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Study design and mark-recapture estimates of dispersal: a case study with the endangered damselfly *Coenagrion mercuriale*

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Abstract

Accurate data on dispersal ability are vital to the understanding of how species are affected by fragmented landscapes. However, three factors may limit the ability of field studies to detect a representative sample of dispersal events: (i) the number of individuals monitored, (ii) the area over which the study is conducted and (iii) the time over which the study is conducted. Using sub-sampling of mark-release-recapture data from a study on the endangered damselfly *Coenagrion mercuriale* (Charpentier), we show that maximum dispersal distance is strongly related to the number of recaptured individuals in the mark-release-recapture study and the length of time over which the study is conducted. Median dispersal distance is only related significantly to the length of the study. Spatial extent is not associated with either dispersal measure in our analysis. Previously consideration has been given to the spatial scale of dispersal experiments but we demonstrated conclusively that temporal scale and the number of marked individuals also have the potential to affect the measurement of dispersal. Based on quadratic relationships between the maximum dispersal distance, recapture number and length of study, we conclude that a previous study was of sufficient scale to characterise the dispersal kernel of *C. mercuriale*. Our method of analysis could be used to ensure that the results of mark-release-recapture studies are independent of levels of spatial and temporal investment. Improved confidence in dispersal estimates will enable better management decisions to be made for endangered species.

Keywords: damselfly, dispersal, dragonfly, mark-release-recapture, movement, study design.

Introduction

Landscape-scale conservation measures, particularly the design and implementation of networks of nature reserves, require knowledge of the dispersal abilities of species which are to be the focus of those conservation measures. The quantification of dispersal requires a substantial investment of resources due to the need to consider a sufficient spatial and temporal scale within which the full range of dispersal events can be observed. Consideration of scale is vital since the costs associated with carrying out such studies increase with the size of the study area (Slatkin 1985). Where resources are limited there is a desire to maximise data while minimising investment, although insufficient investment can lead to misleading results (Koenig et al. 1996).

A simple solution to the problem of finite spatial scale is to design the dispersal experiment at a scale that is sufficient to encompass the range of dispersal events of the subject species. However, this requires exactly the kind of a priori knowledge of dispersal that many such experiments are attempting to establish. A second method is to correct observed dispersal distances according to the likelihood of detecting them given the size of the study area and the number of unsurveyed, suitable habitat patches outside of the study area (Baker et al. 1995; Barrowclough 1978). However, such corrections thicken the tail of the dispersal distribution but do not extend it and knowledge of the suitability of the landscape beyond the study area is required. This method cannot be applied in cases where the study area constitutes an isolated habitat fragment, i.e. there is no more suitable habitat within a reasonable distance of the study area. Finally, post-hoc methods may be used to check that the results of dispersal studies are independent of the scale of the study. Such methods may include randomised sub-sampling of the data to investigate relationships with the area of the study site (Franzén and Nilsson 2007). Post-hoc validation is clearly less preferable than incorporating dispersal knowledge into the study design or correcting for finite study area, as the results may demonstrate conclusively that the study was unable to provide meaningful data aside from the observation that the study was not of sufficient scale. However, this validation does constitute a method that can be used in all cases. While limitations on the quality of data imposed by study design are almost universal, there are relatively few studies explicitly investigating them. Exceptions include inter-study comparisons of mark-release-recapture studies of the butterfly *Maniola jurtina* (L.) showing that the mean dispersal distance recorded was strongly correlated to study area size (Schneider 2003) and evidence of a similar effect for the damselfly *Coenagrion mercuriale* (Hassall and Thompson 2008a).

In Odonata the primary mechanism for dispersal is flight. While there have been documented cases of dispersal in the egg and larval forms these are thought to comprise a negligible proportion of dispersal events (Angelibert and Giani 2003), although it is possible that passive dispersal in lotic systems could be common. Teneral (newly-emerged, reproductively immature) individuals are known to exhibit a negative taxis with respect to reflecting surfaces, including water (Corbet 1999). This results in emigration from the natal water body. However, this “maiden flight” rarely involves distances of more than a few tens of metres (Corbet 1962). Mark-release-recapture studies of odonate dispersal have focused primarily on networks of lentic water bodies (Angelibert and Giani 2003; Conrad et al. 1999). The discontinuous distribution of potential movement distances between those water bodies means that the dispersal kernel cannot be accurately quantified along its entire length. Species inhabiting networks of linear water bodies such as water meadow ditch systems (e.g. Allen and Thompson 2009; Purse et al. 2003) provide an easier system within which to calculate dispersal. Even when adequately designed to encompass the maximum dispersal distance of a species, the chances of catching one of the rare individuals that actually make that movement are low (Corbet 1962). This highlights the rarely-considered aspect of recapture number in mark-release-recapture or the number of tagged individuals in radio-tracking.

Despite a growing number of large-scale studies of dispersal in Odonata, there have been relatively few attempts to validate the results of those studies. We seek to validate data from a mark-release-recapture study on the endangered odonate *Coenagrion mercuriale* (Rouquette and Thompson 2007; Watts et al. 2004), which reaches the edge of its range in southern England and generally occurs in isolated populations. The species is classified as “near threatened” on the IUCN’s Red List (Boudot 2006) as well as featuring in Annex II of the EU Habitats Directive. Habitat for *C. mercuriale* is well-characterised and scarce (Rouquette and Thompson 2005), with none found within several kilometres of the study site. For this reason we do not apply a mathematical correction using Baker et al's (1995) methods. This original study detected a median dispersal distance of 31.9 m and a maximum dispersal distance of 1.79 km, with 66% of individuals moving <50 m in their lifetimes. By sub-sampling the spatial extent of the study area and the temporal length of the study, we test two hypotheses: (i) the accuracy of the detection of maximum and median dispersal distances of *C. mercuriale* increases with diminishing returns as both spatial extent and temporal length of the study increase, and (ii) the original study was of sufficient temporal and spatial scope to accurately characterise the dispersal kernel of *C. mercuriale*. The first hypothesis is motivated by a lack of knowledge concerning the effect of the nature of study design on the results of dispersal experiments. The second hypothesis is motivated by evidence suggesting that the spatial scale of previous studies has influenced the maximum dispersal distance that can be measured in this species (Hassall and Thompson 2008a). The results presented here also address concerns of conservation agencies about the extent of the original study.

