked individuals, which might have died during the first or second day after marking were not recorded in this study.

Our mark-resight study detected a maximum movement distance of 500 m and found that this short-distance dispersal was restricted to the preferred (reproductive) habitat of *C. mercuriale*. In contrast, genetic analysis showed low global genetic differentiation and low genetic differentiation among adjacent populations (Keller *et al.*, 2012). Thus, genetic analysis suggested that dispersal over larger distances occurred occasionally and populations were (at least historically) well connected. Two possible explanations can be given for the different results from mark-resight and genetic analyses. First, low genetic differentiation can be maintained by only few migrants (Wright, 1943), which are difficult to detect in a mark-resight study, especially if only a small proportion of

individuals within local populations were marked (Hassall & Thompson, 2012). A study in southern England, where 8708 individuals of *C. mercuriale* had been marked, found a three times higher maximum movement distance of 1790 m (Rouquette & Thompson, 2007a). Yet, Rouquette and Thompson (2007a) only found very few recaptured individuals moving farther than 500 m (1.3%). Translated to our study with 220 individuals resighted, the 1.3% rate detected by Rouquette and Thompson (2007a) would result in only three far-moving individuals in our study, which could easily have been overlooked. This was also indicated by a study evaluating mark-recapture estimates of dispersal in *C. mercuriale* (Hassall & Thompson, 2012). The study found that detected maximum dispersal distances are mainly related to the number of recaptured individuals and the time length of the study. Interestingly, the statistical analysis found only a minor effect of the extent of the study area. Therefore, it is necessary to mark a large number of individuals to increase the chance of recapturing a substantial number of individuals. Furthermore, marked individuals should be observed for a long enough time period, as done in this study. The potential of *C. mercuriale* to move farther than 500 m in our study area is supported by the finding of a recently established population more than 1 km away from the closest colonised stream (C. Forrer, Büro Kappeler, unpubl. data). A second reason for the different dispersal distances detected by mark-resight and genetic analyses in our study might be the fact that we only observed adult male damselflies, and that females and teneral would move further and more often. Nevertheless, earlier studies found no difference in dispersal distances between sexes of *C. mercuriale* (Purse *et al.*, 2003; Rouquette & Thompson, 2007a), although long-distance dispersal of *C. mercuriale* teneral has not specifically been investigated.

Dispersal paths

The genetic analysis, based on R^2 -values and AIC weights of statistical models explaining pairwise F_{ST} -values among populations, found that short and medium distance (<3 km) dispersal behaviour differs from long distance (>3 km) dispersal behaviour. R^2 -values generally favour models with more predictor variables (Johnson & Omland, 2004) and AIC values can be inflated by the

non-independence of observations such as in distance matrices (Burnham & Andersson, 2002). Nevertheless, if both measures, that is AIC weights and R^2 -values, show congruent results, as we found for the models in this study, one can assume that these results are valid.

For short distances, model B, assuming paths along streams, clearly outperformed model A, based on straight-line geographic distance. For this model, we also found a high model fit ($R^2 = 0.42$), providing good support for dispersal along streams. This result is also supported by findings of mark-recapture studies on *C. mercuriale* that recorded dispersal along streams up to 1.8 km (Hunger & Röske, 2001; Rouquette & Thompson, 2007a). Furthermore, the additional highly significant positive correlation of the variable distance through matrix (d_{gap}) in model B, showed that gaps within continuous habitat (length ≤ 1 km) act as barriers for short-distance dispersal. For long distances (>3 km), model A representing dispersal along straight lines had higher support than model B. Yet, model fit was markedly lower ($R^2 = 0.13$). Possibly, individuals use various movement paths when moving over long distances and straight-line paths give the best averaged representation of the landscape encountered by the dispersing individuals. Different behaviour in short- and long-distance dispersal was reported in previous studies on odonates (Stettmer, 1996; Purse *et al.*, 2003; Ward & Mill, 2007), but also on other species such as tree frogs (e.g. Angelone *et al.*, 2011). Although our genetic study indicated dispersal along streams for distances up to 1.5 km, Purse *et al.* (2003) detected overland dispersal already at 300 m in a mark-recapture study on *C. mercuriale*. Several possible explanations for this discrepancy can be given. First, the number of population pairs limited the definition of different distance classes in this study. In particular, as only few population pairs were <1.5 km apart from each other, the threshold could not be set below 1.5 km. In spite of this, even if the threshold could have been lowered, significance and model fit of model B would most likely even increase compared to model A. Second, the studies were conducted in different landscapes and the influence of the particular study landscape might have caused the different thresholds. It has, in fact, been shown that landscapes have a substantial impact on dispersal behaviour in animals (e.g. Taylor & Merriam, 1995; Anderson *et al.*, 2010). Third, different measures of dispersal, that is direct mark-recapture or indirect genetic measures like pairwise F_{ST} -values, might give different results. As indirect genetic measures also reflect past dispersal events and only assess dispersal that results in mating and gene flow, they might come up with different dispersal distances than mark-recapture studies that directly track contemporary movements (Allendorf & Luikart, 2007).

