

Fine-scale movement behaviors of calopterygid damselflies are influenced by landscape structure: an experimental manipulation

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We explore the effect of differences in landscape structure, arising from habitat loss, on the fine-scale movement behaviors of two congeneric damselflies – *Calopteryx aequabilis* and *C. maculata*. Both species require streams for breeding and naiad development and both often use forest for foraging. We compare movement behaviors across three types of landscape: forested landscapes, where stream and forest habitat are adjacent; partially forested landscapes, where streams and forest habitat are disjunct, and non-forested landscapes, where little to no forest habitat is available. We employ a reciprocal transplant experiment to determine the extent to which movement along and away from streams is influenced by landscape structure and historical behavior or morphological adaptations. For both species, we show that both the propensity to move away from streams and rates of net displacement differ among landscape types. Both species move away from streams on landscapes with high or moderate levels of forest cover but neither moves away from streams on landscapes with little or no forest. Furthermore, *C. maculata* native to predominantly forested landscapes are more likely to move away from streams, regardless of the landscape structure they encounter, than are individuals native to moderately forested or non-forested landscapes. There was no effect of natal landscape on *C. aequabilis*. Comparisons with microlandscape studies suggest that there may be some general similarities among the different systems but these are clouded by uncertainty regarding the similarity of the underlying processes responsible for observed behavioral responses to landscape structure. Despite this uncertainty, animal movement behaviors are contingent upon the structure of the broader landscape, regardless of the absolute scale of the landscape.

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Movement is a fundamental process that influences the dynamics of spatially divided populations of many organisms (Fahrig and Merriam 1985, Kareiva 1987, Turchin 1989, Wiens et al. 1993). Most animals move in search of resources such as food, mates, and shelter and to avoid predation. These movements arise from fine-scale behavioral decisions made by animals in response to heterogeneity at multiple spatial and temporal scales (With 1994a).

Habitat fragmentation alters the spatio-temporal structure of landscapes both by removing habitat and by disrupting its continuity (Lord and Norton 1990). Portions of destroyed habitat are often replaced with novel habitat types. Animals may utilize these novel habitats or view them as either neutral or inhospitable habitat (i.e., matrix). Thus, from the animal's perspective, fragmented landscapes may differ from non-fragmented ones in both the composition and configuration

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of habitat patches (Dunning et al. 1992). The degree to which connectivity (Merriam 1984, Taylor et al. 1993) differs among landscapes depends on how animals perceive, utilize, and move through the various habitat patches present and how these patches are configured. These decisions, in turn, affect how individuals are distributed over landscapes (e.g., With and Crist 1995, With et al. 1997) and, ultimately, may influence population dynamics (Fahrig and Merriam 1985, Kareiva 1987) at larger spatial scales (Wiens et al. 1993). In other words, behavioral decisions made at fine spatial or temporal scales may influence processes at broader spatial scales and/or higher levels of organization (i.e., population dynamics) (Levin 1992).

Bowers et al. (1996) point out the need for more experimental studies of habitat fragmentation in which comparisons are made between unfragmented and fragmented landscapes, rather than large and small habitat patches. That fine-scale movement behavior may be contingent on the structure of the surrounding landscape (Wiens et al. 1997) stresses the importance of conducting studies beyond simple small- and large-patch comparisons. To date, most experimental studies of behavioral responses to spatial structure have been conducted using a microlandscape approach (Wiens and Milne 1989, Crist et al. 1992, With 1994a, b). This approach is a powerful tool for testing ecological theory regarding animal movement (e.g., Wiens et al. 1997) and such studies may be used as models for broader-scale systems (Wiens and Milne 1989, Ims et al. 1993). Comparisons between microlandscape and broader-scale systems must be attempted if important processes identified at fine spatial scales are to be linked to the population processes that occur at broader spatial scales (May 1994, Kareiva and Wennergren 1995).

Here we explore the relationship between fine-scale movement behaviors and landscape connectivity for two adult calopterygid damselfly species (Odonata: Calopterygidae), *Calopteryx aequabilis* Say and *C. maculata* (P. de Beauvois), which utilize both stream and forest habitats. Both species are found along streams that flow through: (1) completely forested landscapes, where stream and forest are adjacent; (2) partially forested landscapes, where stream and forest are disjunct; and (3) non-forested landscapes, where there is little ($\leq 10\%$) or no forest. However, the two species are most abundant at opposite amounts of forest cover (Jonsen 1998). *C. aequabilis* is most abundant on non-forested landscapes while *C. maculata* is most abundant on forested landscapes. Both species have intermediate abundances on partially forested landscapes. On the partially forested landscapes we studied, pasture or cropland separate stream and forest habitats. On these landscapes, foraging *C. maculata* females can move over distances of 500 m or more to access forest habitat (Taylor and Merriam 1995). Less

is known about the movement behaviors of *C. aequabilis*, however our preliminary observations suggest that it too is capable of moving over similar expanses of pasture. Sexually immature (teneral) adult males and females often are found foraging at various distances away from streams before they are ready to mate (Waage 1972, Taylor and Merriam 1995). Thus streams and forest appear to be focal resources for these two species. The composition of partially forested landscapes differs from completely forested ones since a new element – pasture or cropland – is present. In our study we quantify the amount of forest on landscapes, therefore our analyses focus on effects of forest area rather than forest fragmentation per se.

