

An experimental assessment of landscape connectivity

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Pither, J. and Taylor, P. D. 1998. An experimental assessment of landscape connectivity. - *Oikos* 83: 166–174.

We experimentally assess the relative movement abilities of two sympatric, ecologically similar species of damselfly, *Calopteryx maculata* and *Calopteryx aquabilis* (Odonata: Calopterygidae), within two structurally dissimilar habitat types, forest and pasture. For both species, streams are required resources, forest is a potential resource, and pasture is neutral habitat. Experimental manipulations were conducted at a spatial scale approaching typical inter-stream distances within our study region. A portion of the individuals was displaced away from its required stream habitat within its native landscape, and the remaining individuals were transferred to another landscape of alternate habitat structure (either forest or pasture). Within each habitat type we equate relative movement ability, an essential component of landscape connectivity, with the proportion of displaced individuals observed to have reached the stream, as measured against reobservation rates of control individuals released at the stream. We found that *C. maculata*, the species more consistent in its use of forest as a resource, moved significantly more readily through 700 m of pasture habitat than through the same distance of forest, while *C. aquabilis* moved with equal abilities through both habitat types. Historical behavior – whether or not the individuals typically used forest as a resource before the manipulations – did not have a statistically significant effect on the movement abilities of individuals of either species in either habitat type. There was, however, some evidence that *C. maculata* individuals native to non-forested landscapes moved more readily through forest than their forest-inhabiting counterparts. Both sexes moved with equal abilities irrespective of habitat type, but male *C. aquabilis* moved with greater ability through forest than females, while the reverse was true within pasture landscapes.

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Landscape connectivity is of fundamental importance to the dynamics of spatially structured animal populations (Fahrig and Merriam 1985, 1994, Stacey et al. 1997). It represents the degree to which the landscape facilitates or impedes the movement of individuals among resource patches and populations (Merriam 1984, Taylor et al. 1993). For many systems, quantifying landscape connectivity requires spatially explicit methods that are sensitive to the possibility of complex interactions between the behavior of individual animals and landscape structure (Wiens 1997). Individual-tracking techniques (e.g. Fahrig and Merriam 1985, Merriam and Lanoue 1990, Crist et al. 1992, Andreassen et al. 1996), mark-release-recapture experiments (e.g. Fahrig

and Paloheimo 1987, Harrison 1989, Bennett et al. 1994, Sutcliffe and Thomas 1996), and manipulations of habitat or individuals within experimental model systems (EMS) (e.g. Ims et al. 1993, Wiens et al. 1997) have all had some success in this regard (for a review in a slightly different context see Ims and Yoccoz 1997). With these few exceptions, however, it is rare to find empirical data that directly describe key parameters of landscape connectivity, such as the habitat-specific movement patterns, rates, or capabilities of animals (Kareiva 1990, Ims 1995). Even more rare are data comparing movement behaviors among landscapes that differ in structure (e.g. amounts or configurations of suitable habitat, Wiens 1997, Wiens et al. 1997), or that

Accepted 13 February 1998

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ISSN 0030-1299

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describe movements occurring at spatial scales coincident with the particular species' population dynamics (Kareiva and Wennergren 1995).

We believe, however, that combining information about those processes with fine-scale movement data will allow for better predictions of connectivity and population dynamics in heterogeneous landscapes (Merriam 1991, Fahrig and Merriam 1994, Ims and Yoccoz 1997). Several examples help illustrate this point. Extensive mark-recapture and tracking studies of white-footed mice (*Peromyscus leucopus*) showed that movement among spatially subdivided populations was essential to maintaining regional population persistence in farmland mosaics, and was facilitated by the use of wooded fencerows as movement corridors (Middleton and Merriam 1981, Fahrig and Merriam 1985, Merriam and Lanoue 1990). In the same system Merriam and Lanoue (1990) presented some evidence that historical behavior influenced the responses of mice to novel landscape structure. Fencerow use depended somewhat on how the experimental groups of mice used habitats (including fencerows) before being manipulated. This provides an example of how behavioral context, in addition to structural context, may matter to measures of landscape connectivity (Wiens 1997). In contrast, Harrison (1989) found that random movement behavior through open habitat by the butterfly *Euphydryas editha* was likely responsible for the colonization of small habitat patches near a large source population. In another butterfly system, Thomas and Harrison (1992) demonstrated that the colonization of isolated habitat patches by *Plebejus argus* was limited by their dispersal capability (less than 1 km), but facilitated by the presence of stepping stones of suitable habitat patches. Using similar methods, Solbreck (1995) showed that weather, host-plant quality, and movement capability interacted to affect the long-term spatial and temporal dynamics of lygaeid bugs in a patchy landscape. In these latter situations where habitat patches are highly variable in quality or are transient, or when weather conditions introduce added risk (as in many ectotherm systems), high demographic connectivity (sensu Stacey et al. 1997) is essential to population persistence (Harrison and Taylor 1997).

