

Interactive effects of distance and matrix on the movements of a peatland dragonfly

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We conducted a mark–release–recapture survey of a peatland dragonfly (*Leucorrhinia hudsonica*) in each of two years (2002; 2003) in a harvested forest landscape in western Newfoundland, Canada. The odds of an individual male moving between peatlands was influenced by both the distance between peatlands and the type of intervening habitat (the matrix). Specifically, at meso scales (>700 m) there was a positive effect of the amount of cut matrix between peatlands on the odds of moving, but at fine scales (<700 m) there was the opposite effect; proportionally fewer individuals moved between peatlands. The odds of moving out of a peatland decreased as the surface area of water in the peatland increased. Multi-state mark–recapture models showed that the daily probability of a male moving between any two peatlands was 1.9% in 2002 and 6.9% in 2003 ($n = 1527$ and 1280 marked individuals). The results suggest that additional empirical studies that directly measure patterns of movement with respect to landscape structure at multiple spatial scales in other taxa and situations are needed in order to uncover other possible non-linear changes in behavior.

Insects and other animals respond to immediate threats and needs through the process of movement. Individuals move to forage (Ward and Saltz 1994), access habitat (Dunning et al. 1992), escape unfavourable conditions (McIvor and Odum 1988, Holt 1990), or find mates (Hilton 1984). Many empirical studies show that individuals typically move in highly localized areas through their lifetime (Harrison 1989, Roland et al. 2000, Purse et al. 2003) but, for logistical reasons, few studies directly assess long-distance (i.e. broad-scale) movements. This is in spite of the fact that these movements, among other things, allow for the colonization of new habitats and may well ensure the long-term survival of populations (Gustafson and Gardner 1996). Obtaining direct measures of broad-scale movements will improve our insight into processes such as landscape connectivity (Taylor et al. 2006) and patch boundary dynamics (Schtickzelle and Baguette 2003) which are both necessary for understanding how to manage populations in heterogeneous or changing landscapes.

For many individuals, altered landscapes have been shown to influence movement behaviors beyond what is expected from simple distance measures (Gustafson and Gardner 1996, Conrad et al. 1999, Roland et al. 2000, Jonsen et al. 2001). Additional factors that are known to alter movement behavior include the conditions in the patch an individual currently occupies (such as resource levels and population density; Larsen and Boutin 1994, Bowler and Benton 2005), the land types that separate resource patches (i.e. the matrix; Jules and Shahani 2003, Matter et al. 2003), an individual's physiological state

(McIntyre and Wiens 1999), and the perceived cost of undertaking a movement (e.g. mortality risk balanced against present needs). The actual responses of an organism to an altered landscape will vary with both the types of habitats it encounters and the spatial scale over which it is moving. These variable responses are at least in part due to the fact that an individual's perceptual range is likely to be related to the relative openness of the habitat it occupies (Zollner 2000). Most importantly, these multiple factors, acting at different spatial scales, are likely to interact, producing potentially complex behavioral responses from even simple changes to patterns of underlying landscape structure.

At least in part because of this potential complexity, there is a need for additional empirical studies that directly assess the amount of both small and broad-scale movement in altered landscapes. Such studies will allow us to paint a broader picture of how organisms interact with their environments through the process of movement, which is crucial to understanding how anthropogenic changes to landscapes influence population dynamics (Roland et al. 2000, Ricketts 2001). Such direct movement assessments need to be conducted at sufficiently broad spatial scales, that are often much greater than simple intuition might suggest. For example, indirect assessments of the movement of small Diptera in peatland landscapes (Miner and Taylor 2002, Krawchuk and Taylor 2003) suggest that we should attempt to study movement behaviors over scales of multiple kilometers.

Such broad-scale movement in altered landscapes has been studied in some insect taxa (Roland et al. 2000, Jonsen et al. 2001, Ricketts 2001) but relatively rarely in odonates. This is in spite of the fact that most are good fliers and are known to move over large spatial extents (700–4000 m) (Stettmer 1996, Conrad et al. 1999, Purse et al. 2003). Odonate movements have been shown to vary with sex (Utzeri et al. 1988), age (Angelibert and Giani 2003), wing length (Conrad et al. 2002), parasite load (Conrad et al. 2002), environmental conditions (Utzeri et al. 1988), population density (Rouquette and Thompson 2007), and distance between resources (Conrad et al. 1999). Previous experiments on *Calopteryx* species (Pither and Taylor 1998, Jonsen and Taylor 2000) and studies of *Coenagrion mercuriale* (Purse et al. 2003) suggest that altered landscapes can influence movement in odonates in potentially complex ways, and over broad spatial scales.