Our initial observations indicated that both species access forest habitat on forested and partially forested landscapes but not on non-forested landscapes. Thus, we hypothesized that damselflies might vary in their abilities or propensity to move over the different types of landscape, which might have broader-scale consequences for population dynamics. Furthermore, others (Merriam and Lanoue 1990) have demonstrated that in addition to landscape structure, historical behavior or behavioral context (sensu Wiens 1997) may also influence landscape connectivity for a given animal. Over time, behavioral responses to altered landscape structure may lead to distinct morphological adaptations that may further influence landscape connectivity. For example, Taylor and Merriam (1995) demonstrated that damselflies native to fragmented landscapes had longer forewings than those native to unfragmented landscapes. They suggested that the increased distances required to access forest habitat on fragmented landscapes may have selected for damselflies with larger wing sizes. We therefore hypothesized that movement responses to a novel landscape may, at least in part, be influenced by place of origin. Place of origin refers to historical behavioral responses and/or morphological adaptations to an individual's native landscape.

Our objectives were twofold: (1) to explore the extent to which specific fine-scale movement behaviors interact with broader-scale landscape structure; (2) to explore the role of place of origin on responses to landscape structure. To address these objectives, we experimentally manipulated damselflies by capturing and transplanting them to landscapes with different structures and subsequently following their movements. This transplant experiment allowed us to simultaneously test for effects of landscape structure and place of origin on damselfly movement behaviors. We address both objectives by fitting statistical models to test the predictions that the propensity of damselflies to move away from streams (i.e., cross a stream boundary) and the rates of net displacement along and away from streams are influenced by the landscape structure they encounter and their place of origin.

Methods

Study area and species

Our study was conducted in the Annapolis Valley region (45°05'N, 64°30'W) of Nova Scotia, Canada from June to August 1996. The valley is bounded by South Mountain, which is dominated by large tracts of continuous forest and sparse agricultural land. The valley bottom is dominated by a mosaic of agricultural land interspersed with remnant forest patches. Streams flow from lakes on South Mountain into the valley. Populations of *C. aequabilis* and *C. maculata* inhabit streams on partially forested and non-forested landscapes in the valley and on forested landscapes on South Mountain.

C. aequabilis and *C. maculata* develop as naiads and mate and oviposit as adults along streams. Most sexually mature males maintain territories along streams and engage in elaborate mating behaviors that often preclude them from leaving streams (Johnson 1962, Waage 1972, Forsyth and Montgomery 1987). Adult females only require streams as a resource when they are ready to mate and oviposit; consequently, they often are found foraging in forest away from streams (Waage 1972, Taylor and Merriam 1995).

A total of six landscapes was used for experimental work. We categorized the landscapes by measuring the proportion of forest within a circle of 750-m radius around the mid-point of a stream section (approximately 50 m long) using 1:10000 scale air photos. All subsequent damselfly release points were located within these stream sections. Forested landscapes (FO) consisted of a stream flowing directly through continuous forest (mean proportion forest: 0.79 ± 0.04 sd). On partially forested landscapes (PF) streams flowed through pasture with forest 50–500 m distant (mean proportion forest: 0.38 ± 0.09 sd). Throughout this paper we refer to pasture as any grassy, non-forested habitat. On non-forested landscapes (NF) streams flowed through pasture with little to no forest within 750 m of the release point on the stream (mean proportion forest: 0.10 ± 0.03 sd).

Experimental design

Damselflies were captured on each (NATAL¹) landscape and a portion were transplanted to novel (RELEASE) landscapes (Fig. 1). We conducted reciprocal transplants between all three landscape types. Additionally, some individuals were released back onto their NATAL landscapes to act as controls for the transplant treatment. We replicated the experiment on an additional three landscapes. Thus we used six different landscapes,

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

two in each of the three levels of forest cover. No transplants between the two replicate sets were conducted.

Both control and transplanted damselflies were captured along streams and held in plastic vials on ice before release. Damselflies were released individually at streams and followed for a maximum of 30 min. All damselflies were released between 0900 and 1700 which corresponds to their daily activity period (personal observation). The position of the released damselfly was marked each minute using numbered surveyor's flags and the associated habitat type (stream, pasture, or forest) was noted. Thus for the purposes of our experiment, we defined a move as the straight-line distance covered by a damselfly within a 1-min interval. To avoid influencing movement behavior, damselflies were followed at a distance of 5–10 m and flags were placed only after they had moved. Movement pathways were mapped as a series of end-to-end vectors using a tape measure and compass.

