The movement responses of three libellulid dragonfly species to open and closed landscape cover

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Abstract. 1. The land cover between habitats (i.e. matrix environment) can affect connectivity by impacting organismal movement. Many animals, however, have preferences for specific matrix environments, which can affect their movement through the landscape.

2. We examined how different terrestrial matrix environments impacted the fine-scale movement of adult dragonflies. Based on previous studies of adult dragonfly dispersal and larval distributions, we hypothesised that dragonflies would prefer to enter fields rather than forests and that forests would be a barrier to dragonfly movement, due to forests' structural complexity, low understory light availability, and lower air temperatures.

3. To test how adult dragonflies responded to various terrestrial environments, we released 108 *Leucorrhinia intacta*, a mixture of 108 *Sympetrum rubicundulum* and *obtrusum/rubicundulum* hybrids, and 108 *Sympetrum vicinum*, at field-forest ecotones and assessed their preferences for fields or forests. Individual behavioural responses were recorded, including their probability of taking flight, their direction of movement with respect to the two matrix types, and flight time.

4. The likelihood of adult dragonflies taking flight was species-specific in response to release location. Adults moved more frequently towards fields than forests when released at a forest edge. Individuals released within forests had shorter flight times, but again this response was species-specific.

5. The presence of an open matrix (field or meadow) is likely important for facilitating movement in dragonflies; however, forests are not movement barriers for all dragonfly species. Integrating assays of matrix and habitat preferences can provide insight into how landscape connectivity can be maintained for actively dispersing species.

Key words. Behaviour, dispersal, forest cover, matrix, Odonata.

Introduction

In heterogeneous landscapes, patches of habitat where a focal species lives are surrounded by compositionally similar and dissimilar (i.e. matrix) environments (Forman & Godron, 1981, 1986; Kracker, 1999). A matrix environment can promote or restrict organismal movement

(Ricketts, 2001; Murphy & Lovett-Doust, 2004; Prugh *et al.*, 2008). The behavioural responses of individuals to a matrix environment can therefore provide critical insight into how species move through, use, and distribute themselves across heterogeneous landscapes. Few studies connect individual-based behaviour to processes seen at the community and landscape scale (Lima & Zollner, 1996; Bélisle, 2005; Gordon, 2011). Yet, observations of these behaviours at a local scale have been useful in explaining organismal movement (e.g. pumas; Zeller *et al.*, 2014), dispersal (e.g. butterflies; Haddad, 1999), and species coexistence (e.g. warblers; Toms, 2013). Indeed, the integration of behaviour and larger-scale patterns can be

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informative in predicting species' distributions and responses to environmental change (Knowlton & Graham, 2010).

Heterogeneous matrix environments may provide differential costs and benefits to individuals moving through the landscape (Chardon *et al.*, 2003). The suitability of, or preference for, specific types of matrix environments by species and individuals can vary depending on the risks and gains that organisms experience while moving through these environments, whether during rare and long-distance movements from a source habitat to a new habitat (i.e. dispersal) or during short-distance movements that occur frequently (e.g. daily foraging). This landscape of costs and benefits may be complex and drive non-intuitive patterns of movement. For example, matrix environments that provide resources or refuge may be preferred to ones that are easy to move through, despite the costs imposed by the difficulty of moving through these environments (Haynes & Cronin, 2006; Prugh *et al.*, 2008; Kuefler *et al.*, 2010). One type of matrix in terrestrial landscapes that has dramatic effects on the movement of organisms is forest cover (e.g. Ricketts, 2001; Driscoll *et al.*, 2013; Damschen *et al.*, 2014). Some species preferentially move through forests. For example, green hermit hummingbirds (*Phaethornis guy*, Apodiformes) prefer to move through forested corridors, possibly due to increased resource availability (Volpe *et al.*, 2016), and some species of the *Ambystoma* salamander (Caudata) preferentially move through forests rather than fields in order to avoid desiccation (Rothermel & Semlitsch, 2002; Rittenhouse & Semlitsch, 2006). Yet, forests can also increase the risk of mortality (e.g. *Phengaris* spp., Lepidoptera; Nowicki *et al.*, 2014) or restrict movement (e.g. *Leucorrhinia hudsonica*, Odonata; Chin & Taylor, 2009). Forests can also be energetically costly for organisms to manoeuvre through due to their structural complexity (e.g. for *Bombus impatiens*, Hymenoptera; Crall *et al.*, 2015), and in the case of ectotherms, due to the reduced solar radiation available for thermoregulation (e.g. large-bodied dragonfly species; De Marco *et al.*, 2015). Forest cover is also rapidly changing worldwide: some regions are experiencing high levels of forest regrowth, whereas in other regions, forest is being lost (Foster *et al.*, 1998; Hansen *et al.*, 2013). Both types of changes may alter how organisms move in the landscape.