The above examples demonstrate how a more thorough understanding of landscape connectivity could emerge from conducting empirical studies over sufficiently large spatial scales so as to encompass the movement capabilities of the subject organism(s) (Thomas and Hanski 1997). Additionally, such methods are less bound to the many assumptions inherent to predicting responses across scales (e.g. Turner et al. 1989, King et al. 1991). This is especially desirable in light of recent EMS studies that demonstrated complex, non-linear interactions between individual movement behavior, spatial scale, and the structure of landscapes (e.g. Crist et al. 1992, With and Crist 1995, Wiens et al. 1997).

Here we make use of a system involving the adults of the stream-dwelling damselflies *Calopteryx maculata* (Beauvois) and *Calopteryx aequabilis* Say (Odonata: Calopterygidae) to explore empirically key components of landscape connectivity. Specifically, we experimentally determine each species' relative ability to move through forest and pasture habitats. We conducted experiments at a spatial scale that corresponds to both maximum foraging extent of these insects, and the lower limit of inter-stream distances within our study region. Our results, therefore, provide key insights into processes acting at relatively broad spatial scales, such as the relative likelihood of successful inter-stream movements within predominantly forest or pasture landscapes.

Background

There are a number of spatial scales at which *C. maculata* and *C. aequabilis* respond to the spatial patterning of resources. At fine spatial scales, both species are locally abundant where host plants required for oviposition (emergent aquatic vegetation) are abundant (Waage 1972, Meek and Herman 1990). Males are territorial at clumps of oviposition resources (ca 1 m²) and exhibit resource-defense polygyny (Alcock 1987; but see Forsyth and Montgomerie 1987). Experiments have shown that adults perceive and respond to the amount, quality, and dispersion of oviposition resources along the stream (Alcock 1987, Waage 1987, Meek and Herman 1990, Gibbons and Pain 1992). Subtle differences exist in those responses between the species, and adult distributions at these fine spatial scales (i.e. scale of meters along streams) reflect those differences (Meek and Herman 1990).

At medium spatial scales, forest is a potential foraging resource for both species (Taylor and Merriam 1995). Within patchy forest landscapes some adult *C. maculata* will make directed, transient movements through several hundred meters of pasture habitat in order to access forest patches (Taylor and Merriam 1995). We have observed this behavior in some *C. aequabilis* individuals, though not as frequently. When they inhabit streams within continuous forest landscapes, the damselflies do not make extended inter-habitat movements (because forest is situated immediately adjacent to the stream). Surveys have shown that *C. maculata* individuals are distributed at greater distances away from streams (scale of hundreds of meters) within fragmented forest landscapes as compared to continuous forest landscapes (Taylor and Merriam 1995).

Thus, just as adult distributions along a given stream are influenced by reproductive behaviors (i.e. movement for defending or finding territories) and the spatial patterning of oviposition resources, distributions within

a given landscape are influenced by the interaction between the damselflies' foraging behaviors and the spatial patterning of streams and forest within the landscape. As a consequence, the size of a damselflies' ecological neighborhood (*sensu* Addicott et al. 1987) may be larger within fragmented landscapes.

We were interested in how landscape spatial structure interacts with the movement behaviors of the damselflies at medium spatial scales to govern connectivity in our study region. Based on the landscape-specific foraging behaviors described previously, we suggest that – all else being equal – the likelihood of inter-stream movements is higher within fragmented landscapes (where extended foraging bouts occur) than within continuous forest landscapes. We predict that the success with which an individual moves between streams will be influenced by both the distance between streams and the nature of the inter-stream habitat. To test this prediction we performed manipulative mark-recapture experiments that were designed to directly measure the relative abilities of the two species to move through either forest or pasture habitat, over a distance comparable to inter-stream distances in the valley (700 m). More specifically, our experiments were designed to address the following points:

1. Of primary interest is whether forest and pasture facilitate movement to different degrees for these ecologically similar species. We predict that individuals of both species will move more readily through pasture habitat than through forest habitat. This is based upon observations of movement behaviors within each habitat type: within pasture habitat both species make transient movements only.