By capturing and releasing damselflies only in stream habitat, our experimental design allowed individual damselflies to make behavioral decisions based on fine-scale (i.e., within stream habitat) and/or broader-scale (i.e., landscape) information. Individual damselflies defined how they interacted with landscape structure by (1) choosing to remain along streams or to move away (and move through other habitat types) and (2) by increasing or decreasing their rates of net displacement. The movements we recorded thus had the potential to transcend scales (i.e., fine-scale within-stream versus broader-scale between stream and forest movements).

To check for cumulative measurement error (e.g., Turchin et al. 1991) we used a backsight from the end

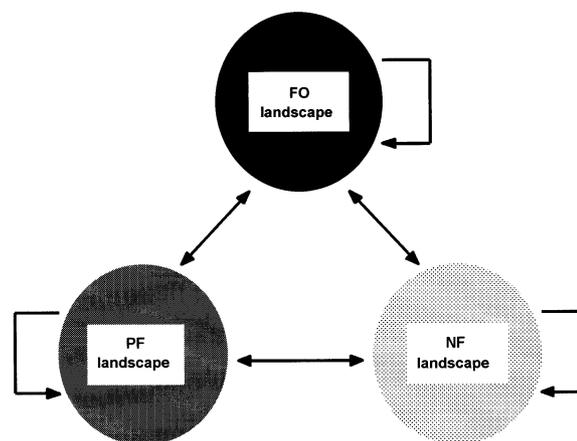


Fig. 1. Schematic diagram of experimental transplants of damselflies among landscape types. Double-headed arrows represent reciprocal transplants among pairs of landscapes. Feedback arrows represent control damselflies, captured and released back onto natal landscapes. We used two replicates of this design, for a total of six landscapes. No transplants were conducted between the two replicates.

of the pathway to the release point. When a pathway was plotted with this final bearing and distance (net displacement) it formed a polygon and the degree to which the polygon was open represented the cumulative measurement error. The mean estimated error (as a percent of the net displacement) was $3.4 \pm 0.5\%$ (1 sd) and never exceeded 19%, so no correction was deemed necessary. Removal of two pathways (14 and 19% error) from statistical analyses did not alter results noticeably, so they were not removed from the results presented here.

Movement behaviors

We calculated two variables that described the pathways of each individual damselfly: (1) the probability of moving away from the stream and (2) the rate of net displacement. The probability of moving away from stream is a measure of the propensity of damselflies to cross stream – forest or stream – pasture boundaries. Damselflies that moved more than 5 m away from streams by the end of their pathways were scored as ‘away from stream’. Thus the probability of moving away from stream is a binary variable based on the outcome of individual damselfly pathways. We frequently observed individuals momentarily fly (< 5 m) off streams only to return immediately and so we ignored these movements when assessing whether or not an individual moved away from stream. Net displacement is the straight-line distance between the start and end positions of each pathway. Several individuals were lost before 30 min, therefore we used the rate of net displacement (m min^{-1}) to standardize pathways. The rate was calculated by dividing the net displacement by the total number of minutes an individual was observed.

Statistical models

We assessed the effects of landscape structure on the two movement-pathway variables: (1) the probability of moving away from the stream and (2) the rate of net displacement. For each species we fit two separate generalized linear models (McCullagh and Nelder 1989) for a total of four models. To control for effects of variation in weather, we included in all models the environmental covariates TEMPERATURE, WIND, and CLOUD. TEMPERATURE was measured using a copper-constantan thermocouple placed 1.5 m from the ground. WIND speed was measured using a wind gauge held 1.5 m from the ground. CLOUD cover was estimated as a percent directly overhead of the observer. All three covariates were measured immediately before an individual damselfly’s release. To control for variation in time from capture to release among individuals,

Table 1. Number of damselflies tracked in each level of the factors RELEASE landscape, NATAL landscape, and SEX for the two species, *C. aequabilis* and *C. maculata*. (FO: forested landscapes, PF: partially forested landscapes, NF: non-forested landscapes).

RELEASE	SEX	<i>C. aequabilis</i>		<i>C. maculata</i>		
		NATAL				
		PF	NF	FO	PF	NF
FO	F	3	5	8	1	1
	M	3	5	4	2	1
PF	F	7	4	6	2	3
	M	7	4	4	2	2
NF	F	5	4	4	1	4
	M	8	5	5	2	3

we included in all models the covariate HANDLING TIME (the duration from capture to release that individuals were held). In the models assessing the probability of moving away from streams we also included the covariate PATH TIME (number of minutes an individual was observed), to control for variability in the duration that individuals were followed.