Here, we directly assessed meso-scale movements (between peatlands) for a common peatland dragonfly, *Leucorrhinia hudsonica*, within a heterogeneous, partially harvested, boreal forest landscape. We attempted, with partial success, to do so at a sufficiently broad spatial scale so to capture the full range of lifetime adult movements experienced by individuals. Previous broader-scale (2×2 km) surveys of the species in the landscape (Holder 2001, McPherson 2003) suggested that the presence of scrub and clearcut matrix types were associated with increased incidence and abundance of *L. hudsonica* larvae. We hypothesized that these associations might in part be explained by increased rates of movement through structurally simplified landscapes that contained more open space. Specifically, we predicted that movement would be higher in more open landscapes (as suggested by experiments with *Calopteryx*; Pither and Taylor 1998), but that these higher rates might only be manifested at broader scales, since finer-scale movements would be dominated by different behavioral processes (Jonsen and Taylor 2000). We assessed movement directly, using mark–recapture surveys across multiple scales, which allowed us to quantify the temporal frequency, the spatial extent, and between-peatland scales of movement of individuals, and to relate how those movement behaviors were influenced by matrix types within the landscape.

Methods

Study system and data collection

The Gros Morne Greater Ecosystem in western Newfoundland, Canada, is comprised of boreal forest (dominated by *Picea mariana* and *Abies balsamea*), peatlands, scrub-forest (stunted *P. mariana* and *A. balsamea*, ~ 1.5 – 2 m in height), bodies of water, and areas of harvested forest (Fig. 1). The study organism, *L. hudsonica*, a territorial species, is the most abundant odonate species in the area (Holder 2001). As adults, *L. hudsonica* use forest habitats for roosting, foraging, and sexual maturation (Hilton 1984, Corbet 1999) and occupy peatlands (and the water-filled pools within them) during mating and oviposition. Larval development occurs in pools within those peatlands (Holder 2001).

We conducted mark–release–recapture (MRR) surveys during 2002 and 2003 within a set of 15 peatlands (Fig. 1; A–O) in the Humber River watershed (UTM 5500450 0478000). We chose peatlands to represent a range of sizes, degree of accessibility and configuration within the landscape, as well as a contrasting set of intervening matrix types between pairs of patches at different distances. Peatlands were sampled between 9 July and 29 July 2002 and 7 July and 5 August 2003, i.e. during the peak flight period of *L. hudsonica* (Holder 2001, McPherson 2003). Two different spatial scales were studied in the two years. In 2002, peatlands within an area of ~ 1 km² were sampled (Fig. 1; peatlands A–G). In 2003, 3 peatlands that were surveyed in 2002 were excluded and the study area was spatially expanded to include an additional 8 peatlands resulting in a survey area of ~ 2 km² (Fig. 1; peatlands A, B, D, E, H–O).

On each sunny day between 08:30 and 17:00 during the sampling period, between one and eight people searched each peatland (in a zigzag pattern) for *L. hudsonica*. Peatlands were sampled in a rotating fashion so that each peatland had sampling effort at various times during the day over the course of the survey. To the extent possible, we made an effort to ensure that effort was constant across peatlands. Sexually mature individuals were caught with an aerial net and a unique number was written on their wing with a permanent marker. They were released at the point of capture.

The perimeter and area of each peatland was measured with a Garmin E-trex Venture GPS unit (Datum: NAD 83). We obtained physical measurements for every pool within three peatlands (B, K, M) and for $\sim 30\%$ of the pools in the remaining 12 peatlands. For each of the sampled pools, we recorded pH using an Oakton pHTester 2 meter (with automatic temperature compensation), estimated the percent cover of emergent vegetation (5% increments), the slope of the bank (% steep/gradual in 5% increments), and the surface area of water. Previous studies had suggested that such pool-scale variables might influence peatland choice for *L. hudsonica* (McPherson 2003).