2. We are also interested in how historical behavior (*sensu* Merriam and Lanoue 1990), or behavioral context, may affect landscape connectivity. Based on extensive observations in the field, we assign the damselflies used in this study to two behavioral categories: those that use forest as a resource but need not make extended movements to access them (i.e. individuals inhabiting forested streams), and those that do not use forest as a resource (i.e. individuals inhabiting streams where forest is scarce). Henceforth we refer to the individuals as "forest individuals" and "pasture individuals", respectively. Our experiments are designed to detect net differences (if they exist) in landscape-specific connectivity, brought about by any differential interactions of the movement behaviors of those categories of individuals with landscape structure.

3. Inter-sexual differences in movement behaviors at the stream are attributed to territoriality in the males, which occurs only at the stream (Waage 1972, Conrad and Herman 1990, Meek and Herman 1990). Hence, we have no reason to believe that there should be differences between the sexes in either the overall, or the habitat-specific ability, to move through the two habitats.

Methods

Description of study area

Our study area within the Annapolis Valley region of Nova Scotia, Canada (45°05'N; 64°30'W) is heterogeneous in space and time. Oviposition resources are patchily distributed along streams, and streams are patchily distributed within various amounts of surrounding forest habitat. Within the valley proper (which consists of a mosaic of farmland and woodlots) stream habitat and forest patches are abundant and are in relative proximity (ca 0.5 to 1.2 km apart) with respect to the movement capabilities of these damselflies (ca 1 km within a day; pers. obs.). On the slopes of the valley, streams are typically several kilometers away from each other, and are separated by continuous forest.

Streams change through time with respect to suitability. It is not unusual for a portion of the streams in the region to run dry during the flight season. Under such conditions the extent to which those locales act as sinks (*sensu* Dunning et al. 1992) to adults will depend in part on the abilities of the damselflies to move to more suitable streams.

Field methods

To verify that our desired experimental spatial scale of 700 m would provide reasonable reobservation rates, we performed a preliminary experiment using *C. maculata* (assuming the results would be applicable to *C. aquabilis*). This experiment was very similar in design to the main experiments. We describe it in detail below, reserving an explanation of the key differences in the designs for later.

Preliminary experiment

On 25 June 1996 we captured and marked 50 individual *C. maculata* of each sex at a forested stream (Tupper Lake Brook, UTM Zone 20T: 374500 m E, 4986500 m N). Only reproductive adults in good condition were used (with undamaged wings). Damselflies were caught using a standard insect flight net, and placed in a cooler at approximately 10°C. Alphanumeric markings were painted on the hind wings using thinned whiteout fluid (Forsyth and Montgomerie 1987). We displaced 10 of each sex at distances of 350 and 700 m from the stream at two different locations; one where the most direct route to their required stream habitat (there was only one stream in the vicinity) would take them through continuous forest, and the other where the most direct route was through patchily cut forest. These treatments were included first, to verify that the distance displaced affected reobservation success, and second, to test whether intermittent open areas along a displacement route would produce a detectable difference in

movement abilities as measured by reobservation rates. Ten control individuals of each sex were released at the stream, providing the expected proportion of the released individuals to be reobserved. Releases involved placing the cooled damselflies within a 1-m³ mesh cage, allowing them to acclimatize over 30 min, and opening the cage to allow them to fly away on their own accord. All groups were balanced according to the amount of time each individual endured captivity (all within two hours). Over the first three fair-weather days following the release (up to a maximum of six days), between 0900 and 1700 h, we patrolled the stream for marked individuals. Reobservation effort included walking up and down a 350 m section of the stream while agitating the streamside vegetation. Any marked individuals within sight of the stream counted as a reobservation. These tactics avoid biases in observation rates among sexes experienced by more passive observation (Henderson and Herman 1984). Marked individuals are easily viewed with the naked eye, but 7 × 28 binoculars were used when required.

We analyzed the results using logistic regression, with reobservation success as the binary response variable, and SEX¹, HABITAT and DISTANCE as the explanatory factors. The terms of interest in the resulting models are the interactions between DISTANCE and all other factors. All statistical models presented were fit using the glm procedure in S-Plus (Chambers and Hastie 1992). We assessed the adequacy of fit of all models using residual diagnostics (McCullagh and Nelder 1989).

We justify treating each damselfly as an independent observation in these models in two ways. First, we have seen no evidence to suggest that, when releasing the damselflies in groups away from the stream, they affect one another's movements. Similarly, when releasing them at the stream, where males are territorial, equal numbers are removed and replaced such that the density of damselflies before and after release would be the same (thus minimizing any confounding density-dependent behavior). Second, weather conditions and release times are controlled for, such that each individual in each experiment receives roughly the same amount of manipulation and handling, all under similar environmental conditions.