We then assessed the effect of each of the design factors NATAL, RELEASE, and SEX on the response. NATAL refers to the landscape that damselflies were captured on (irrespective of RELEASE landscape). We used NATAL to assess the importance of place of origin on probabilities of moving away from streams and rates of net displacement. We use place of origin in reference to either historical behavior (Merriam and Lanoue 1990, Pither and Taylor 1998) or morphological attributes (Taylor and Merriam 1995) that represent adaptations to the damselfly’s native landscape. RELEASE refers to the landscape (NATAL or novel) that damselflies were released on. We used RELEASE to assess the overall effects of landscape structure that individuals encountered on probabilities of moving off stream and rates of net displacement (irrespective of the landscape type that individuals were captured on).

Since we did not find any populations of *C. aequabilis* on forested landscapes that were suitable for tracking (due to impassable terrain and/or extremely dense vegetation) the NATAL landscape factor in these models had only two levels (PF and NF). This was not a problem for *C. maculata* since it was found more consistently on FO landscapes than was *C. aequabilis*, we therefore had a greater selection from which to choose two suitable landscapes for tracking.

To compensate for the unbalanced design (see Table 1), we retained only those design factors that had significant effects on the response, and then further tested whether any two-way interactions among these retained design factors also influenced the response. This approach was more conservative than including nonsignificant main effects when testing for significant interactions. For simplicity, we do not present non-significant interaction terms. When necessary we compen-

sated for over- and under-dispersed data by fitting Quasi-likelihood models (McCullagh and Nelder 1989, Bayley 1993). In these situations we used the *F*-test to test for significance of model terms (StatSci 1995).

Since the response: probability of moving away from streams is a binary variable (remained on stream/moved away), we fit quasi-likelihood models with binomial errors. We fit a Poisson model for the rate of net displacement analyses since means and variances were approximately equal and values could only be ≥ 0 ; this is justified even though rates of net displacement are not integer values (see McCullagh and Nelder 1989). Due to small sample sizes, the maximum probability of Type I errors for all tests was set at 0.10.

Results

One hundred and fifteen damselflies were released and followed (60 *C. aequabilis* [32 females, 28 males] and 55 *C. maculata* [25 females, 30 males]) between 13 June and 22 August 1996. The number of damselflies tracked for each level of the factors RELEASE, NATAL, and SEX is presented in Table 1.

Female *C. aequabilis* move lengths were longest and rates of net displacement were fastest on PF landscapes while male move lengths were longest and rates of net displacement were fastest on NF landscapes (Table 2). Both male and female *C. maculata* move lengths were longest and rates of net displacement were fastest on PF landscapes (Table 2). In general, both species had turn angles centered on approximately 0°, except *C. aequabilis* on NF landscapes which had a bimodal distribution of turn angles centered on 21° and 159° (Fig. 2). The dispersion of turn angles on NF landscapes was significantly different than those on FO and PF landscapes for *C. aequabilis* (Kruskal-Wallis rank-sum test, $\chi^2_{0.05,2} = 6.89, p = 0.03$), while *C. maculata* turn angle dispersions were not significantly different among landscape types (Kruskal-Wallis rank-sum test, $\chi^2_{0.05,2} = 4.43, p = 0.11$). The greater frequency of course reversals made by *C. aequabilis* on NF landscapes (Fig. 2) may occur because damselfly movements were

confined to stream habitat (see Probability of moving away from streams, below).

Probability of moving away from streams

There was a significant effect of RELEASE landscape on the probability of moving away from the stream. Both species moved away from streams when released on FO and PF landscapes, but neither species moved away from the stream when released on NF landscapes (Table 3, Fig. 3). For *C. maculata*, however, the effect of RELEASE landscape was confounded by a significant effect of NATAL landscape on the probability of moving away from the stream (Table 3; effect of NATAL). Individuals captured on FO landscapes were more likely to move away from streams than those captured on PF or NF landscapes (Fig. 3). This effect did not vary among RELEASE landscapes (no significant RELEASE \times NATAL interaction, Table 3).

Rate of net displacement

There was a significant effect of RELEASE landscape on the rate of net displacement for both species (Table 4). *C. aequabilis* moved at slightly slower rates on FO landscapes than on PF or NF landscapes (Table 4, Fig. 4), similarly, *C. maculata* had reduced rates of net displacement on FO landscapes compared to PF and NF landscapes (Fig. 4). On PF and NF landscapes, *C. maculata* moved about twice as fast as *C. aequabilis* (Wilcoxon rank-sum test, $Z_{2,df} = 2.17, p = 0.03$) but rates of net displacement were similar on FO landscapes (Wilcoxon rank-sum test, $Z_{2,df} = 1.05, p = 0.29$).

The elevated rates of net displacement on PF relative to FO landscapes (Fig. 4) appeared to be primarily due to the rates at which *C. maculata* moved across pasture in order to access stream and forest resources on PF landscapes. On PF landscapes, individuals of both species that traversed pasture to access forest habitat had significantly higher movement rates than those remaining along streams (Wilcoxon rank-sum tests: *C. ae-*

Table 2. Movement parameters for *C. aequabilis* and *C. maculata* females and males released on FO, PF, and NF landscapes. Values are means \pm 1 se. Turn angles are presented graphically in Fig. 2.