Distance and amount of intervening matrix type between peatland pairs were measured from a recent aerial photograph using ImageTool 3.00 software (ImageTool Development Team 2002) using the following approach. We first classified the aerial photo into peatland and three types of matrix: scrub, forest, and harvested forest (i.e. cut). The amount of matrix between a given pair of peatlands was then measured by connecting the widest points between each pair and calculating the area of each matrix type in between. The proportion of each intervening matrix type was then multiplied by the minimum distance between the two peatlands to estimate the average distance of each matrix type that an individual would have had to travel through when moving between a pair of peatlands.

Statistical analysis

We estimated a crude measure of relative population size using overall catch per unit effort. The total effort (i.e. total number of people \times total number of minutes) in each peatland were divided by the area of water in the peatland

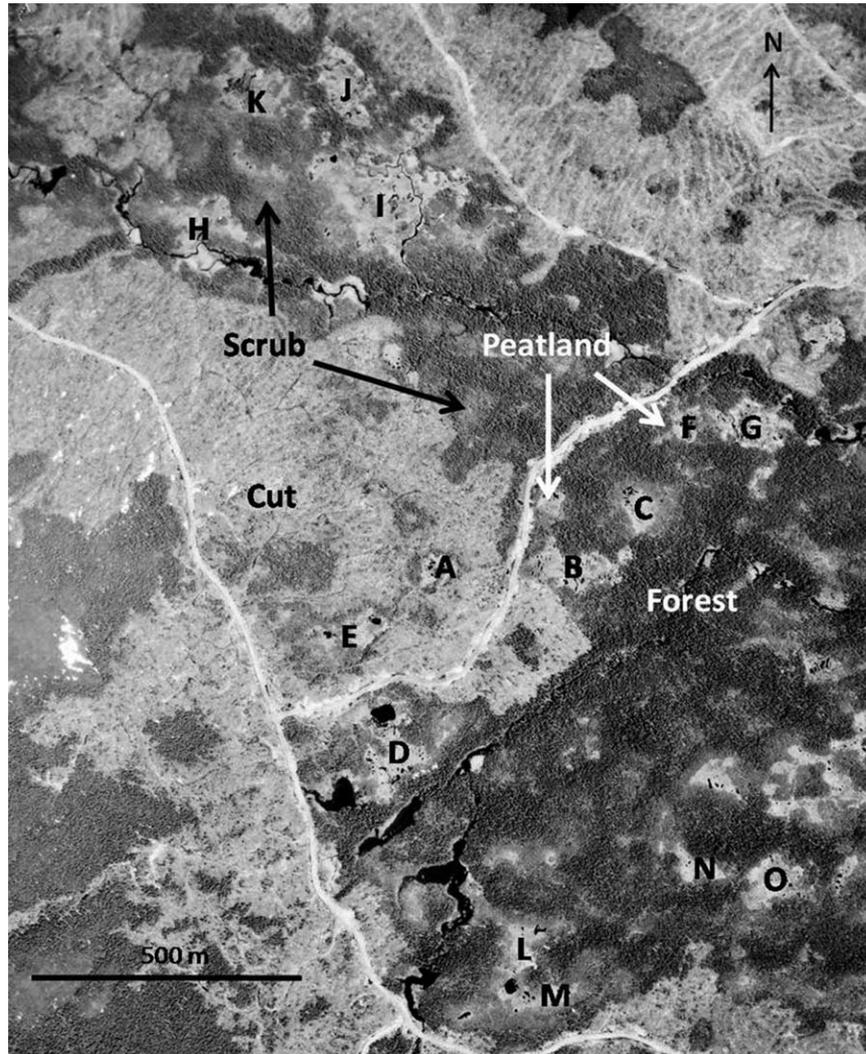


Figure 1. Aerial photograph of the study landscape. The area is composed of forest, scrub, peatlands, small bodies of water, logging roads, and commercially harvested areas (“cut”). Peatlands A–O are identified with letters over the area. Photograph courtesy of Corner Brook Pulp and Paper.

to obtain a measure of effort. Catch per unit effort was calculated as the total number of unique individuals marked in each bog, divided by effort (min m^{-2}). More sophisticated measures of population size were difficult to obtain because we know that large numbers of animals are moving between peatlands, and numbers fluctuated across sampling days.