Main experiments

All experiments were conducted between 28 June and 31 July of 1996. Fig. 1 depicts a schematic representation of our main experiments. They involved capturing and individually marking damselflies, releasing a portion of the individuals within the native landscape, and transferring the others to a structurally different landscape. The

reciprocal manipulations using the same two landscapes are performed simultaneously. Table 1 shows the locations of the experimental streams, and the details of sample sizes and replication for each treatment. Displaced individuals are released 700 m away from a single stream (their required reproductive resource), and control individuals are released adjacent to the stream, providing the expected number to be reobserved. We equate the movement abilities of the damselflies through each habitat type with the proportion of displaced individuals observed to have reached the stream, as measured against the number of control individuals reobserved.

Experimental landscapes were chosen according to two key criteria. They were required to have (1) a 700-m displacement trajectory predominantly homogeneous in structure throughout; i.e. the minimum distance route for the damselflies to fly was either forest or pasture, both along the entire 700-m length, and for a band of several hundred meters wide; and (2) only one stream in the vicinity; i.e. the next nearest stream was more than 1.5 km away from the release point. One forested site – North River – had a quiet, infrequently used dirt road (3 m wide) that crossed the displacement trajectory near the stream. Concurrent work (Ian D. Jonsen unpubl.) found that all of the forested streams used in our experiments had over 75% forest cover within a 500 m radius, while our pasture streams had more than 75% of non-forest cover (i.e. hay fields or pasture) within the same distance radius.

As in the preliminary experiment, we analyzed the results using logistic regression, with reobservation success as the binary response variable, and SEX, SOURCE, and RELEASE as the explanatory factors. Control and

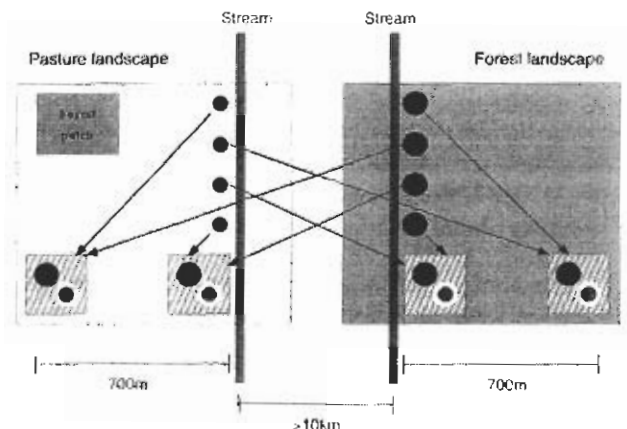


Fig. 1. Schematic diagram of one replicate of the main manipulation experiments. Each circle represents a group of males and females (at least 5 of each, at most 10). Black circles represent individuals caught within forest landscapes, and grey circles are pasture individuals. Arrows indicate displacements within, and transfers between landscapes. Diagonally hatched boxes represent 1-m³ cages. Reobservation effort was balanced by time of day among landscapes.

¹ Throughout the text, factor names included in statistical models are in SMALL CAPS font.

Table 1. Names and locations of streams used for experiments, with their respective numbers of females and males used for manipulations. "P" and "F" denote pasture and forest respectively, so the sample sizes accompanying P-P would indicate the number of individuals captured *and* released in the pasture landscape, while P-F would indicate the numbers captured in the pasture landscape but released in the forest landscape. The same pattern follows for F-F and F-P.

| Species | Pasture stream | Forest stream | Female "N" | Male "N" |
|---------------------|--|---|-----------------------------------|-----------------------------------|
| <i>C. aquabilis</i> | Tributary of Canard River 383200 m E, 4987300 m N | North River 370800 m E, 4980800 m N | P-P 10, P-F 10, F-F 10, F-P 10 | P-P 10, P-F 10 F-F 10, F-P 10 |
| <i>C. aquabilis</i> | Graves Brook 354300 m E, 4990200 m N | North River 370800 m E, 4980800 m N | P-P 18, P-F 20, F-P 13 | P-P 20 |
| <i>C. maculata</i> | Black River 345600 m E, 4977100 m N | Fales River 349800 m E, 4976000 m N | not used | P-P 14, P-F 14, F-F 16, F-P 17 |
| <i>C. maculata</i> | Graves Brook 354300 m E, 4990200 m N | South River 358100 m E, 4980700 m N | P-P 10, P-F 10, F-F 12, F-P 12 | P-P 18, P-F 18, F-F 20, F-P 20 |
| <i>C. maculata</i> | Graves Brook 354300 m E, 4990200 m N | Tupper Lake Brook* 374500 m E, 4986500 m N | F-F 10, F-P 10 | F-F 10, F-P 10 |