Release landscape	Sex	<i>C. aequabilis</i>		<i>C. maculata</i>	
		Move length (m)	Rate of net displacement (m min ⁻¹)	Move length (m)	Rate of net displacement (m min ⁻¹)
FO	F	6.24 \pm 2.68	0.71 \pm 0.29	4.92 \pm 0.63	0.83 \pm 0.19
	M	5.97 \pm 1.93	0.63 \pm 0.26	5.08 \pm 1.04	0.76 \pm 0.30
PF	F	7.57 \pm 1.76	1.02 \pm 0.30	14.25 \pm 3.41	2.74 \pm 1.18
	M	7.71 \pm 1.51	0.92 \pm 0.38	20.40 \pm 6.12	2.10 \pm 0.90
NF	F	3.51 \pm 0.80	0.26 \pm 0.08	14.21 \pm 3.39	1.99 \pm 0.45
	M	14.83 \pm 3.69	1.42 \pm 0.57	11.33 \pm 2.61	1.66 \pm 0.60

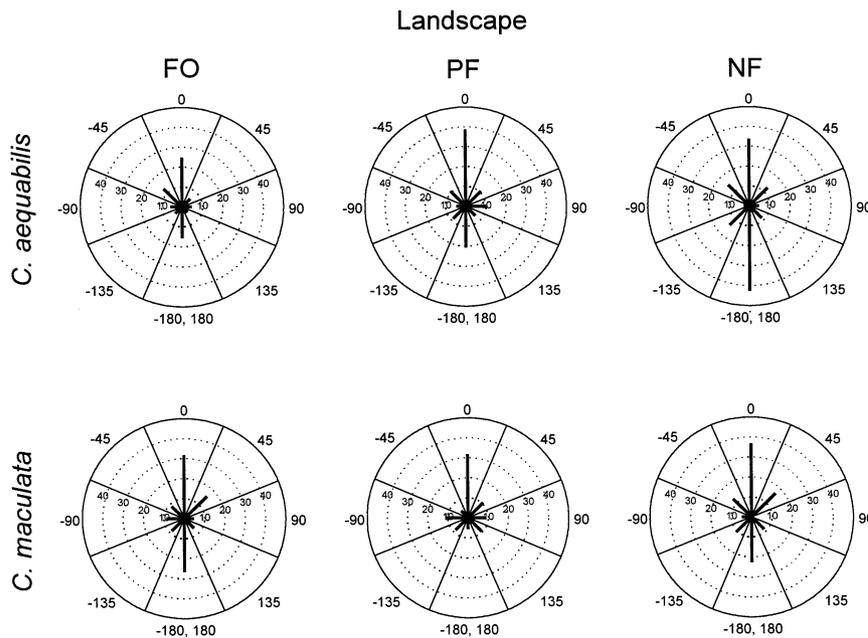


Fig. 2. Circular histograms of turn angles for *Calopteryx aequabilis* and *C. maculata* released on FO, PF, and NF landscapes. Turn angle labels indicate center points of each sector. Inner labels indicate frequency of turn angles. Observations are individual turn angles pooled across all damselfly pathways within a landscape type.

aequabilis: $Z_{2,df} = 2.81$, $p = 0.005$; *C. maculata*: $Z_{2,df} = 1.85$, $p = 0.06$). In contrast, on FO landscapes, where stream and forest habitat were contiguous, there were no differences in movement rates between individuals moving from stream to forest and those remaining along streams (Wilcoxon rank-sum tests: *C. aequabilis*: $Z_{2,df} = -0.67$, $p = 0.50$; *C. maculata*: $Z_{2,df} = 0.43$, $p = 0.67$). Movement rates on NF landscapes were not a function of movement through pasture since damselflies rarely moved off streams and none moved between stream and forest habitats.

Discussion

Interactions between movement behaviors and landscape structure

Both *Calopteryx* species obligately use streams for mating and naiad development and facultatively use forest for foraging and nocturnal roosting (Johnson 1962, Waage 1972, Forsyth and Montgomery 1987, Taylor and Merriam 1995). Hence streams and often forest are focal resources for these two closely related species. Our results indicate that both species respond to the relative proportions of these focal resources on different landscapes by altering their fine-scale movement behavior.

Our analyses provide evidence that place of origin influences how *C. maculata* move over the landscape but not *C. aequabilis*. *C. maculata* individuals native to forested landscapes are more likely to move away from streams than those native to partially forested or non-forested landscapes but *C. aequabilis* native to different landscape types all respond similarly. The result for *C.*

maculata suggests that a behavioral difference in the propensity to move away from streams exists among populations inhabiting forested landscapes versus partially or non-forested landscapes. Place of origin had no influence on rates of net displacement for either species.

Our analyses did not identify any differences in movement responses between sexes. However, this result was based on an unbalanced design that limited our ability to test for interactions between sex, release landscape structure, and place of origin. Therefore, the exploration of differences in behavioral responses between the sexes to landscape structure may benefit from further experiments.