We fit a multi-strata model for live recaptures using MARK 5.1 (White and Burnham 1999) to the data to obtain a broad idea about movement, apparent survival, and recapture probabilities within the system. Multi-strata models allow for the estimation of an overall daily movement rate among peatlands (ψ), while accounting for daily “apparent” survival (Φ) (e.g. survival plus permanent emigration from the study area) and variable recapture rates (p) in each peatland. We fixed (p) at zero for all days where no sampling occurred within a peatland. The resulting measures of (ψ) give a broad indication of daily movement rates between peatlands corrected for effort and re-sighting probabilities. We measured the goodness of fit of the overall model using \hat{c} , (an estimate of dispersion,

suggesting whether the model accounts for sufficient variability within the data). We did not attempt to fit simpler or more complex models to the data using the multi-strata framework since our intent was only to gain broad insight into a set of parameters of biological interest. Furthermore, with these data, more complex models quickly become intractable due to the sparse data and large number of possible parameters.

We fit generalized linear models (GLMs) using the binomial family (R base package v. 2.1; R Development Core Team 2006) to the odds of an individual moving between each pair of peatlands (the number of recaptured individuals that were observed to move versus the number observed not to move) using a combined backwards and forwards stepwise approach (Faraway 2005). We fit separate models for each year due to the large difference in sampling scale. For each model we first used backwards step-wise elimination from a full model including peatland-scale characteristics for both the source and destination peatlands (pH , area, slope, and emergent vegetation), catch per unit effort and distance between peatlands. Elimination of terms

was determined by considering both the relative contribution of the terms to the overall fit of the model (F-test, max type-I error = 0.05) and the stability (i.e. no fitted values close to 0 or infinity) and significance of parameter estimates (t-test, max type-I error = 0.05). After a best fit model was obtained, we tested for additional effects of the amount of cut matrix (as described above) between pairs of peatlands, and the interaction between cut distance and total distance (as suggested by plots of raw data).

Results

Overall demographic parameters

We marked 1527 and 1280 male, and 206 and 201 female *L. hudsonica* in 2002 and 2003 respectively. In 2002 we re-observed 431 (28.2%) males and 19 (9.2%) females. In 2003 we re-observed 230 (18.0%) males and 22 (10.9%) females. Of those re-observed, 81 (18.8%) males and 3

(15.8%) females had moved between peatlands in 2002 while 43 (28.7%) males and 2 (9.1%) females did so in 2003. For males, movement was observed for 30/42 (2002) and 28/132 (2003) pairs of peatlands. For females, movement was observed for 3/42 (2002) and 2/132 (2003) pairs of peatlands (Table 1). In both years, the longest movement observed was the full extent of the study area (840 m in 2002 and 1560 m in 2003) with an average distance moved of 210 ± 21 m (2002) and 432 ± 78 m (2003) (mean \pm SE) for males. Because few female *L. hudsonica* were observed to move between peatlands, we focused our analysis on males.

GOF tests in MARK using multi-strata models with a quasi-likelihood approach showed overdispersion ($\hat{c} = 5.983$ (2002) and 5.565 (2003)) suggesting that a simple, overall parameter for movement did not adequately capture all of the variation observed. Unfortunately, the relative sparseness of the data (many zeros) and large number of possible state transitions meant that more complex models would not converge. None-the-less, we estimated apparent survival

Table 1. Total numbers and proportion of adult *L. hudsonica* marked and recaptured (on subsequent days) in each peatland and observed movement between sites.

