

Movement behaviours of a forest odonate in two heterogeneous landscapes

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ABSTRACT

The results from an empirical survey of *C. maculata* along streams in both a largely forested landscape and a more open, agricultural landscape are compared so simple measures of landscape structure, and the output from a behavioural simulation model based on a set of simple rules that govern how *C. maculata* accesses resources in the two landscapes. In the more open landscape, only proximity of the forest to the stream explains the empirical pattern of distribution, but in the more forested landscape, only simulated use of streams does. Further, populations are aggregated at broader spatial scales in the more open landscape. Collectively, the results suggest that *C. maculata* move more extensively when compared to the more closed, forested landscape, which has implications for landscape-scale population structure.

INTRODUCTION

Humans can influence the structure of forested landscapes over very large spatial scales. Activities such as farming permanently remove forest habitat and replace it with open pasture or crops. Forest harvest removes standing timber which is replaced by new forest that will have a younger age structure and may also have a radically different species composition. In both cases, the underlying structure can also vary through time. Most importantly, human-induced processes such as these typically occur at very broad spatial

scales; scales that may encompass typical population-level processes such as dispersal and mating, for a variety of taxa.

For many odonates, forest is an essential habitat – a home for species that typically are not or can not be found anywhere else (Corbet 1999). But for many odonates, forests are just one of several habitats where important components of the life-cycle can occur. For example, forests may serve as ‘resting’ habitat for teneral, so they can mature away from areas where they may otherwise be harassed by adults or subjected to greater predation (Corbet 1999). For yet more species, forests provide foraging and daily roosting sites that are distinct from oviposition and mating sites (Corbet 1999). In these latter situations, daily or seasonal movements must occur so that individuals can access not only patches of forest habitat but other habitats where oviposition and mating take place.

Population persistence is the key issue for management and conservation of many species. In heterogeneous landscapes, persistence of populations depends not only on the presence of a complete suite of resources patches in a particular area, but further, on the collective ability of individuals (a population) within that area to move and access all of those resources. For taxa that have life stages in both terrestrial and aquatic environments (such as odonates) improving our understanding of their ability to move through landscapes and ‘string together’ sets of resources in order to survive, is key to gaining an understanding of how their populations persist in human-modified landscapes. Studies of landscape connectivity (Taylor et al. 1993; Belisle 2005) aim to do just that.

Considerable research has tackled the issue of how individual animals respond to patterns of altered forest structures arising from human activities. In odonates, such studies have typically focussed on behaviours at fine or medium spatial and temporal scales (e.g. Pither & Taylor 1999). Fine scales as those where behaviours occur within a single day and over moderate distances (up to 500 m for example for many odonate species). Activities such as territorial defence and daily foraging are included in this set. Medium scales are broader (500-2000 m), and encompass movement behaviours that typically only occur every day or second day, for example decisions regarding movement from oviposition to resting sites. Such movements are typically thought of as within population movements. Finally, landscape scales (> 2000 m), are scales over which population-level processes such as dispersal or migration occur. Such movements may occur only once or twice in an individual’s lifetime.

Of interest in these fine- and medium-scale studies are questions about how processes (for example, the movement of individual damselflies between forested and non-forested habitat) differ depending on the distribution and amount of habitat at the landscape scale (e.g. Jonsen & Taylor 2000a) and how the behaviours translate into patterns of distribution at

landscape scales (e.g. see Levey 2005). These are questions that are difficult to tackle directly, because of the large spatial and long temporal scales involved. As a consequence, it is useful to explore alternate means by which we might gain insight into these broad-scale processes that might then suggest new avenues of inquiry.