Materials and Methods

Data collection

A mark-release-recapture study to quantify the dispersal ability and population genetic variation of *C. mercuriale* was carried out in southern England for 43 days beginning on 12

June 2001. The study site comprised a series of eight sub-sites located along the Itchen Valley, of which five were directly adjacent (Fig. 1). Mature adult damselflies were caught and marked with a dot of paint on the dorsum of the thorax and a unique alphanumeric code on the wing. The locations of each capture as well as subsequent recaptures or sightings were recorded using GPS to the nearest meter (m). For details of this study see Watts et al. (2004) and Rouquette and Thompson (2007).

Sub-sampling

The dataset was divided according to the five contiguous sub-sites (A, B, C, D and E, Fig. 1) and these were used in combinations to give study areas of varying spatial extents (Fig. 2). Since individuals moved between adjacent sub-sites, only adjacent sub-sites could be combined while preserving these movements in the resulting data. This resulted in 15 combinations of sites with areas (calculated by taking the area of the convex hull surrounding the recorded GPS locations) varying from 0.13 km^2 (Itchen Valley Upper only) to 1.34 km^2 (all sub-sites). Data were also divided according to the week of recording (with the extra day included in the final week), with adjacent time periods being combined. This resulted in a sample of 21 time periods varying from 7 to 43 days (Fig. 2). Study areas and time periods were combined in a factorial design to give 315 subsets of the original data relating to a range of different study site areas and temporal lengths. Each of these constitutes a "simulated study".

Data analysis

For each simulated study the gross dispersal distances (sum of Euclidean distances between sightings) were calculated for each individual and the maximum and median gross dispersal distances were calculated for the population. Gross dispersal distances can be considered the most ecologically relevant dispersal measure in the context of metapopulations, as they provide an estimate of the total potential distance that an individual can move. Alternative measures are the "net dispersal distance", measuring the distance between the locations at which each individual was first and last seen and "individual dispersal distances", measuring the distances covered between sightings. However, the ecological relevance of net dispersal distance is unclear given the varying rates of philopatry and uncertainties over what factors affect the tendency to disperse (Beirinckx et al. 2006). Thus an individual may gravitate back to approximately the same location where it was first sighted, but this tells us nothing about its ability to move between habitat patches. In a similar way, individual movements may involve short patrol flights along stretches of stream which fulfil an entirely different function (e.g. territoriality, mate searching) than directed dispersal. In contrast, by calculating the sum total of these individual flights, the potential distance that an individual could move can be calculated.

Gross dispersal distances were plotted against spatial extent (area in km^2) and recapture number to evaluate the relationships between each of these factors. We acknowledge that there is a lack of independence between data from the results of the 315 simulated studies (Fig. 2 demonstrates that different simulated studies use the same data). For example, if there are large movements in a given week, there will be large movements in all models involving data from that week. We therefore need to account for variation between datasets that include or do not include the data from that week. We introduce a random factor to account for the variation between the datasets due to the shared presence of the movements from each week or sub-site. Therefore, in each model, the presence or absence of the five sub-sites or six sampling weeks were included as random effects, leading to 11 random effect terms in total. Finding that the main effects are still significant even accounting for the variation between weeks and sub-sites suggests that the main effects are significant regardless of the lack of independence in the data. LMEs were constructed to explain maximum gross dispersal distance and median gross dispersal distance in each of the simulated studies. Fixed effects in each model were the area of the study site, the length of the study (in weeks) and the number of recaptured individuals.

The correlation between recaptures and length of study was $r=0.656$, $p<0.001$, and the correlation between recaptures and area of the study site was $r=0.491$, $p<0.001$. This raises a potential problem of multicollinearity in the models. To test for this, we would usually calculate variance inflation factors (VIFs) for each term in the model. However, it is not clear how this should be done in the case of mixed effect models. When we calculate the VIFs for the models without the random effects (i.e. as multiple linear regression models), the VIFs are 1.77 (area), 2.31 (time) and 3.05 (recaptures). A variety of thresholds for "high" multicollinearity have been proposed, but none of these exceed VIF=4 (for a review see O'Brien 2007). Thus we can tentatively suggest that the collinearity in the variables is not contributing to inflated variance in parameter estimates in our mixed effects models. Instead, the inclusion of the three variables in the models allows us to determine which exhibit the strongest relationship with dispersal distance when the other two variables are accounted for.

Along with investigating those aspects of study design that affect the detection of dispersal, there is also an interest in verifying the results of the original study. Verification was attempted by testing for the difference in goodness-of-fit between models with and without quadratic terms which might indicate that an asymptote had been reached. Significant terms from the previous pair of LMEs were entered into further LMEs both with and without the corresponding quadratic terms. Model fit was assessed using the difference in Akaike's Information Criterion (ΔAIC) between the two models judged according to the rules of thumb set out by Burnham and Anderson (2002: ΔAIC 0-2 = little difference between models, ΔAIC = 4-7 much better performance by one model, ΔAIC>10 = essentially no support for the worse model).