Our results can be conceptualized as an interaction among landscape structure, patch boundary permeability (Stamps et al. 1987, Wiens 1997, Wiens et al. 1997) and patch viscosity (With 1994b, Wiens et al. 1997). *C. maculata* on completely forested landscapes readily accesses forest adjacent to streams but *C. aequabilis* does not; the permeability of the boundary between stream and forest is high for *C. maculata* but quite low for *C. aequabilis*. On partially forested landscapes both species are capable of moving away from streams through pasture to access forest. The permeability of the stream/pasture boundary on these landscapes is similar to that of the stream/forest boundary on predominantly forested landscapes for *C. maculata* but is much higher for *C. aequabilis*. Neither species utilizes pasture as a resource (Taylor and Merriam 1995, pers. obs.) so animals tend to move relatively quickly and directionally through the open habitat. In other words, the viscosity of pasture patches is low. On primarily non-forested landscapes neither species appears to access the

small amount of forest habitat present. Other experiments demonstrate that both species are capable of moving through the larger extents of pasture (Pither and Taylor 1998) so presumably the animals do not detect the presence of forest at such large distances from the stream (i.e., > 500–750 m) or choose not to venture away from the stream when there is so little forest present. Alternatively, both species may still move between stream and forest but with much reduced frequency than similar movements on forested and partially forested landscapes. If movements between stream and forest on predominantly non-forested landscapes occur very infrequently, they could go undetected within our experimental design. However, the typically observed diurnal rhythm in damselfly occupancy and mating behaviors along streams was not evident on non-forested landscapes (pers. obs.); damselflies were observed perching on riparian vegetation as early as 0630, well before daily flight activity commenced. Regardless, the permeability of the stream/pasture boundary on non-forested landscapes is very low.

The key result is that the propensity of damselflies to leave stream habitat (patch boundary permeability) depends not only on the elements comprising the boundary (represented here as stream-forest or stream-pasture) but also depends on the amount and configuration of those elements within landscapes. This relationship between patch boundary permeability and landscape structure indicates that for a given animal the connectivity of a landscape is influenced by that animal's behavioral responses to spatial structure at multiple scales. That *C. maculata* native to forested landscapes had higher propensities to move away from streams suggests that historical behavior or a morphological adaptation to forested landscapes may also be an important component of landscape connectivity for these populations.

Comparisons with microlandscape studies

A key result of this study – patch boundary permeability varies as a function of the amount and configuration

of habitat (here comprised of both stream and forest patches) on a landscape, rather than simply as a function of the elements comprising the boundary – parallels a finding by Wiens et al. (1997); the viscosity of grass patches for tenebrionid beetles increased as the overall coverage of grass on the landscape decreased. In the present study patch boundary permeability differs between partially forested and non-forested landscapes (see Fig. 3). Wiens et al. (1997) inferred from movement rates that patch viscosity decreased noticeably as the percent grass cover on microlandscapes decreased from 40% to 20%. The proximal mechanisms appear different (patch viscosity versus patch boundary permeability), however, Wiens et al. (1997) suggested that beetle movement rates within habitat may decrease as a function of an increased number of edge encounters. In other words, beetles may move more slowly through a rare landscape component (grass habitat) because they frequently pause when encountering patch edges or are reluctant to cross patch edges – patch permeability decreases as a function of amount of habitat on the landscape. Thus the fine-scale behavioral responses to both patch- and landscape structure alter landscape connectivity for beetles and damselflies in a similar way, at two very different absolute spatial scales.

Comparisons between the current study and other microlandscape studies (Crist et al. 1992, With 1994a, With and Crist 1995, 1996) are less straightforward because movement patterns in each microlandscape study were related to vegetation heterogeneity rather than amount of habitat. However, some general comparisons can be made if we consider that in the microlandscape studies the amount of grass habitat decreases with increasing heterogeneity of microlandscapes (e.g., With 1994a, b). In a study of grasshopper responses to microlandscape (25 m² in extent) and broader-scale heterogeneity, rates of net displacement of one species were highest on homogeneous microlandscapes (where preferred grass habitat was most abundant) but those of another species were highest on moderately heterogeneous microlandscapes (With 1994a). However, this relationship among rates of net displacement and microlandscape structure varied as a

Table 3. Analysis of deviance table. The response variables are probability of moving way from stream for *C. aequabilis* and *C. maculata*. Individuals were released and tracked in two sets of three landscapes representing a range of forest cover. The models are Quasi-likelihood models fit with logit link and $\mu(1 - \mu)$ variance functions. The estimated dispersion parameters are 0.70 (*C. aequabilis*) and 0.92 (*C. maculata*). Environmental covariates are the combined df and deviance for the factors: WIND, TEMP, PTIME, HTIME, and CLOUD (see Methods for description).