Different dispersal behaviour across short and long distances has also been found in other insects (e.g. in a butterfly; Hovestadt *et al.*, 2011) and has been suggested in other landscape genetic studies (Segelbacher *et al.*, 2010; Storfer *et al.*, 2010). Until now, most landscape genetic

analyses have focused on only one general dispersal type and have not distinguished between distance classes. For instance, corridor analysis (Emaresi *et al.*, 2011) assumes more or less straight-line dispersal and detects landscape effects within a straight buffered line between populations. Hence, for short-distance dispersal this approach would have erroneously considered the landscape along straight lines instead of the landscape along streams to explain genetic differentiation. It therefore seems to be important that dispersal studies first identify different types of movement and analyse each type separately.

Conclusions

This study showed that short-distance (≤ 500 m) within-habitat dispersal frequently occurs between local populations of *C. mercuriale* and that it can be detected in mark-recapture studies. A landscape genetic analysis indicated that dispersal being restricted to reproductive habitat even occurs over larger distances (≤ 1.5 km). Moreover, populations were more differentiated when the habitat was not continuous and matrix had to be crossed. On the contrary, long-distance dispersal events (3–4.5 km) could only be detected with genetic analysis and most likely occur only rarely. This long-distance dispersal is, however, important for maintaining functional connectivity in fragmented landscapes and for counteracting genetic isolation of more distant populations and enabling re-colonisations of isolated sites. The results of the present study suggest that short- and long-distance dispersal should be differentiated when planning connectivity measures in conservation management for *C. mercuriale*. Habitat maintenance and connection of present populations by restoring contiguous streams will enhance short-distance dispersal within streams. As these short-distance dispersal events occur regularly, especially if the habitat is continuous, restored sites will most likely be colonised after a short time. In contrast, long-distance dispersal only occurs rarely, but does not depend on continuous habitat. Long-distance dispersal resulting in gene flow was suggested to be characterised by higher directionality, following more or less a straight line. A previous study has detected landscape elements that enhance or hinder dispersal for this movement type in *C. mercuriale* (Keller *et al.*, 2012). This study showed that areas of forest and substantial elevation change, such as hilly landscape, were barriers, but that open agricultural land enhanced dispersal and gene flow. Thus, the findings of this study complement the existing knowledge on dispersal of *C. mercuriale*. Moreover, it shows how the combination of mark-resight and landscape genetic studies may enhance the understanding of insect dispersal in fragmented landscapes. In particular, the identification of different dispersal habitats for short- and long-distance dispersal helps planning conservation measures for threatened species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12016:

Table S1. Multiple regression results of two dispersal models (A and B) for three distance classes and four matrix cost values among populations of *Coenagrion mercuriale* from Switzerland. Significance and sign (in brackets) of each regression coefficient, model fit (R^2) and Akaike weights (AICw_i) are given for each model. *P*-values: *** ≤ 0.001 , ** ≤ 0.01 , * ≤ 0.05 .

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