In this paper, I present an example of one such means to explore links between fine-scale behaviours and landscape-scale patterns. The system I use involves the damselfly *Calopteryx maculata* (Odonata, Calopterygidae). The species is typically found along forested streams, but can also be found in partially forested landscapes where it makes frequent flights traversing open areas to access nearby patches of forest (Taylor & Merriam 1995). It is known that fine-scale movement processes in this species (such as travel between forest habitats used for foraging, and oviposition sites) differ depending on the arrangement of those habitats (the distance between them) in the landscape. For example, Jonsen and Taylor (2000a) showed that *C. maculata* had higher rates of net displacement in landscapes that were partially or non-forested compared to those that were forested. Moreover, Jonsen & Taylor (2000b) suggested, using a simulation modelling approach, that the medium-scale patterns of dispersion in the species arose from fine-scale movement behaviours that were not only related to within-habitat characteristics, but also to characteristics of the broader landscape. They showed that, at least for *C. maculata*, that landscape 'context' influenced fine-scale behavioural decisions suggesting a kind of cross-scale interaction (Allen & Holling 2002) in behaviour.

I hypothesize that such cross-scale interactions will produce patterns of distribution unique to particular landscape types, and could also influence population structure. Consider three types of landscapes, all containing a network of streams separated from one-another by distances of 1-2 km. All streams are inhabited by *C. maculata* but the landscapes differ in the amount of forest between the streams. In landscapes with large amounts of forest between the streams, individuals will venture off the streams frequently to forage in the forest, but will rarely move from one stream to another. In landscapes with little forest, individuals will rarely move off the streams, and so again, will rarely move from one stream to another. However, in landscapes where the space between streams is partially covered with forest, individuals will move over broader spatial extents (i.e. they will have expanded ecological neighbourhoods; Addicott et al. 1987) and therefore interact more frequently with more distant populations. In the two extreme cases (completely forested and largely non-forested landscapes) it might be hypothesized that the population structure in a forested landscape will be more like a true metapopulation (sensu Harrison 1994) whereas in landscapes with partial forest cover, there will be more of a 'patchy population' (sensu Harrison 1994).

If these fundamental processes were indeed correct, then we could infer that landscape-scale patterns of distribution of odonates might relate to landscape-scale patterns of forest structure through the influence of that structure on fine-scale processes. Such ‘cross-scale effects’ are of interest because they may, because of thresholds and non-linearities, alter the broad-scale structure or even behaviour of systems in unexpected ways (Allen & Holling 2002). Such effects are of particular importance to landscape managers who may, for various reasons, continue to view systems as stable or linear, even when confronted with evidence that they are unstable and non-linear (Walters 1997). A clearer understanding of such complexity in empirical systems is invaluable.

However, even if they were common, such effects may be difficult to identify simply because they will likely be manifested over broad-spatial or longer temporal scales. In spite of this, it may be possible to detect the signatures of such effects through combinations of statistical models of distributions at large scales, and simulation models that relate patterns to processes across scales. Here, using a data set on the distribution of *C. maculata* within two landscapes dominated by different types of forest landscape structure, I use a simple simulation model to explore whether and how fine-scale behaviours may be translated across scales in ways consistent with the hypothesis that landscape-scale patterns of distribution of a forest damselfly are a function of fine-scale habitat attributes, meso-scale habitat, and interactions between fine-scale behaviours and meso-scale habitats.

I first sampled the distribution of *C. maculata* along most streams in two landscapes that differed in their overall pattern of forest cover and land use. I then derived two measures that could potentially explain the observed pattern of distribution of the species: 1) the distance between the stream and the edge of the nearest forest patch (of three different size classes) and 2) an index of the frequency of use by individuals of different streams within each landscape derived from a model that simulated, using a small set of very simple rules, the movement of individual damselflies within the landscape in relation to the same patches of forests and streams. I used statistical models to explore how the empirical pattern of stream occupancy related to both variables.

Of particular interest was whether the measures of simulated stream use was better at explaining the empirical distribution of damselflies when compared to the simple measure of distance between stream and forest, and whether the importance of each measure differed between the two landscape types. If simulated numbers of individuals did predict incidence, it would suggest that fine-scale individual behaviour interacted with broader-scale landscape structure (sensu Taylor et al. 1993) and that in these situations empirical distributions could not be predicted simply from knowledge of the scale of a set of particular behaviours.