<i>C. aequabilis</i>					<i>C. maculata</i>				
Term	df	Deviance	F	p(F)	Term	df	Deviance	F	p(F)
Null	59	60.05			Null	52	56.70		
Environmental covariates	5	8.38	Environmental covariates	5	5.66
RELEASE	2	8.84	6.34	0.003	RELEASE	2	14.53	7.92	0.001
Residual	52	42.38			NATAL	2	5.06	2.76	0.07
					Residual	43	31.45		

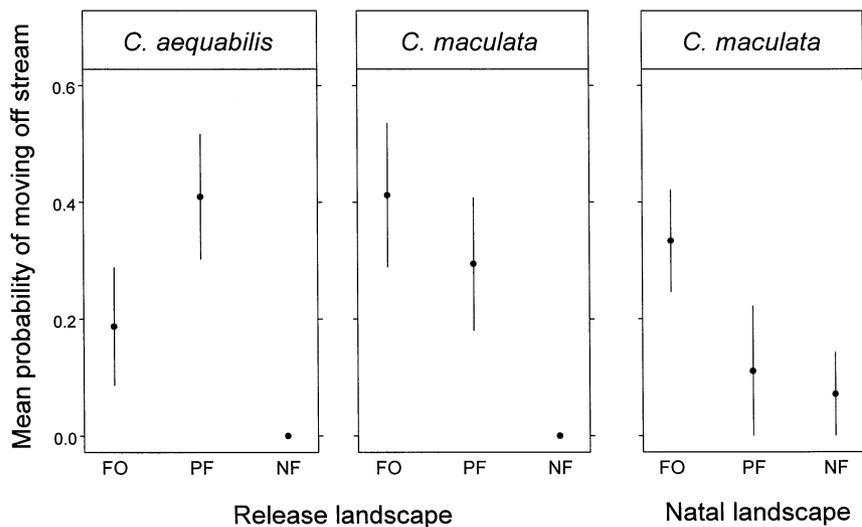


Fig. 3. The mean probability of moving from stream to forest for *Calopteryx aequabilis* and *C. maculata* released on FO, PF, and NF landscapes and *C. maculata* captured on FO, PF, and NF landscapes. Error bars are ± 1 se. Note that neither species of damselfly moved away from streams when released on NF landscapes (mean = 0 ± 0 se).

function of cattle grazing intensity at a broader scale. When homogeneous microlandscapes were a rare (8%) component of the broader landscape, transition probabilities (the probability of moving out of a given microlandscape; see With and Crist 1995) were low but when homogeneous microlandscapes were more common (21%), transition probabilities were as high or higher than on moderately or very heterogeneous microlandscapes (With and Crist 1995, 1996). This result, in some respects, parallels a key finding in the current study; damselflies have a high probability of remaining in stream habitat when the amount of forest habitat on the landscape is low. However, it is unclear whether grasshopper movement responses to broader-scale structure (i.e., pasture grazing intensity) arise from foraging behavior, as they do for damselflies in the current study, or rather from broader-scale habitat preferences (which encompass a variety of life history requirements).

In contrast to the grasshopper studies, Crist et al. (1992) found that tenebrionid beetles had higher net displacements in bare ground and grass microlandscapes but as fine-scale structural complexity increased (e.g., cactus and shrubs became more prevalent), net displacements decreased. In other words, beetles were responding to structural complexity rather than amount of habitat within the 25-m² microlandscapes. This is perhaps because tenebrionid beetles are generalist herbivores and detritivores (Wiens et al. 1997). Beetles also responded to differences in structure arising from cattle grazing at a broader scale (i.e., within pastures), however, this response was not consistent among the species observed.

A feature common to the microlandscape studies outlined here and the current, broader-scale study is the response of animals to spatial structure at more than a single scale. Animal movements are contingent upon

the internal structure of habitat patches and upon the structure of the broader landscape. Despite this broad generality, there are also fundamental differences among species within a single study and between microlandscape studies and the current study. The comparisons above highlight how difficult it can be to draw general similarities among studies conducted at different absolute scales and on different taxa.

Two features of calopterygid damselfly natural history set them apart from tenebrionid beetles and acridid grasshoppers. First, calopterygid damselflies are tied strongly to stream habitat; nymphs develop completely within streams, males defend breeding territories and mate with females exclusively along streams and females obligately oviposit on aquatic vegetation (Johnson 1962, Waage 1972, Forsyth and Montgomery 1987). Thus movements away from streams are generally transient (perhaps at the temporal scale of one or a few days) and in some respects similar to 'central place foragers' (e.g., ants and honey bees). In the microlandscape studies outlined above, beetles and grasshoppers are not tied to any specific landscape element and forage more freely over the landscape. Second, calopterygid damselflies are highly mobile insects that link stream and forest resources by sustained flight rather than by crawling, hopping, or short flights. However, others (Henderson and Herman 1984, Conrad and Herman 1990) have shown that adults of both *Calopteryx* species respond to spatial structure at similarly fine-scales (< 1 m) as tenebrionid beetles and acridid grasshoppers. The speed and nature of damselfly flight allows them to forage at broader spatial scales than less mobile species. Therefore, damselflies are not likely to be as strongly influenced by fine-scale structural complexity as, for example, tenebrionid beetles appear to be (Crist et al. 1992, Johnson et al. 1992).