* This site was used for the preliminary experiment also.

displaced individuals are distinguished in the models using the binary factor DISPLACE, so the terms of interest in the resulting models are the interactions between DISPLACE and all other factors. SOURCE, referring to the source landscape of the damselflies, was the term used to assess the importance of historical behavior on movement abilities, i.e. do attributes (like behavior) specific to the damselflies' native landscapes lead to net differences in movement abilities within the two habitat types? RELEASE refers to the release landscape, and was used to assess overall effects of habitat type on movement abilities. For both species we fit models including the main effects and all two- and three-way interactions. In view of the relatively small sample sizes, we consider results to be biologically meaningful if associated type-I error rates are less than 0.1. Results falling near this value warrant further investigation.

One full replicate experiment included displacements of groups of both sexes within and among the pasture and forest landscapes (Fig. 1). On some days and at some sites limited numbers of one sex allowed for only partial replicates (i.e. treatments on one sex) to be performed; i.e. it would take too long to capture enough of both sexes in one day. In these instances we attempted to complete the unfinished portion of the experiments on the next day, while allowing for continual reobservation by using an additional experienced observer. The resulting sample sizes and details of replication are shown in Table 1. We were required to use different landscapes for each species, therefore we analyze each species separately.

Results

Preliminary experiment

A total of 17/50 (34%) of the males and 7/50 (14%) of the females were reobserved in the preliminary experiment. Based on the reobservations of control individuals (9/10 for males, and 4/10 for females), the expected

proportion of each release group to be reobserved was 0.9 and 0.4 for males and females, respectively. We reobserved an average of 35% of the expected number of individuals released at 350 m, and 10% of those released at 700 m. Thus DISTANCE had a significant effect (deviance explained = 22.67 on 110.2 Null deviance; $P(\chi^2) < 0.001$), but there was no significant difference in the likelihood of reobserving individuals released in the continuous forest as compared to the patchy forest (effect of HABITAT, deviance explained < 1; $P(\chi^2) > 0.1$).

Thus, reobservation rates were low, but sufficient for us to continue to use 700 m as the experimental displacement distance.

Main experiments

C. aquabilis individuals moved with similar ease through forest and pasture habitat (Table 2; no effect of RELEASE \times DISPLACE, Table 3), while *C. maculata* individuals moved much more readily through pasture habitat than through forest (Fig. 2; effect of RELEASE \times DISPLACE ($P(\chi^2) < 0.01$), Tables 4 and 5). Thus, our first prediction was supported for *C. maculata* but not for *C. aquabilis*.

Historical behavior did not have a statistically significant effect on the relative movement abilities of either species in general, nor within either habitat type (effects of SOURCE \times DISPLACE and SOURCE \times RELEASE \times DISPLACE, for both $P(\chi^2) > 0.1$; Tables 3 and 5). However, Fig. 2 suggests that pasture *C. maculata* individuals from pasture landscapes exhibited slightly better relative movement abilities than forest individuals in forest habitat, and also to a lesser extent in pasture habitat (effects of SOURCE \times DISPLACE and SOURCE \times RELEASE \times DISPLACE, for both $P(\chi^2) = 0.13$; Table 5).

Males and females of both species generally moved with equal abilities, irrespective of habitat type (no effect of SEX \times DISPLACE, Tables 3 and 5). A significant interaction of SEX \times RELEASE \times DISPLACE was found for *C. aquabilis* individuals (Table 4, $P(\chi^2) = 0.015$); males

Table 2. Experimental reobservation rates (RR) for *C. aequabilis* individuals. Provided are the percentage and actual numbers (reobserved/released) for each treatment group. The last column shows the calculated relative reobservation rates.

| Treatment | RR of control individuals | RR of displaced individuals | Relative RR (RR displaced - RR controls) |
|----------------------|---------------------------|-----------------------------|--|
| Released in forest* | 43.3% (13/30) | 6.9% (2/29) | 15.9% |
| Released in pasture* | 68.1% (32/47) | 10.6% (5/47) | 15.6% |
| Taken from forest† | 48.1% (13/27) | 11.5% (3/26) | 23.9% |
| Taken from pasture† | 64% (32/50) | 8% (4/50) | 12.5% |

* Effect of RELEASE landscape on reobservation rates, irrespective of SEX and SOURCE landscape.