METHODS

Calopteryx maculata primarily inhabit streams that flow through forest. Two resource patches are required by the species: the flowing streams (along which they mate and oviposit, and within which the larvae develop) and forested areas (within which adults roost and forage for prey) (Johnson 1962). The species is also found in fragmented-forested landscapes, where populations are present along streams that run through pastures. Individuals are capable of moving between forest and stream resource patches on a daily basis (Pither & Taylor 1999; Jonsen & Taylor 2000a).

Regional distribution. The regional distribution of *C. maculata* was surveyed in 1991 in the area around Ottawa, Ontario, Canada. All road-stream intersections in two landscapes (one north and one south of the Ottawa River; Figure 1) were visited during the middle of the day (1000-1500) during the month of July (the period of day and month when the species is most active).



Fig. 1. Classified Landsat image of study area showing open areas (light gray), forest (medium gray) and water (dark grey). The image represents an area of approximately 100 km by 200 km near the City of Ottawa, Ontario, Canada. The major river in approximately the middle of the image is the Ottawa river which roughly divides the northern and southern landscapes.

The two landscapes contrasted one another; the northern landscape was primarily forested, with small intermittent areas of agricultural land whereas the southern landscape was more open, with a more patchy distribution of forest. At each intersection, I recorded the number of male and female *C. maculata* present within 50 m of the intersection and whether the stream at that location was flowing. 85 stream/road intersections were surveyed in the northern landscape and 147 were surveyed in the southern landscape.

A Landsat image (25 m pixel size) of the Ottawa-Hull region was classified into three classes: forest, large bodies of water and non-forest (Figure 1). The area of each patch of contiguous forest was calculated, and three maps were created, one map containing all forest patches greater than 100 m², a second containing all patches greater than 1000 m² and a third map containing all patches greater than 10,000 m². The first map therefore included all patches on the second and third maps; and the second map included all patches on the third. Within these maps, I reclassified all forest below the threshold sizes as non-forest. For each of these three maps I then also created a further set of maps that showed, for each 25 × 25 m pixel, the distance and direction to the edge of the nearest forest patch. Similarly, all streams in the region were digitized from topographic maps (1:50000 NTS series) and I created a fourth 'map' giving the distance and direction of the nearest stream for each pixel. The complete set of maps thus allowed me to determine the presence of, distance and direction to three sizes of forest patch and streams for every 25 × 25 m pixel in the landscape.

Simulation model of landscape connectivity. I simulated movement of many individual female *C. maculata* within the landscape at a fine scale (i.e. movement in non-forest *vs.* movement in forest) through a single generation (a 30 day period). The simulation model was made deliberately simple since I was not interested in recreating the precise dynamics of the species' movement, but rather, in exploring how relatively simple measures of movement influenced distribution across scales.

Within the model, each female lived for 30 days (approximately the maximum lifetime for adults). Reflecting the general biology of the species, animals spent the first 8 days of their life feeding, then subsequently alternated between feeding and oviposition states. While in a feeding state, animals moved towards nearby patches of forest; while in the oviposition state, animals moved toward streams. Individuals moved in single pixel steps (~25 m) up to a maximum that depended on their state. Individuals could detect streams or forest from distances of up to ~1000 m; when further than 1000 m from either, or in forest, individuals moved according to a correlated random walk (Turchin 1998). While in a feeding state, and not in forest, individuals could move a minimum of 1500 m plus an additional amount drawn from a lognormal distribution (median distance of 300 m) in an attempt to find

forest. While in an oviposition state, individuals were effectively allowed to move until they detected a stream and then, after reaching a stream, individuals could move up or down the stream in a random direction for a maximum of 500 m. If an individual could not find the appropriate habitat within the time/distance constraints noted, it persisted in the same state for a subsequent 'day'. All individuals survived regardless of habitat. The specific parameters outlined above were estimated based on observations of the biology of the species in the area (Taylor 1993); their suitability within the model was assessed by graphically comparing the simulated distribution of damselflies in forest and non-forest sites with local-scale measures of density obtained from 750 m transects perpendicular to streams at two sites.