Peatland	Year	Sex	Marked	Recaptured		Movement events	
				Individuals	Proportion	Departure	Arrival
A	2002	M	170	82	0.48	12	15
		F	32	2	0.06	0	1
	2003	M	92	35	0.38	5	4
		F	13	2	0.15	0	1
B	2002	M	401	136	0.34	22	37
		F	62	6	0.10	1	0
	2003	M	171	38	0.22	4	5
		F	28	3	0.11	1	0
C	2002	M	128	54	0.42	15	10
	F	18	1	0.06	0	0	
D	2002	M	520	154	0.30	38	13
		F	57	6	0.11	1	2
	2003	M	207	35	0.17	2	2
		F	35	2	0.06	0	0
E	2002	M	161	37	0.23	10	12
		F	19	2	0.11	0	0
	2003	M	126	22	0.17	3	7
		F	8	1	0.13	0	0
F	2002	M	61	29	0.48	8	9
	F	6	0	0.00	0	0	
G	2002	M	77	19	0.25	3	12
		F	12	2	0.17	1	0
H	2003	M	48	18	0.38	8	4
		F	7	1	0.14	0	0
I	2003	M	206	75	0.36	3	9
		F	32	4	0.13	0	0
J	2003	M	51	15	0.29	4	0
		F	6	1	0.17	1	0
K	2003	M	63	18	0.29	4	1
		F	16	1	0.06	0	1
L	2003	M	37	11	0.30	5	5
		F	10	1	0.10	0	0
M	2003	M	151	69	0.46	9	8
		F	14	2	0.14	0	0
N	2003	M	19	7	0.37	1	3
		F	13	2	0.15	0	0
O	2003	M	106	42	0.40	5	5
		F	19	2	0.11	0	0
Mean	2002	M	216.9	73	0.36		
		F	31.3	3	0.089		
	2003	M	106.4	32.1	0.31		
		F	16.8	1.8	0.11		

(daily) for male *L. hudsonica* to be 0.89 ± 0.007 (2002) and 0.86 ± 0.014 (2003) and probability of recapture (daily) was estimated to be 0.14 ± 0.022 (2002) and 0.16 ± 0.058 (2003). The average daily movement rate (the probability that, on each day, an individual animal would leave a peatland and move to another within the sampled area) was estimated to be 0.019 ± 0.011 (2002) and 0.069 ± 0.048 (2003).

Logistic models of the 2002 movement data suggested that the odds of males moving between peatlands were higher for larger populations (estimated by the catch per unit effort), for pairs of peatlands close together, and when the peatland of origin had less water (Table 2). Contrary to our prediction, there was no evidence that the area of cut matrix between peatlands was related to movement. However, there was marginally significant ($p = 0.08$) evidence for an effect of an interaction between cut matrix and distance on the odds of moving, suggesting that cut matrix did indeed influence movement rates, but only at scales at or around the maximum extent of movement we were able to observe in 2002.

Logistic models of the 2003 data also suggested that the odds of males moving between peatland was higher for pairs of peatlands close together, and when the peatland of origin had less surface area of water (Table 2). Supporting our prediction, there was evidence that the effect of distance on the odds of moving depended on the amount of cut matrix between peatlands. Long distance movements were more likely, and short-distance movements were less likely, when there were larger amounts of cut matrix between peatlands (Table 2; Fig. 2).

Discussion

Influence of the matrix on movement

The results support our prediction that an open matrix increases the odds of a male *L. hudsonica* moving between peatlands, and that influence is dependent upon distance. At short distances ($< \sim 700$ m) the odds of moving between peatlands separated by a matrix comprising predominantly harvested forest are lower than those moving through a non-harvested (primarily forest) matrix. However, at long distances ($> \sim 700$ m), the opposite is true. In other words, the effect of the matrix on landscape connectivity for the species is dependent upon the spatial scale at which the system is viewed. The fact that we were

only able to detect this effect in 2003 when we had expanded the spatial scale of the study, strongly argues for additional empirical studies of patterns of movement at very broad spatial scales.

Previous studies of insect movement have shown an effect of matrix type on movement behaviors and landscape connectivity. For example, Pither and Taylor (1998) showed that *Calopteryx* dragonflies moved more readily through open habitats compared to forested habitats. Ricketts (2001) showed that for four species of butterflies, conifer matrix was 3–12 times more resistant to movement than willow matrix. Goodwin and Fahrig (2002) showed that goldenrod beetle *Trirhabda borealis* movement was related to matrix types. We expand on this body of evidence, and further suggest that relationships between landscape connectivity, matrix and scale may be complex. Such complex (i.e. non-linear) relationships could readily emerge from feedbacks between individual behavioral decisions at fine scales interacting with broader-scale patterns and process.