Table 4. Analysis of deviance table. The response variables are the rate of net displacement (m min^{-1}) measured from individual pathways of *C. aequabilis* and *C. maculata*. Individuals were released and tracked in two sets of three landscapes representing a range of forest cover. Model 1 (*C. aequabilis*) is a Poisson model fit with a log link function, model 2 (*C. maculata*) is a Quasi-likelihood model fit with log link and μ variance functions. The estimated dispersion parameter is 1.90. Environmental covariates are the combined df and deviance for the factors: WIND, TEMP, HTIME, and CLOUD (see Methods for description).

<i>C. aequabilis</i>				<i>C. maculata</i>				
Term	df	Deviance	$P(\chi^2)$	Term	df	Deviance	F	$p(F)$
Null	59	77.28		Null	52	114.33		
Environmental covariates	4	3.46	...	Environmental covariates	4	12.80
RELEASE	2	5.83	0.054	RELEASE	2	16.24	4.41	0.018
Residual	53	67.99		Residual	46	85.29		

Despite the difficulties in making comparisons between fine-scale, experimental model system studies (e.g., Wiens and Milne 1989, Ims et al. 1993) and broader-scale studies, we suggest such comparisons, where feasible, be attempted to determine the generality of interactions between movement behaviors and spatial structure. Identifying when such generalities do and do not exist will greatly enhance our knowledge of the functioning of ecological systems and how best to manage them (Wiens et al. 1993). However, because many responses change unpredictably across scales (Wiens 1989, Levin 1992) we must ensure that similar processes underlie the responses observed in the different systems for such comparisons to be valid.

Fine-scale movements and connectivity

Our exploration of the relationship between fine-scale movement behaviors and connectivity indicates that spatial structure at multiple scales influences the ability or propensity of damselflies to traverse landscapes. Results elsewhere (Pither and Taylor 1998) demonstrate that both damselfly species are capable of travelling between streams in our study region (ca 750 m) and that pasture facilitates the ability of *C. maculata* to complete these movements successfully while *C. aequabilis* movement is neither facilitated nor impeded by pasture or forest habitat. These results suggest that, for *C. maculata*, interactions among streams (i.e., local populations) may be enhanced by moderate loss of forest habitat but for *C. aequabilis* interactions among streams should remain similar regardless of the amount of forest habitat present. However, we demonstrate that a fine-scale behavior, the decision to move away from a stream, is strongly influenced by the amount of forest habitat on the landscape. When little or no forest is present within 750 m of the stream, damselflies do not move away from the stream. Thus we predict that exchange of individuals among streams may be enhanced on partially forested landscapes but will be greatly reduced on non-forested ones. The implication is that landscape structure mediates exchanges of individuals among populations via fine- and broader-scale

(dispersal) movement behaviors. The extent to which such a prediction is upheld will depend upon the similarity between damselfly movement behaviors for accessing forest (foraging) and for dispersal. At present we have no evidence to suggest that these movements are fundamentally different (i.e., governed by different sets of behaviors). For example, female damselflies moving large distances away from streams to forage in distant forest may be just as likely to encounter and affect the demography of local populations on other streams as individuals dispersing from streams that have become uninhabitable. Regardless, our prediction outlines how a fine-scale behavior that is contingent upon landscape structure, may influence broader-scale population processes and demonstrates the importance of studying movement patterns at multiple scales.

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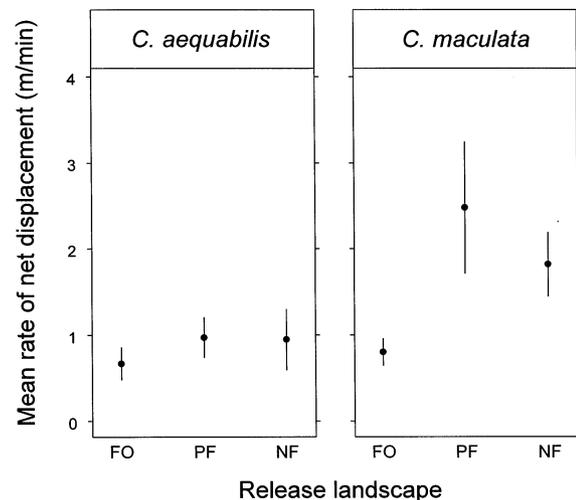


Fig. 4. The mean rate of net displacement (m min^{-1}) for *Calopteryx aequabilis* and *C. maculata* released on FO, PF, and NF landscapes. Error bars are ± 1 se. Note that despite overlapping standard error bars, *C. aequabilis* rates of net displacement were significantly different among landscapes once environmental covariates were statistically controlled for (see Table 4).

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