The patterns of movement of *C. maculata* were then simulated by populating the simplified forest/stream landscapes discussed above, with 1 individual per 50 m of stream and aggregating all points visited by all damselflies across the landscape over 30 simulated days. I term this 'simulated stream use'. The purpose of the simulation was to determine, when subjected to the specific behavioural rules outlined above, on which streams' individuals spent most of their time. The model makes no attempt to include additional factors that might influence behaviour including: density dependence, competition with con-generics or other factors associated with streams that are known to be important to the species. As such, it is highly simplified, but also overly conservative, since, if incorporated into the model, such additional elements would most likely improve the overall probability of detecting an effect.

Statistical models. All analyses were done using the R statistical package (v 2.1.0; R Development Core Team 2005). First, the spatial point pattern (random vs. clumped) was determined by calculating Ripley's K across a series of distance classes using the *Kfn* function in the *MASS* package (Venables and Ripley 2002). The values were compared to randomized distributions (1000 replications) based on the underlying distribution of sample points. Logistic regression models were fit using the *glm* function with binomial errors and logit link. Three models were fit for each of the northern and southern landscapes, one for each of the three categories of forest patch size (100 m²; 1000 m²; 10,000 m²).

Each model included a term indicating whether the stream was flowing at each empirical sample point, and pairs of the terms for proximity of forest of the three minimum size classes, and an index of the relative use of the stream at the sample point by simulated individuals (simulations run with forest patches at that scale). Fitting the term for simulated stream use after fitting the term for proximity of forest is a conservative test of the effect of simulated stream use. Such a conservative test is important, since the two terms will clearly be correlated. Overall goodness of fit of the models was assessed by examining residual plots and the dispersion parameter, and terms in models were considered of interest if their value was > 2 times their estimated standard error.

RESULTS

Female *C. maculata* were present at 32% (27/84) points in the forested northern landscape and at 12% (17/145) points in the more open southern landscape. Across both landscapes, individuals were present at ~50% of survey points where large patches of forest were closer than 750 m versus 18% of other points.

At fine scales, the empirical distribution of female *C. maculata* in the forested northern landscape was clumped at distances of ~250 m compared to the open southern landscape, where it showed a clumped distribution at scales of ~500 m (Figure 2). Beyond a scale of ~750 m, the distribution of female *C. maculata* in the southern landscape was consistently and significantly clumped whereas in the northern landscape, the distribution was not significantly different from random.