For example, Jonsen and Taylor (2000) compared the movement behavior of two species of *Calopteryx* along streams in forested, partially forested, and non-forested landscapes. They found that both the tendency to move away from streams and rates of net displacement differed among landscape types with individuals having a higher rate of displacement in a non-forested than a forested matrix. Pither and Taylor (1998) suggest that the distribution of *Calopteryx maculata* in a given landscape was influenced by the interaction between the damselfly's foraging behaviour (small scale) as well as the configuration of the resources within the landscape (broader scale). Both of these studies suggest interacting effects of a broad-scale feature of the landscape (the context) with a behavior at a fine scale. Such "cross-scale" effects have been suggested for other taxa (e.g. birds, Norris 2005) and provide a reasonable mechanism for the results mentioned above.

In a similar way, the different responses that *L. hudsonica* exhibits to behavior at different scales could be surmised as being the result of an interaction between behaviour and landscape structure. When undertaking fine scale movements within peatlands (e.g. territorial behaviour, foraging and subsequent roosting) *L. hudsonica* would presumably readily cross an edge into forest, since individuals forage and roost in forest (Hilton 1984). Once in forest, individuals would be relatively safe from predators and the elements, and provided the matrix consisted primarily of forest, could wander considerable distances foraging or looking for an appropriate roosting site and end up, by chance, in

Table 2. Parameter estimates and standard errors of the co-variables for the GLM with a binomial distribution estimating the influence of peatland and landscape characteristics on male *L. hudsonica* movement in 2002 and 2003.

	Estimate	SE	$p(> z)$
2002			
Catch per unit effort	0.04	0.016	0.01
Log area of water at origin (m ²)	-1.0	0.52	0.05
Distance (km)	-2.2	-0.69	0.003
2003			
Log area of water at origin (m ²)	-0.54	0.25	0.03
Total distance (km)	-3.5	1.0	<0.001
Distance through cut matrix (km)	-4.4	2.2	0.18
Total distance × distance through cut matrix	6.7	2.4	<0.001

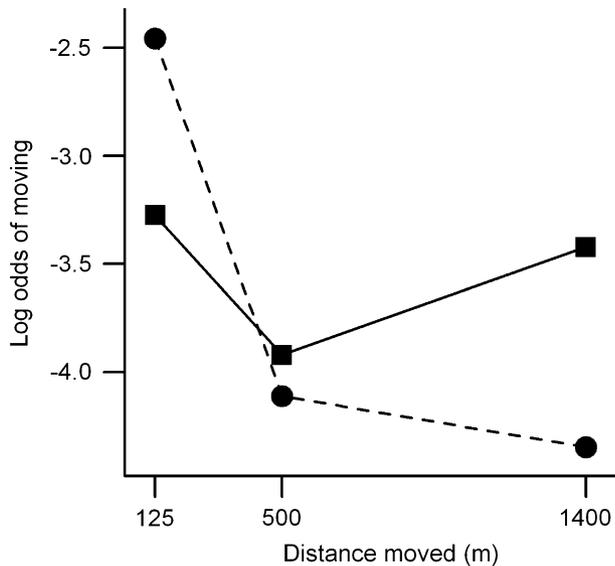


Figure 2. Interaction plot of the log(proportion) of male *L. hudsonica* moving between peatlands of various distances. Circles represent peatlands that are separated by <40% cut matrix (i.e. separated by mainly forest and scrub matrix). Squares represent peatlands that are separated by >40% cut matrix.

other peatlands. However, if individuals intent on foraging or roosting encountered an edge composed of harvested forest, they would likely remain in forest because it would provide them with the required resources (Jonsen and Taylor 2000). Longer-distance movements on the other hand, likely result from behaviors other than foraging; for example, *L. hudsonica* males likely move between peatlands to increase mating opportunities and to avoid competition for resources (Van Dyck and Baguette 2005, Chin 2006). When these individuals enter a harvested landscape, the lack of structural interference may give them more or better information about their surroundings and thus allow them to move more readily in a single direction (Zollner 2000). Because long-distance movement is usually deliberate, as opposed to accidental, it would be ideal to move through a matrix type that does not obstruct long-distance vision.