Results

Detection of dispersal distance

Linear mixed effects models demonstrated that maximum dispersal distance was highly positively related to the number of recaptures (t_{304}=10.69, p<0.001, Figure 3) and positively related to the length of the study (t_{304}=3.31, p=0.001). Maximum dispersal was marginally, though not significantly, related to study area (t=1.92, p=0.056, Figure 4). While a substantial increase in maximum dispersal distance is recorded when the length of the study increases above seven days, little further improvement is observed. The noise associated with the patterns suggests that spatial extent has relatively little explanatory power (Figure 4). However, an asymptotic relationship appears to be present between maximum dispersal distance and the number of recaptured individuals (Fig. 4). At low temporal extents (seven days), studies would give approximately linear relationships between the number of recaptures and the maximum dispersal distance recorded. As the temporal length increased towards 42 days, the relationship increasingly resembled the kind of asymptote that would be expected if the study was accurately sampling dispersal.

Median dispersal distance was highly positively related to the length of the study (t_{304}=6.53, p<0.001) and highly negatively related to the number of recaptures (t_{304}=-3.55, p<0.001) but not significantly related to the area of the study site (t_{304}=1.10, p=0.274). Median dispersal exhibited a relationship that appears as dampening oscillations around an average with increasing recapture number around a final value (Fig. 3, top panels), rather than approaching that value asymptotically. However, the positive relationship with the temporal scale of the study is made clear when the average values for each temporal extent of study were compared (Fig. 5).

Assessment of original study

Asymptotic relationships appear to be present in maximum dispersal distance (Fig. 3) and a consistent value of median dispersal distance is maintained over increasing recapture number (Fig. 3) and temporal scale (Fig. 5) supporting the conclusion that the original study was of sufficient scope to detect the entire range of potential dispersal distances (i.e. up to and including the maximum dispersal distance). That maximum dispersal distance is accurately recorded for this particular landscape is further supported by data from the full study that included three additional northern sites at varying distances from the complex included here. The full dataset still only recorded a maximum dispersal distance of 1790m despite increasing the number of recaptures to 2523 compared to a total of 1823 in the subset of the data used here.

The AIC values for the models describing maximum dispersal (maximum dispersal = recaptures + time vs. maximum dispersal = recaptures + recaptures^2 + time + time^2) were 4359 for the linear model and 4331 for the quadratic model. The ΔAIC of 29 suggests far greater support for the quadratic and the conclusion that the results demonstrate the actual maximum dispersal distance of *C. mercuriale*. Solving the quadratic function for the maxima of the equation describing the relationship between maximum dispersal distance and length of study and number of recaptures gives a maximum dispersal of 1832m, only 42m greater than empirical observations. This maximum is found with a recapture number of 1875 and a study length of 3.621 weeks. For median dispersal distance, the AIC values for the models describing maximum dispersal (median dispersal = recaptures + time vs. median dispersal = recaptures + recaptures^2 + time + time^2) were 2601 for the linear model and 2622 for the quadratic model. The ΔAIC value of 21 suggests that the quadratic model for median dispersal performs substantially worse than the linear model.

Discussion

Contrary to previous assumptions and the results of previous studies (Franzén and Nilsson 2007), we present results that show that the ability of a mark-release-recapture study to measure a species' dispersal ability may not be dependent on the spatial extent of the study area. However, we note that the key result – the relationship between study site area and maximum dispersal distance – was marginally non-significant (p=0.056), which means that we cannot confidently accept the null hypothesis that area has no effect on the detection of dispersal. This is further supported by the solutions of the quadratic functions describing maximum dispersal, which provide estimates which are slightly greater than those that were detected. However, the methods of analysis presented in this study permit the quantification of this effect so that the results of the study can be weighed against the limitations of scale.

Spatial extent may be important in its own right in providing space within which monitored individuals can move. However, spatial dimensions may also determine the number of individuals that can be recaptured (based on population density), which in our analysis is the most important factor in estimating maximum dispersal ability. We also show that the temporal scope of a study, an often overlooked aspect of study design, is important in determining both median and maximum dispersal distances. It is commonly assumed that a study area of greater spatial extent will enhance the tails of dispersal kernels, thus providing better estimates of what is occurring at those extremes. In the case of *C. mercuriale,* while additional LDD events are observed, it may serve also to increase the number of individuals that are recaptured. The sufficiency of the scale of the original dispersal study (described in Rouquette and Thompson 2007) is supported by low estimates of gene-flow between sub-sites (Watts et al. 2004) as well as the support for and solutions from quadratic functions of study scale against maximum dispersal distance. Low dispersal in *C. mercuriale* is further supported by evidence from other sites of genetic differentiation over small spatial scales (Watts et al. 2006) and an unsuccessful search for long-distance dispersal in the periphery of another study site (Thompson and Purse 1999).

The differentiation of these three components of study design – number of individuals observed, spatial extent and temporal extent – is important. Spatial extent limits the distance over which the study can detect dispersal and temporal extent limits the time over which observed individuals can make dispersal movements. While the relationship between recapture number and dispersal distance is less intuitive, plotting the maximum dispersal distances recorded in this study alongside those detected in other studies suggests that the pattern may not be unique to this study (Fig. 6). The location of some studies below the general trend is likely due to the shorter study length in some cases (four studies were conducted for four weeks or fewer). A similar relationship has been demonstrated in a meta-analysis of the spatial extent of study areas and recorded dispersal distance (Schneider 2003), with the two shown to be significantly correlated.