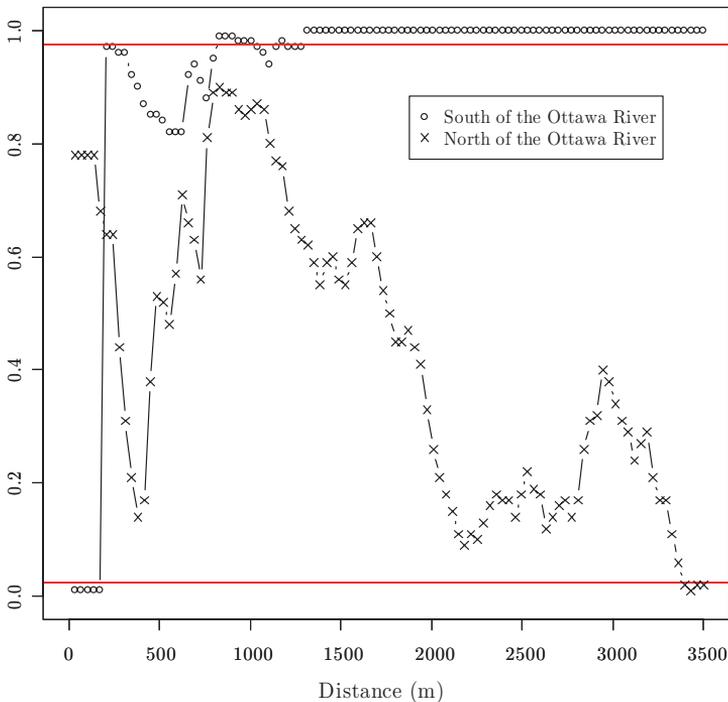


Fig. 2. The extent to which the spatial point pattern for occupied points in the southern and northern study areas are clumped, random or uniform. Shown is the deviation of the Ripley's K value calculated from points occupied by *Calopteryx maculata* from the expected value calculated from all points surveyed (y axis) compared across distance classes. Points near the top of the plot (above the horizontal line) suggest a clumped distribution; points near the bottom suggest that points are uniformly distributed.

Stream flow was positively correlated with the presence of female *C. maculata* for all models at all scales (Table 1) reflecting the fundamental importance of that resource type to the species (flowing streams are used for oviposition). In both landscapes proximity of forest or simulated stream use

Table 1. Parameter estimates (estimated standard error in brackets) from generalized linear models (binomial errors; logistic regression) fitting the presence/absence of female *Calopteryx maculata* to three variables: stream flow at the sampling site, distance to the nearest large (> 10,000 m²) forest patch and the density of animals from the simulation model. Only parameter estimates significantly different from zero (t-test) are shown.

	North	South
Flow	2.90 (1.10)	2.70 (1.00)
Distance to large forest patches	ns	-0.05 (0.02)
Simulated density	0.02 (0.01)	ns

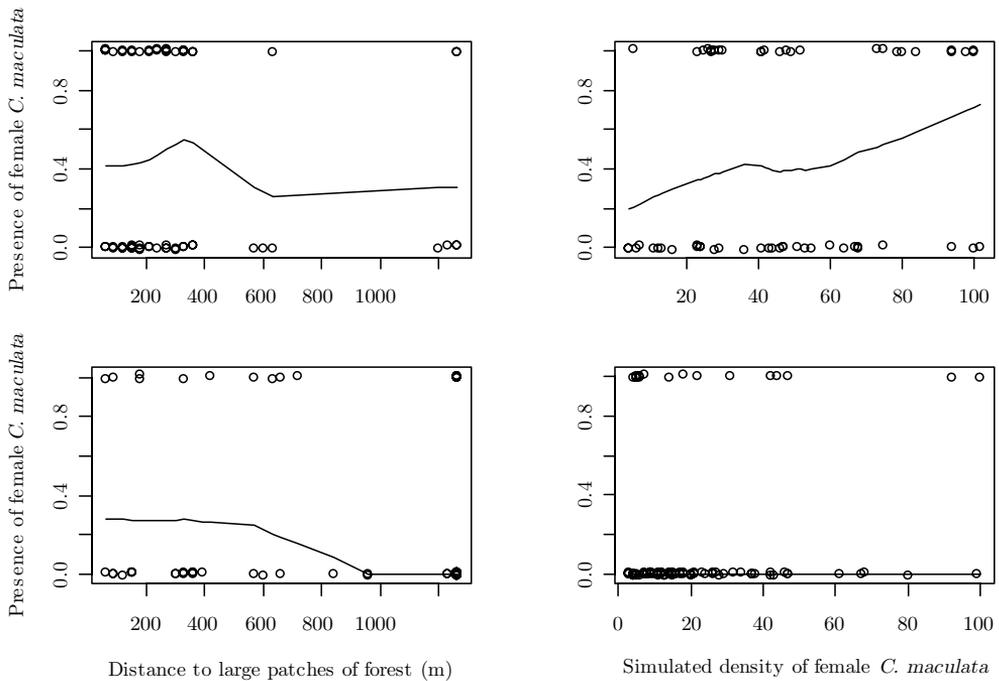


Fig. 3. Presence of female *C. maculata* in relation to Distances to large patches of forest, and to simulated stream use. Lines are locally-weighted regressions showing the probability of incidence as a function of the distance to forest patches (10,000 m²; left panels) and simulated stream use of individuals (right panels). The top two panels show results from the northern landscape; the bottom two show results from the southern landscape.

of damselflies were only found to be important when considering large forest patches ($>10,000 \text{ m}^2$). In the open, southern landscape, incidence increased with increasing proximity of large forest patches but there was no additional effect of simulated stream use. In the more forested northern landscape, there was no effect of distance to forest, but incidence increased with the index of simulated stream use (Table 1; Figure 3).