Terrestrial matrix conditions are similarly important for semi-aquatic insects, many of which have an aquatic larval stage and a terrestrial adult life history stage. In these taxa, survival and post-colonisation distributions can depend on the permeability of the matrix (e.g. Joly *et al.*, 2001; Semlitsch, 2008). Our study taxon, dragonflies (three species in the family Libellulidae), use terrestrial systems as adults to make frequent daily movements of over 50 m for activities such as foraging and moving between roosting and reproductive habitats (Eason & Switzer, 2006) and also to disperse to aquatic habitats where they mate and lay eggs (Switzer, 2002). Dragonflies are a good model taxon for understanding behavioural responses to

changes in the landscape, as adults frequently disperse to and establish at new aquatic habitats (Oertli, 2008), and may exhibit differential responses to habitat heterogeneity. For example, forests can obstruct adult dragonfly dispersal to aquatic reproductive habitats at distances ≥500 m (Chin & Taylor, 2009) and can restrict their arrival at aquatic habitats (Remsburg *et al.*, 2008; French & McCauley, 2018). At shorter distances, however (e.g. 125 m), forests do not seem to impede movement to aquatic habitats (Chin & Taylor, 2009). The behavioural mechanisms behind this pattern of increased connectivity at small scales, among dragonfly breeding habitats with an intervening forest matrix, remain unclear. Forests may be beneficial at these small scales, whether by facilitating dragonfly movement (Chin & Taylor, 2009) or by providing resources or refuge. Some species of dragonfly use forest edges to roost during their inactive overnight period (Corbet, 1999; Timofeev, 2016), to take refuge from the heat and/or to bask (Paulson, 2009), and to forage (Corbet, 1999). It is also possible that once dragonflies enter a region with both substantial forest cover and aquatic habitats, dispersal out of the region to new aquatic habitats by current and future generations may be limited. For example, individuals may perceive it to be too costly to search for new aquatic habitats (e.g. Stamps *et al.*, 2005), particularly if navigating around forests increases travel time.

We therefore sought to determine whether a behavioural preference by dragonflies for forest or field environments at small scales might explain their previously observed patterns of dispersal, as these preferences could also contribute to observed patterns of dragonfly distributions across ponds with varying levels of surrounding forest cover (e.g. McCauley *et al.*, 2008). We tested whether dragonflies preferentially moved in and into field versus forest matrix environments and observed dragonflies' behavioural responses to forest edges. Specifically, we used three species which were expected to have generalist responses to forest cover, as they inhabit ponds across a gradient of surrounding forest cover as larvae (McCauley *et al.*, 2008), and are associated with forests to varying degrees as adults (Walker & Corbet, 1975; Paulson, 2009; Mead, 2017). We hypothesised that dragonflies would prefer to move in and enter field environments and that forests would be a barrier to movement, as dragonflies may face difficulties in navigating the structural complexity of forests during flight (e.g. Crall *et al.*, 2015), and the conditions of lowered light and air temperature imposed by the forest canopy (Chen *et al.*, 1999) would reduce dragonfly flight activity (e.g. Csabai *et al.*, 2006; De Marco *et al.*, 2015). Conversely, the open and less structurally complex field habitats, with higher air temperatures and light intensity, were expected to be preferred because they facilitate movement (e.g. Csabai *et al.*, 2006; Crall *et al.*, 2015). Specifically, we predicted that across species, dragonflies would have a higher probability of flying towards fields versus forests, and that they would move more and for longer time periods in fields versus forests. We tested

these predictions by releasing three species of adult dragonflies near the boundaries between fields and forests and by observing their likelihood of taking flight, and their direction and time of flight.