The number of recaptured individuals may affect dispersal estimates in one of two ways. First, while capable of larger movements, many individuals may be sedentary through lack of necessity for dispersal. Thus finding individuals that fulfil their dispersal potential may require sampling of larger number of individuals. Secondly, there may be a proportion of individuals that are pre-disposed to philopatry and a proportion that are dispersive, leading to a bimodal distribution of dispersal distance. Sampling from the dispersive individuals requires greater sample sizes which, in turn, provide better estimates of dispersal. Estimates of philopatry in odonates vary markedly between species, from 1.5% recaptures to 90.2% recaptures (Beirinckx et al. 2006), while this study found a recapture rate of 29.0% (Rouquette and Thompson 2007). Philopatry is also present in mammals (Waser and Jones 1983) and birds, where a review of passerine birds showed levels of philopatry between 0% and 39.7% (Weatherhead and Forbes 1994). A wide variety of factors have been implicated in affecting the extent to which odonates disperse. These include body size (Anholt 1990; cf. Conrad et al. 2002; Thompson 1991) – a pattern which is seen across taxa (Jenkins et al. 2007) – immune activity (Suhonen et al. 2009), ectoparasitic mite burden (Conrad et al. 2002), sex (Beirinckx et al. 2006; Conrad et al. 2002) and age {Michiels, 1991 #1340}. This age-dependent dispersal tendency could potentially result in increased dispersal later in the season. However, we find no evidence of this in the present study. Female polymorphisms (Bots et al. 2009), proximity to range margins (Hassall and Thompson 2008b) and landscape structure (Taylor and Merriam 1995) have also been suggested as factors affecting flight ability via changes in morphology.

The logistical constraints placed on studies that seek to characterise dispersal may be eased with the development of novel technologies. Chief among these is radio-tracking, the use of which is generally limited to larger vertebrates and some terrestrial invertebrates. However, the technology has also been adapted for terrestrial beetles (Rink and Sinsch 2007), bees (Sumner et al. 2007) and even aquatic fly larvae (Hayashi and Nakane 1989). Radio frequency identification (RFID) tags have now been used to track the movements of individual *Anax junius* (Drury) on their annual migration over North America (Wikelski et al. 2006), although this species is one of the largest and strongest flyers out of the Odonata. An alternative method which has successfully been applied to smaller insects, including bees

(Riley et al. 1996) and butterflies (Cant et al. 2005) is harmonic radar. The recent, preliminary application of this technique to odonates (*Libellula fulva* (Müller) and *Aeshna mixta* (Latreille)) suggests that this may be a profitable area of research in the future (Hardersen 2007). However, the current limits to the range of the radar (1 km, Cant et al. 2005) make it unsuitable for detecting LDD. The alternative group of methods rely on the quantification of genetic variation across the landscape (e.g. Watts et al. 2007). Arguably this is the more valuable technique in terms of conservation management, as it incorporates the movement of genes and not just the movement of individuals. However, the measurement of gene-flow depends on the magnitude of genetic variation within and between the studied populations, which, in the case of *C. mercuriale*, can be very low (Watts et al. 2006). Furthermore, there is conflicting evidence for a correlation between "direct observations" of dispersal (i.e. mark-recapture studies) and "indirect observations" of dispersal (e.g. gene-flow estimates) (Koenig et al. 1996; but cf Bohonak 1999).

In order to make full use of dispersal data (Rouquette and Thompson 2007), knowledge about habitat requirements (Rouquette and Thompson 2005) and population genetics (Watts et al. 2006) of *C. mercuriale*, information is required concerning its rates of persistence in habitats. Currently this exists only for a handful of North American odonates (Gibbons et al. 2002). Incorporating persistence with dispersal, habitat and population genetics data would permit both metapopulation modelling and population viability analysis approaches to be used in the prediction and management of *C. mercuriale*. This is of particular relevance given the current decline of the species (Boudot 2006) and the low genetic variability found in some populations (Watts et al. 2006).

The “pandemic lack of data” not only in dispersal ecology but in conservation biology as a whole has led to the application of theory without due consideration to its limitations (Doak and Mills 1994). Despite the enormity of the dispersal literature, “there are...disappointingly few available estimates of dispersal variables from natural populations” (Macdonald and Johnson 2001). This is particularly the case with LDD, which is the aspect of dispersal that is both the most important to conservation biology and most difficult to measure (Trakhtenbrot et al. 2005). The amount of money required to produce a viable, long-term network of habitat conservation areas in the United States has been estimated at $5-8 billion per year over 40 years (Lerner et al. 2007). However, the implementation of networks of habitat conservation areas is undermined by the current lack of understanding concerning how animals may move between (Schultz 1998) and even within (Woodroffe and Ginsberg 1998) those areas. Clearly planning for the allocation of such a vast sum of money requires a firm evidence base from which to draw.

In addition to the design of static nature reserves, the onset of global climate change has enhanced the need to understand how species move through the landscape. Range shifts have been well-documented in a range of taxa (Hickling et al. 2006; Parmesan 2006), but it is unclear whether these species are keeping pace with shifting isotherms. Synergistic effects of climate change and habitat loss have been demonstrated using modelling approaches (Travis 2003), with range shifts hindered by poorly connected habitat (Opdam and Wascher 2004). This has led to concerns that static nature reserves may be insufficient to protect wildlife in the face of climate-induced range shifts (Araújo et al. 2004).

Mark-recapture or capture resight methods have been used to study dispersal in invertebrates such as beetles (Turchin and Thoeny 1993), snails (Baur 1986) and odonates (Rouquette and Thompson 2007), as well as in small (Diffendorfer et al. 1995) and large mammals (Støen et al. 2006), birds (Haas 1995) and whales (Smith et al. 1999). Many such studies produce data which is amenable to validation using our methods. Future study design should include aspects of the dispersal of the focal species that have previously been studied, such as the maximum dispersal distance recorded with different numbers of recaptured individuals. The spatial scale of the experiment may still be important but this importance may lie in ensuring a sufficient number of individuals are included. Analyses of results of these types of studies should include sub-sampling of data to ensure that the final results are independent of the scope of the study.