† Effect of SOURCE landscape on reobservation rates, irrespective of SEX and RELEASE landscape.

moved more readily through forest habitat than did females, while the reverse was true in pasture habitat (Fig. 3).

Discussion

Determining the habitat-specific movement abilities and tendencies of animals is crucial for a better understanding of landscape connectivity (Merriam 1991). Several field studies have provided fine-scale data regarding the way in which vegetation structure affects the movement patterns of animals (e.g. Crist et al. 1992, Wiens et al. 1997). At larger spatial scales most data have come from tracking and mark-recapture studies within patch systems interconnected by movement corridors (e.g. Fahrig and Merriam 1985), habitat of varying quality (e.g. Duelli et al. 1990, Thomas and Harrison 1992), or some combination of both (e.g. Wegner and Merriam 1979, Machtans et al. 1996). In the few cases where the spatial scales were sufficient to encompass the movement capabilities of the subject organism(s), a strong understanding of the relationship between movement behavior and observed spatial dynamics was gained (e.g. Fahrig and Merriam 1985, Thomas and Harrison 1992).

We used a novel experimental design to measure directly the relative abilities of two ecologically similar damselflies to move through forest and pasture habitat. We knew that under natural conditions both species moved through each habitat type as part of their daily activities. While forest holds some value as a foraging resource to the damselflies, pasture is a non-resource habitat. We conducted our assessments over a distance comparable to the extreme foraging range of these insects, which corresponds to minimum inter-stream distances in our region.

We found that *C. maculata*, a species relatively consistent in its use of forest as a resource (Taylor and Merriam 1995), moves significantly more readily through 700 m of pasture habitat than through the same distance of forest (Fig. 2). *C. aequabilis*, a species

peculiar to open stream habitats (Walker 1953), moved through pasture and forest with equal abilities.

These results have important implications for the regional dynamics of *C. maculata*, given the spatial structure of habitat in our study region. Specifically, our results suggest that, all else being equal, *C. maculata* will move more *successfully* between streams separated by 700 m of pasture than between those separated by 700 m of forest. More generally, we predict that movements among streams that are separated by mixed pasture-forest habitat are more *likely to occur* than analogous movements in landscapes where streams are separated by continuous forest.

Other observations lend strength to these predictions. Surveys elsewhere showed that *C. maculata* occurred more frequently at greater distances away from pasture streams than forest streams (Taylor and Merriam 1995). Furthermore, *C. maculata* have frequently been observed making extensive, directed flights between streams and forest patches that are separated in space (Taylor and Merriam 1995; this study). Taken together, these results suggest that the removal or fragmentation of forest that surrounds stream habitat may act to enhance interactions among local populations at broad spatial scales. In contrast, the results also suggest that at the finer, foraging scales, the removal of forest habitat for foraging might have negative consequences for the

Table 3. Analysis of deviance table. Results are from a logistic regression of the success of reobserving *C. aequabilis* individuals according to experimentally controlled effects. Only those terms including the displace factor are shown.

| Term | Df | Deviance | $P(\chi^2)$ |
|-----------------------------|-----|----------|-------------|
| Null | 150 | 193.14 | |
| DISPLACE | 1 | 45.16 | <0.001 |
| SEX × DISPLACE | 1 | 1.65 | 0.198 |
| SOURCE × DISPLACE | 1 | 0.86 | 0.353 |
| RELEASE × DISPLACE | 1 | 0.42 | 0.516 |
| SEX × SOURCE × DISPLACE | 1 | 1.17 | 0.279 |
| SEX × RELEASE × DISPLACE | 1 | 5.97 | 0.015 |
| SOURCE × RELEASE × DISPLACE | 1 | 0.13 | 0.720 |
| Residual | 136 | 129.10 | |