Quantile-quantile plots comparing the distribution of simulated stream use in the northern and southern landscapes show that, across the entire distribution, simulated stream use is higher in the northern landscape (points above the line in Figure 4). Since streams were populated with the same initial densities of individuals, this result demonstrates that, with the given set of behavioural rules and at the points sampled empirically, simulated damselflies spend more time along streams in the northern landscapes than in the southern landscape.

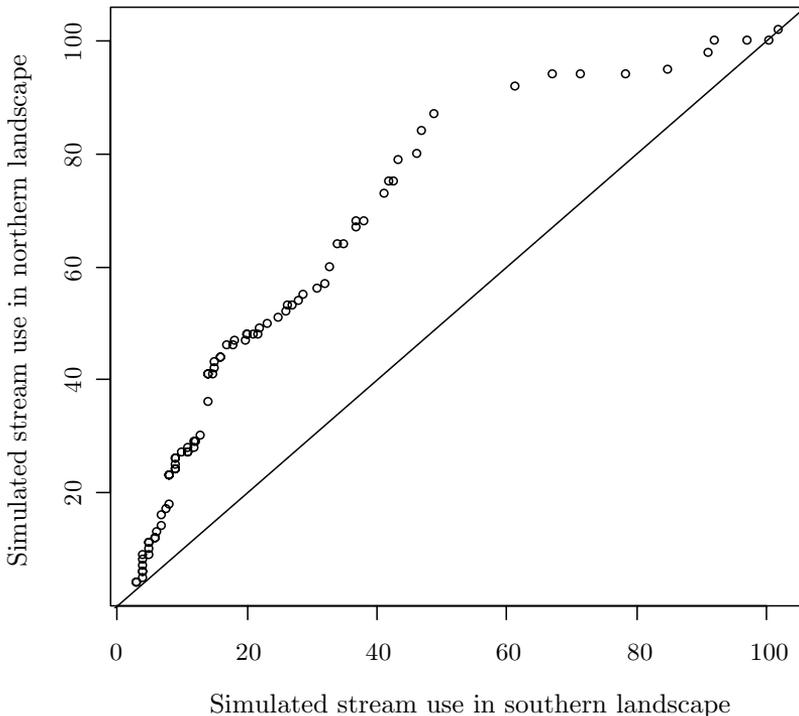


Fig. 4. Quantile-Quantile plot comparing the distributions of numbers of *C. maculata* visiting simulated streams in the southern *versus* the northern landscape. The straight line is the expected pattern when the distributions are the same. Points lying above the line indicate a larger numbers of individuals in the northern landscape compared to the southern landscape.

DISCUSSION

Collectively, the results are consistent with the scenario that in the more open, southern landscape, where resources are likely more patchily distributed, female *C. maculata* move over greater spatial extents to access resources compared to the more forested northern landscapes. Three lines of evidence support this proposition: 1) population incidence was correlated over broader spatial scales in the south; 2) proximity of large forest patches was only an important predictor of incidence in the south, and 3) quantile plots of simulated stream use showed that individuals spent less time at streams in the south than in the north.

Importantly, the results also demonstrate that a measure of landscape use, based on a small, simple set of behavioural rules, adequately explains variation in the incidence of the species in the northern (forested), but not the southern (open) landscape. The result also suggests that the presence of the species along streams in the northern landscape results from a more complex function of resource use than simple availability or proximity of resources. The converse was true for the southern landscape; proximity of the resource was the only predictor, and there was no need for additional information of how behaviour interacted with landscape structure to result in a given pattern of distribution.