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Figures

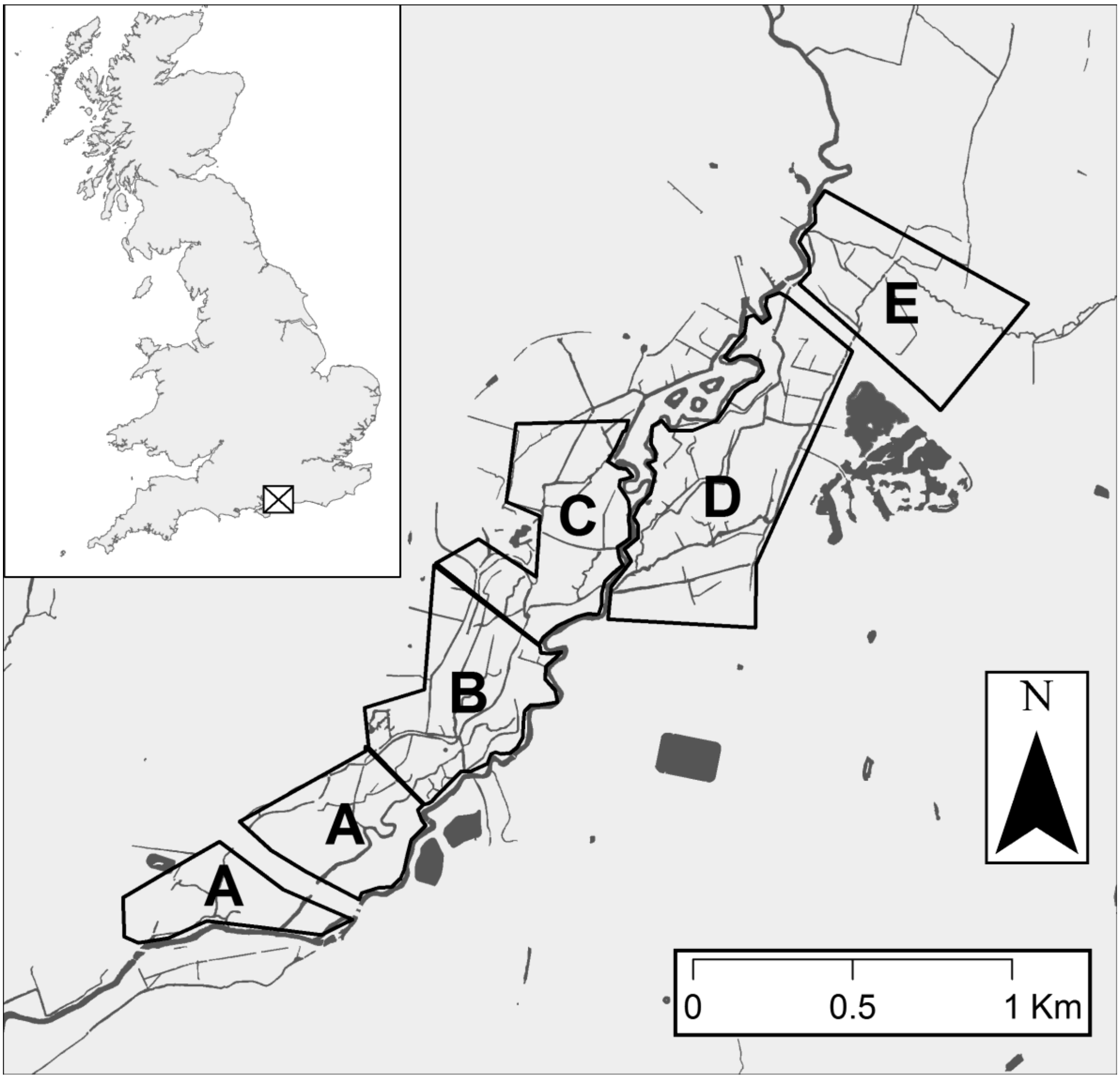

Fig. 1 – Map of the *Coenagrion mercuriale* mark-release-recapture study site in the Itchen Valley, southern England, with sub-sites labelled: A = Itchen Valley Lower, B = Itchen Valley Mid, C = Itchen Valley Upper, D = Allington Manor, E = West Horton Farm.