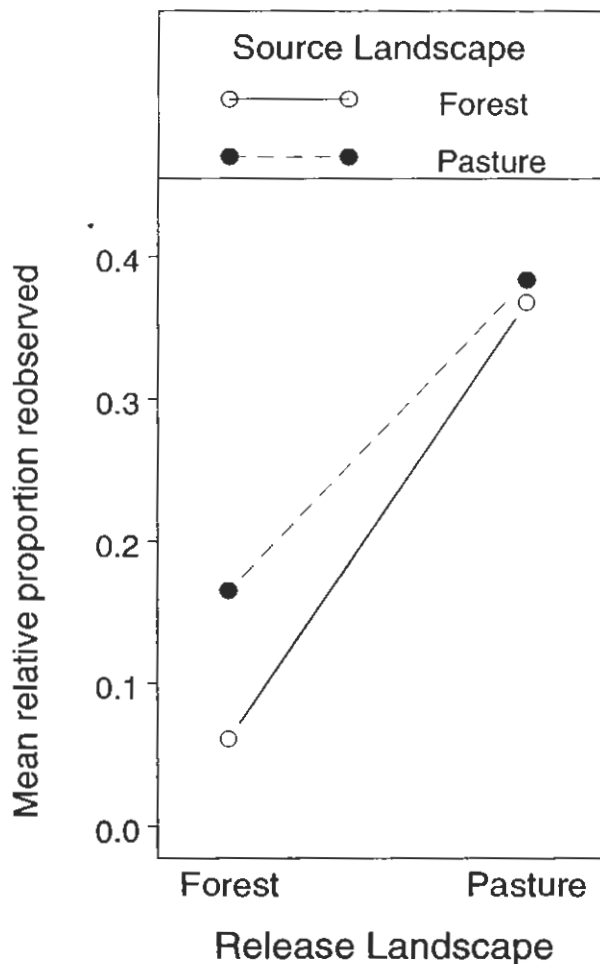


Fig. 2. Plot of the mean relative proportion (proportion of displaced individuals reobserved divided by the proportion of control individuals reobserved) of *C. maculata* individuals reobserved (see Table 3 for data) according to SOURCE and RELEASE landscapes. The difference in the relative proportions reobserved among RELEASE habitat types is significant ($P(\chi^2) = 0.005$). For example, a relative proportion of 0.17 of the individuals native to pasture landscapes (filled circles) that were released in forest landscapes were reobserved.

damselflies. The important point is that altering landscape structure may affect population-level processes in different ways at different scales.

Table 4. Experimental reobservation rates (RR) for *C. maculata* individuals. Provided are the percentage and actual numbers (reobserved/released) for each treatment group. The last column shows the calculated relative reobservation rates.

| Treatment | RR of control individuals | RR of displaced individuals | Relative RR (RR displaced ÷ RR controls) |
|----------------------|---------------------------|-----------------------------|--|
| Released in forest* | 71.6% (48/67) | 6.4% (4/63) | 8.9% |
| Released in pasture* | 56.8% (25/44) | 21.3% (10/47) | 37.5% |
| Taken from forest† | 69.6% (48/69) | 10.3% (7/68) | 14.8% |
| Taken from pasture† | 59.5% (25/42) | 16.7% (7/42) | 28.1% |

* Effect of RELEASE landscape on reobservation rates, irrespective of SEX and SOURCE landscape.

† Effect of SOURCE landscape on reobservation rates, irrespective of SEX and RELEASE landscape.

Table 5. Analysis of deviance table. Results are from a logistic regression of the success of reobserving *C. maculata* individuals according to experimentally controlled effects. Only those terms including the DISPLACE factor are shown.

| Term | df | Deviance | $P(\chi^2)$ |
|-----------------------------|-----|----------|-------------|
| Null | 220 | 296.30 | |
| DISPLACE | 1 | 69.79 | <0.001 |
| SEX × DISPLACE | 1 | 0.34 | 0.559 |
| SOURCE × DISPLACE | 1 | 2.28 | 0.131 |
| RELEASE × DISPLACE | 1 | 8.01 | 0.005 |
| SEX × SOURCE × DISPLACE | 1 | 0.03 | 0.855 |
| SEX × RELEASE × DISPLACE | 1 | 0.77 | 0.381 |
| SOURCE × RELEASE × DISPLACE | 1 | 2.30 | 0.130 |
| Residual | 206 | 205.82 | |

Empirical evidence demonstrates that the ability of animals to persist in transient habitats is directly related to mobility (e.g. Solbreck 1995, Denno et al. 1996). Our study system can be considered transient in that the abundance or quality of stream habitat (either oviposition sites or actual stream water) varies both within and between flight seasons. In dry years, for example, adults may be required to move to different streams for mating and ovipositing. The success with which a damselfly moves to an alternate stream will be a function of the inter-stream distance, and the individual's ability to move through the intervening habitat. We predict that the ability of adult *C. maculata* to move to different streams, and thus endure severe seasons, would be higher in the patchy landscapes than in the forested landscapes.