If females interact with landscape structure at broader scales, different fine-scale behaviours would lead to altered patterns of distribution, and potentially, different kinds of spatial structuring of populations. One can envision that if landscapes with population structures that were similar to metapopulations (in the strict sense; Harrison 1994) gradually had resources removed from them (making them more highly fragmented) that those populations might begin to show increased flow of individuals between sub-populations and begin to behave more like patchy populations. The completely random spatial point pattern exhibited in the forested northern landscape contrasts sharply with the clumped pattern in the more open southern landscape. Such a pattern is consistent with a difference in overall population structure between the two landscapes. If animals must move over larger spatial extents to access resources, then population incidence will be spatially correlated over broader scales (Turchin 1998).

Within the more forested northern landscape, most streams are situated within 400 m of a patch of large forest. It is known that the species is readily able to access resources over these scales (Pither & Taylor 1999), however, the positive association between the simulated numbers of animals using the stream and the presence of female *C. maculata* in the forested northern landscape

implies that key elements of their behaviour are captured within the simple simulation rules (essentially, moving between forest and streams up to ~1000 m apart) within that landscape. This also implies that behaviour in the more open southern landscape is *not* captured by those same rules. Assuming that movement is likely occurring over broader spatial scales in the more open landscape, then it suggests that our fine-scale behavioural rules should include 'context' effects (a difference in behaviour that is a function of the overall landscape context; Jonsen & Taylor 2000b). Such an interaction is an example of a cross-scale effect (Allen & Holling 2002). Additional detailed explorations of the simulation model, coupled with additional empirical investigations could be used to more precisely tease apart the specific interactions between landscape structure and behaviour that gave rise to the different patterns observed in the two landscapes.

In addition to possible cross-scale context effects of landscape on fine-scale movement and distribution, there are likely effects of the intervening matrix that may enhance or diminish the observed patterns (Ricketts 2001). For example, experiments on movement abilities of *C. maculata* have been done largely within landscapes dominated by forage crops or pasture, and less frequently in landscapes with open areas dominated by scrub or food-crops. In a different system involving heterogeneous boreal forest in western Newfoundland, McPherson (2003) showed that the Libellid, *Leucorrhinia hudsonica* is less abundant in peatlands surrounded by forest than in peatlands surrounded by scrub or harvested forest. The implication (at least partially supported by direct measurements of movement; Chin 2006) is that movement is facilitated where the matrix between peatlands is more open, thus facilitating inter-peatland movement which has the effect of enhancing populations. Comparable results have been observed in other systems such as in the alpine butterfly system in Alberta, Canada (Roland et al. 2000). Assuming that matrix does generally influence movement, we might expect additional non-linearities within such systems to arise from the combined effects of human activity reducing overall resource abundance, changing its positioning within landscapes, and through changes to the non-resource matrix itself, that will influence movement processes.

The results also suggest that studies of a species' 'habitat' need to incorporate measures from multiple scales. Such multi-scale studies are now relatively commonplace for some taxa such as birds (e.g. Betts et al. 2006) but could be even more prevalent in odonate and other insect studies (e.g. see Cronin & Reeve 2005). Insight into the relative importance or even existence of underlying processes that lead to patterns of distributions will be enhanced by exploring the relationships between correlates of those processes and the patterns of distributions using simple statistical relationships.

Finally, populations of many species inhabiting human-dominated landscapes may be able to cope with moderate amounts of broad-scale habitat change, simply by altering how they link together resource patches through the process of movement. In forest landscapes, this suggests that managers must first pay attention to the amounts of different resource patches that remain on the landscape (that is, that all requisite resources must be present for a given species to survive, but then consider how such resource patches are tied together – the concept of landscape connectivity; Taylor, With and Fahrig *in press*). Managers need to be alert to the fact that altering broad-scale landscape structure may influence population structure in unexpected and possibly non-linear ways.

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