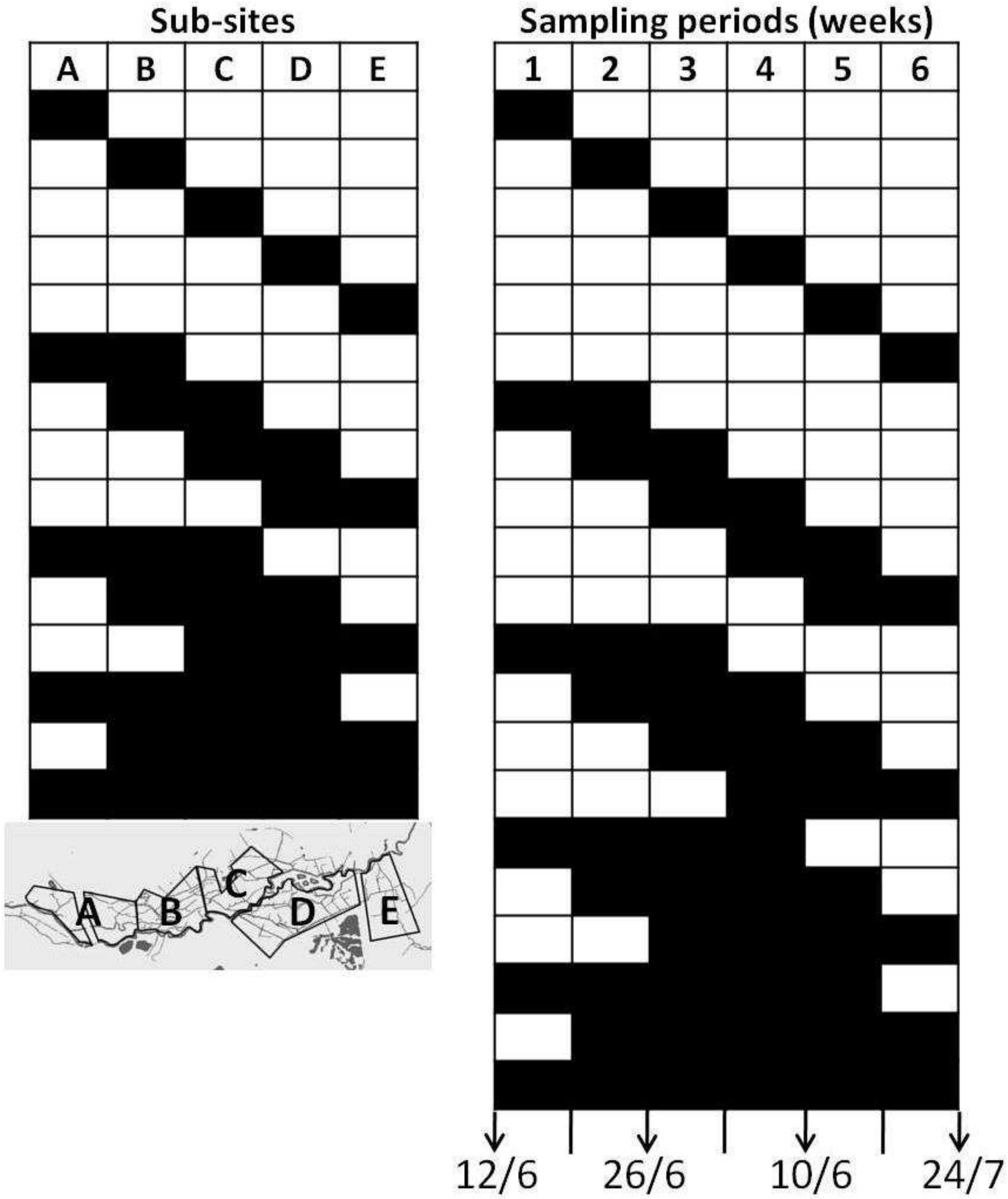

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Fig. 2 – Diagram showing how subsets of the spatial (left) and temporal (right) extent of the original study were defined. Each column corresponds to a different sub-site (see diagram at the base of the columns) or week in the study (see dates at the base of the columns) and shading indicates the inclusion of data from that specific sub-site or week in the model. Each row corresponds to a different combination of the sub-sites or weeks. Each of the 15 spatial configurations is combined with each of the 21 temporal configurations to give the 315 model runs described in the text.