Our experimental design also allowed us to assess the relative importance of historical behavior to the connectivity of forest and pasture habitat types. Merriam and Lanoue (1990) found that groups of white-footed mice selected for specific behavioral tendencies used fencecrosses in slightly different ways. Here we tested whether individuals that do not use forest resources in their host landscapes moved with different abilities than their forest-inhabiting counterparts. Although we did not find any significant differences in movement abilities among those behavioral groups, the power of this portion of the experiments was relatively low because considerably fewer *C. maculata* were taken from pasture landscapes than from forest landscapes. We

suggest that more experiments could reveal further interesting results regarding how historical behavior influences the habitat-specific connectivity.

We found no difference in the movement abilities of the sexes in our experiments. We did, however, find that the relative reobservation rates of male *C. aquabilis* was higher in forest landscapes than in pasture landscapes, while the reverse was true for females (Fig. 3). This particular result is based on comparatively few reobservations, and as such would benefit from further experiments.

Conclusion

We demonstrate a relatively straightforward method to directly assess the habitat-specific movement abilities of

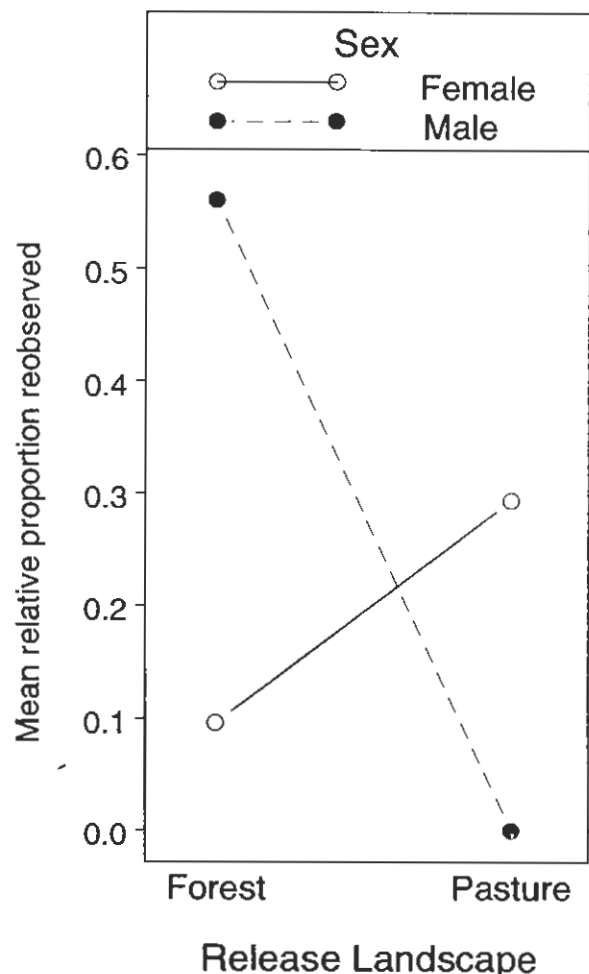


Fig. 3. Plot of the mean relative proportion (proportion of displaced individuals reobserved divided by the proportion of control individuals reobserved) of *C. aquabilis* individuals reobserved according to SEX and RELEASE habitat. The interaction term of SEX \times RELEASE \times DISPLACE was significant ($P(\chi^2) = 0.015$). For example, males (filled circles) were reobserved in higher relative proportions when released in forest landscapes as compared to pasture landscapes.

animals. We were interested in determining the potential for broad-scale movements of damselflies among streams separated by forest or pasture habitat. We performed experiments over a distance comparable to inter-stream distances, thus minimizing the extent to which we were required to extrapolate our findings across spatial scales.

Information gleaned from such an approach would add much to predictive models of population persistence or distributions (e.g. Schippers et al. 1996). In some systems such information may be less critical (e.g. Hanski 1994), but in others this kind of connectivity may largely be defined by subtle interactions between animal behavior and landscape structure that could only be revealed by such spatially explicit empirical techniques (Merriam 1991, Wiens 1997). We suggest that this experimental design could be applied in other similar systems, to further our understanding of the fundamental concept of landscape connectivity. Selecting species and individuals for particular life-history traits or behavioral characters (as we have here) will provide a better mechanistic understanding of landscape structure and its relationship to animal movements (Wiens et al. 1993).

Acknowledgements – We thank Heather Forsythe for assistance in the field, and local landowners for access to experimental sites. This work was supported by an Acadia University Graduate Research Fellowship to JP. PDT acknowledges support from NSERC and Environment Canada (CWS) through their support of the Atlantic Cooperative Wildlife Ecology Research Network (ACWERN).

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