Basic demographic characteristics

In spite of relatively low recapture rates, our estimated daily movement rates are similar to those that have been observed for other odonates (McCauley 2007, Rouquette and Thompson 2007). This result, coupled with the relatively low rates of apparent survival we observed (which include permanent emigration) suggests that individuals in this system are likely moving over an even broader spatial extent than we sampled. Consider for example that even with a low recapture rate, we observed several animals move the full extent of the study area (> 1.5 km) in 2003. The spatial scale over which individuals move regularly (and thus the spatial extent over which these populations are structured) must be broader than the maximum scale we sampled. Although the rates of movement are somewhat high relative to other odonate studies, they are consistent with suggested

high rates of movement for other insect taxa in the region (Miner and Taylor 2002, Krawchuk and Taylor 2003).

Previous studies have shown that female odonates disperse more (Angelibert and Gianni 2003) or move longer distances than their male counterparts (Conrad et al. 2002), so we suspect that female *L. hudsonica* are also capable of moving at least the same distances as male conspecifics. Male and female *L. hudsonica* have different strategies to maximize their reproductive success; males aggregate within peatlands while females tend to be more cryptic, spending extensive periods of time foraging in forests to increase their fecundity and entering a peatland only when they are ready to mate (Corbet 1999). Consequently, females have the opportunity to make relatively long movements while moving about in the forest searching for food and roosting spots.

Influence of non-matrix variables on inter-peatland movement

Because *L. hudsonica* defend territories and breed at pools, competition among males may have been higher in smaller peatlands as smaller peatlands had fewer pools and consequently had a lower surface area of water. Since finding a mate is critical for all sexually reproducing organisms, if an individual was unable to find a mate or hold a territory, or if the costs of holding a territory outweighed the reproductive benefits, the individual would have been pressured into emigrating despite the energy costs and potential risks of dispersing across the matrix and finding a new habitat patch (Switzer 1997, Schtickzelle and Baguette 2003). Previous studies have shown similar findings, where individuals emigrated from smaller habitat patches because of the lack of available resources, to larger ones in hopes of improved reproductive success (Cronin 2003).

Potential population consequences

The relatively high rate of movement between patches and high proportion of animals moving across the greatest extent of the study system suggests that male *L. hudsonica*, in this system, exist as a “patchy population” as opposed to a “metapopulation” of isolated subpopulations (Harrison 1991). It appears that *L. hudsonica* are well-adapted to the patchy distribution of peatlands in the region because of these relatively high rates of movement. However, because of the observed complexity of the response to landscape structure, the effects of such changes in behavior on populations are not necessarily predictable. For example, a change in underlying landscape structure may increase or decrease the amount of movement by individuals in a landscape. Too much movement may be detrimental to population survival if it promotes spatial synchrony in dynamics (Sutcliffe et al. 1997, Earn et al. 2000), which eliminates the opportunity for demographic rescue (Brown and Kodric-Brown 1977, Liebhold et al. 2004). Conversely, a reduction in movement may prevent demographic rescue, promote inbreeding and/or restrict gene flow (Lande et al. 1999, Frankham et al. 2003). In both extremes, populations may become more vulnerable to extinction (Earn et al. 2000, Frankham et al. 2003).

Although connectivity of the Humber River watershed for *L. hudsonica* appears to be influenced by matrix type, peatlands are functionally linked at the scale in which we conducted this survey. Harvested forest was not a barrier to movement and we suspect that *L. hudsonica* is responding to changes in the landscape, which likely has population-level consequences. However, longer-term and larger-scale data sets (replicated in different landscapes) are necessary to fully evaluate changes in population demographics so that the influence of matrix types on the process of movement and consequently on population dynamics can be more directly determined.

The interactive effects of matrix composition and distance on assessments of landscape connectivity have important implications for studies that are conducted on a spatial scale that is not relevant to the organism of study and for studies that assume that patch isolation is independent of landscape structure (Fahrig and Paloheimo 1986, Harrison 1989, Conrad et al. 1999, Bagnette et al. 2000). In the present system, failing to explore the effect of matrix type on movement rates at a broader scale would not have revealed the interactive effect of distance and matrix type on movement of *L. hudsonica*. Such a result has important implications for (meta)population theory, since it shows that patch isolation can be a function of both distance between two patches (Hanski and Simberloff 1997) and matrix type (Taylor et al. 2006) and can include complex (non-linear) behavioral changes to landscapes.

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