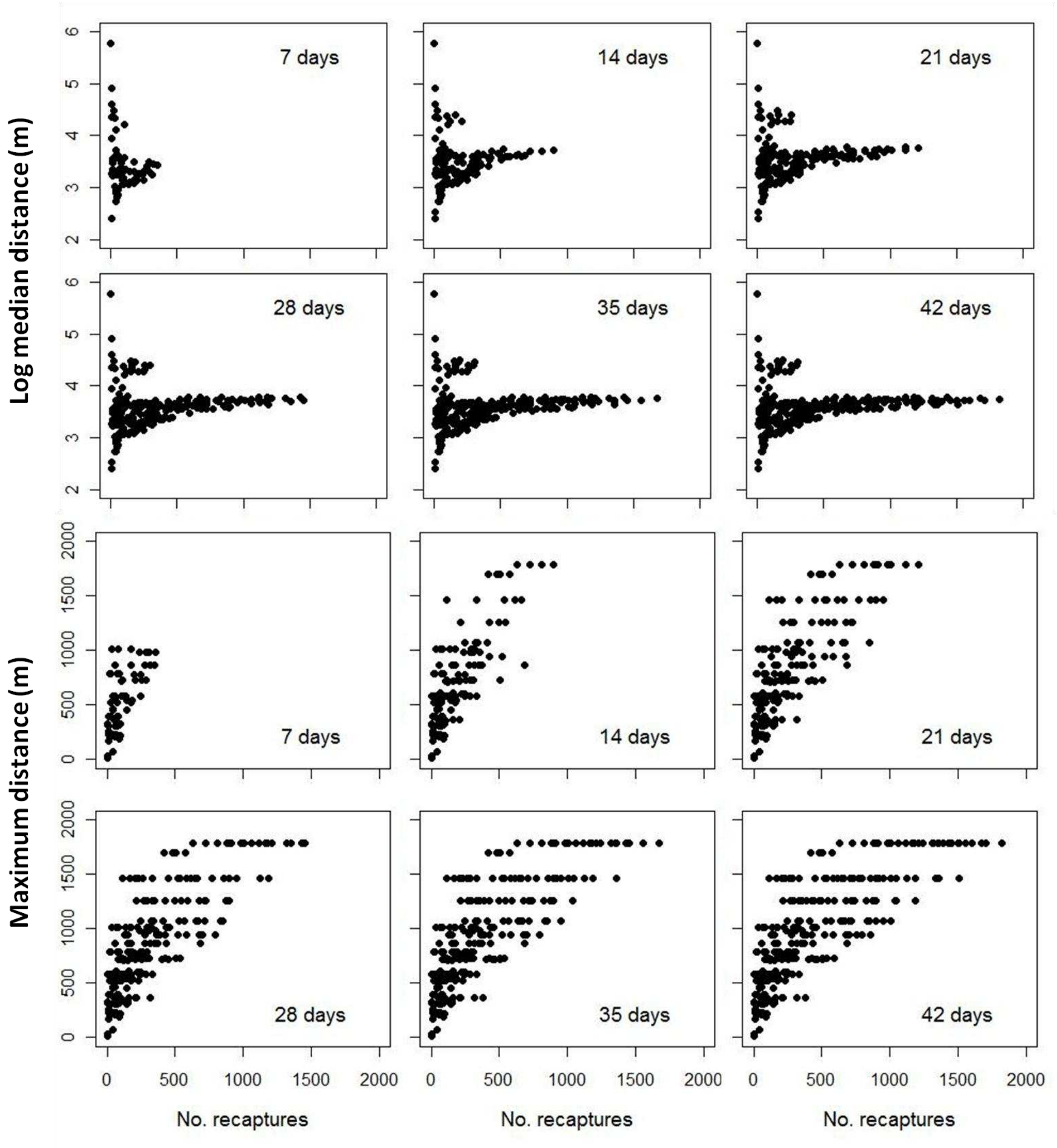

Fig. 3 – Relationships between median and maximum gross dispersal distances and spatial extent of the study site. Panels show different lengths of study. Each point is a simulated study.

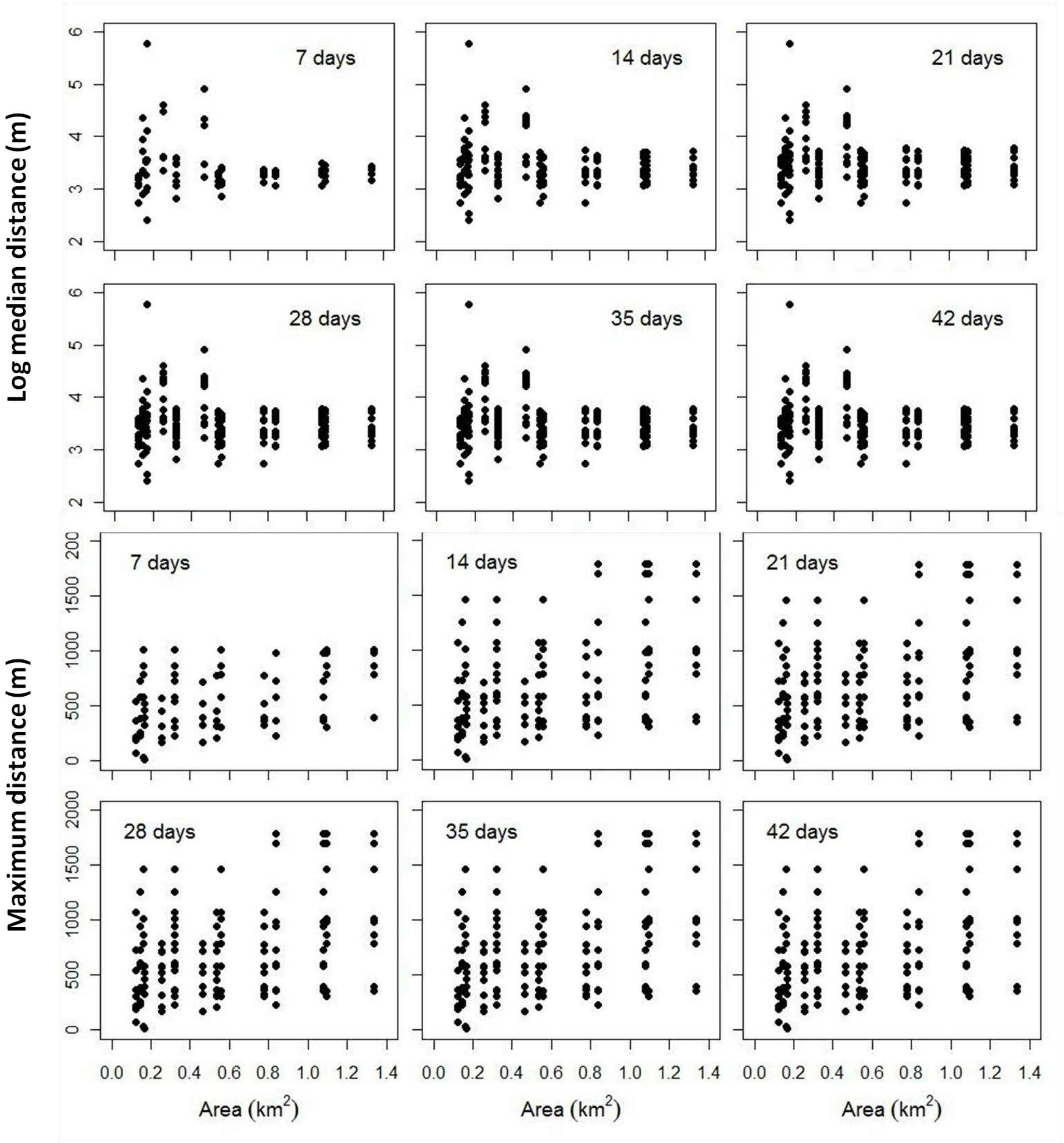

Fig. 4 – Relationship between the median and maximum dispersal distances detected in simulated studies and the number of individuals recaptured. Panels show different lengths of study. Each point is a simulated study.

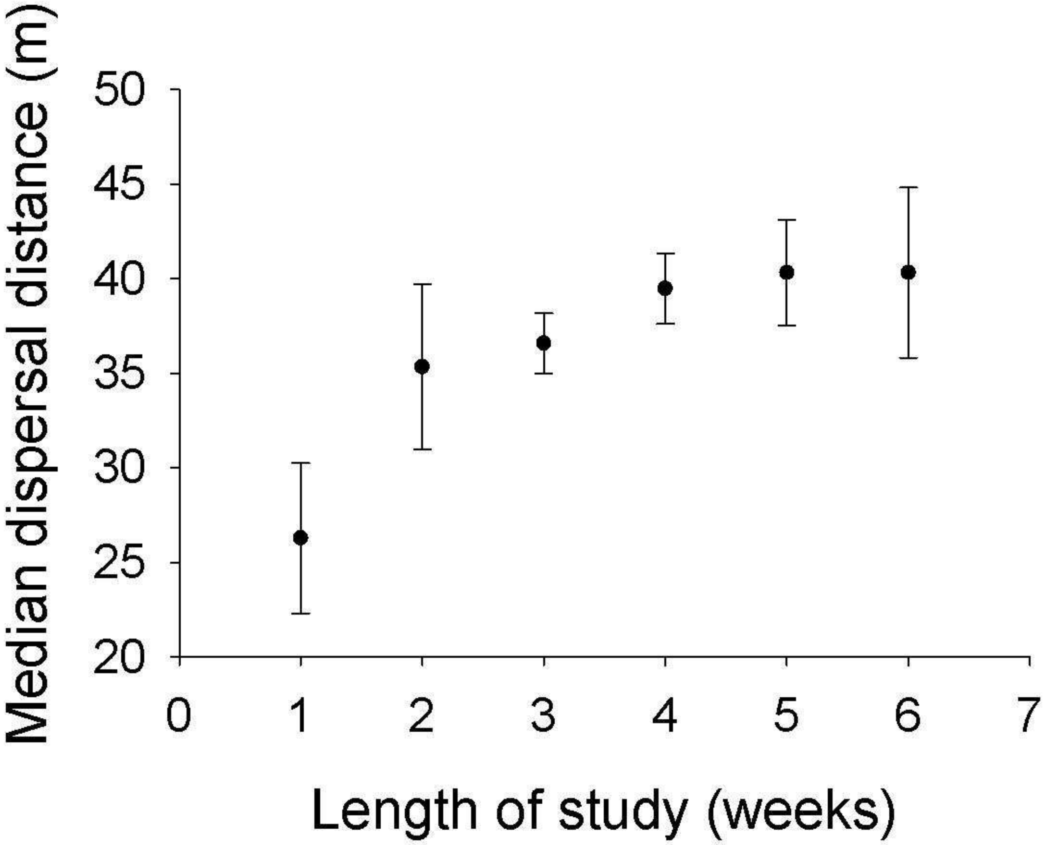

Fig. 5– Effect of length of study on the median dispersal distance recorded for *Coenagrion mercuriale*. Error bars are 1 SE.

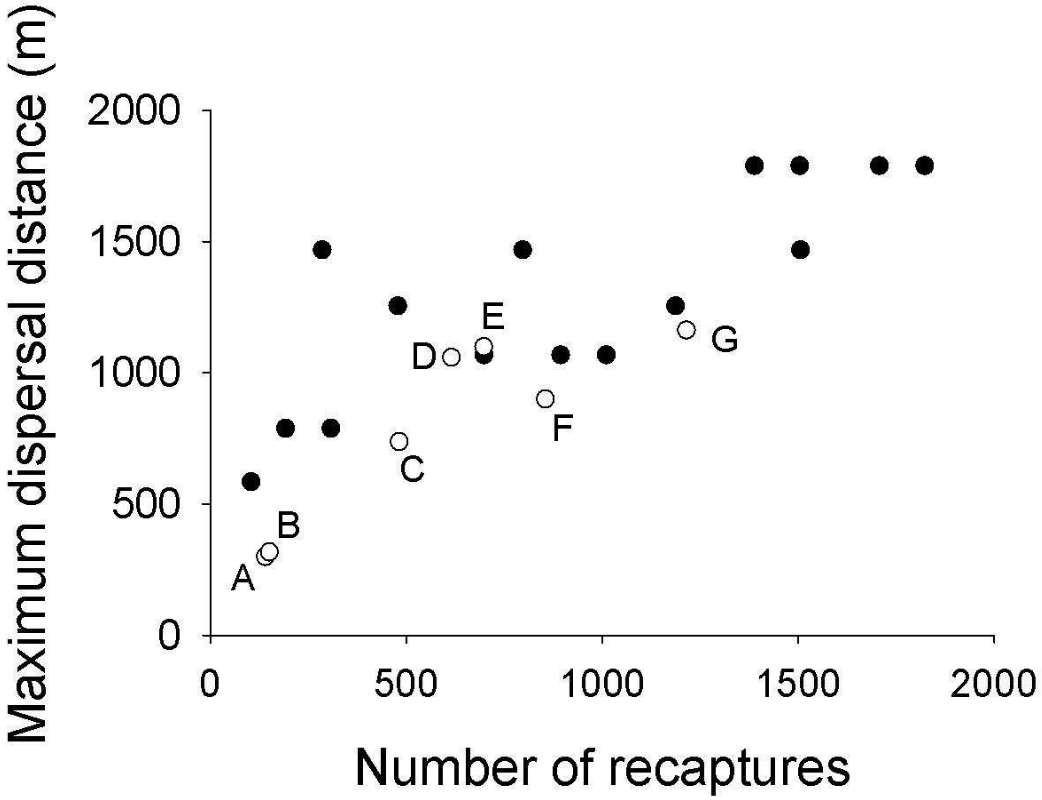

Fig. 6 – Comparison of the relationship between the number of recaptured individuals and the maximum dispersal distance recorded in previous mark-release-recapture studies on damselflies (open circles) with results from this study (closed circles – data shown are for six-week-long studies). Studies are: A=Hunger and Röske (2001), B=Allen and Thompson (2009), C=Ward and Mill (2007), D= Purse et al. (2003), E=Stettmer (1996), F=Purse et al. (2003), G=Allen and Thompson (2009).