Materials and methods

To test how adult dragonflies moved in response to open versus closed environments, we observed flight patterns of dragonflies released in field and forest matrix environments, and at forest edges. Our work was conducted at the University of Toronto's Koffler Scientific Reserve (KSR; King City, ON, Canada, 44.03 N, 79.53 W). The reserve was previously an equestrian property on which forest regrowth has occurred relatively recently. The landscape at KSR, on the western side of the reserve where this study was conducted, has proportionally even amounts of open and closed land cover, with approximately 49% fields and 51% forests.

In the summer of 2015, we collected 324 individual adult dragonflies from local ponds at KSR. Specifically, we collected 108 adult males of each of two distinct species, *Leucorrhinia intacta* (Hagen, 1861) and *Sympetrum vicinum* (Hagen, 1861), as well as 108 adult males of what we deemed 'Sympetrum hybrids', which were likely a mixture of *Sympetrum rubicundulum* (Say, 1839) and *Sympetrum obtrusum* (Hagen, 1867)/*rubicundulum* hybrids. For the purposes of this study, we conservatively treated the 'Sympetrum hybrids' as a species complex with varying levels of hybridisation represented, including hybrid individuals with varying levels of introgression as well as individuals of solely *S. rubicundulum* background, because we could not reliably distinguish between the two.

These three species are all members of the family Libellulidae (Odonata, Anisoptera), their larvae are common in lentic systems in this region, and adults of these species were abundant at KSR. The larvae of all of our study species have been observed across a gradient of pond canopy cover and surrounding landscape forest cover (McCauley *et al.*, 2008). In North America, the adults of these species tend to prefer more open aquatic habitats for reproduction (Walker & Corbet, 1975; Mead, 2017), particularly *L. intacta* (Paulson, 2009). Adult *S. vicinum* individuals, however, have been observed in forests on patches of grass with no overhead canopy cover (Walker & Corbet, 1975), and using forest edges when in proximity to reproductive habitat (Paulson, 2009). *Sympetrum rubicundulum* adults have been observed at ponds surrounded by forests (Walker & Corbet, 1975) but are generally found in more open areas (Paulson, 2009). *Sympetrum obtrusum* adults can be associated with forests (Paulson, 2009; Mead, 2017) and have been observed in forested wetlands (Walker & Corbet, 1975); however, whether this is in the context of reproduction is unclear. The larvae and adults of these species may therefore have generalist responses to canopy and forest cover.

Males were used as they were more readily available than female dragonflies. Little is known about whether the dispersal of dragonflies is sex-biased; however, previous studies have found male-biased arrivals to aquatic habitats (McCauley, 2006) and limited female dispersal among aquatic habitats for some species (Conrad *et al.*, 1999; Chin & Taylor, 2009; McCauley *et al.*, 2010). Adults were used rather than tenerals (i.e. juveniles) as dragonflies may move and/or disperse more readily at the adult stage (Angelibert & Giani, 2003), and adults are less easily damaged during collection and are more identifiable to sex and species than tenerals.

Mature male dragonflies were collected using insect nets from Gazebo Pond and Dufferin Pond at KSR while they were either perching or flying during hours of peak dragonfly activity (~11 h00–13 h00). As they were collected, individuals were placed in covered plastic cups in a cooler and chilled using ice packs to anesthetise them, in order to measure and mark them more effectively. They were stored in the cooler for the duration of the collection. Using digital calipers (to 0.01 mm), we measured individuals' head width as a proxy for body size/mass to test for effects on their ability to take flight (e.g. McCauley, 2005; Serrano-Meneses *et al.*, 2007), and forewing length, as a proxy for their flight ability (e.g. McCauley *et al.*, 2014). Both head width and wing length are positively related to body length, another common measure of body size (Serrano-Meneses *et al.*, 2007). The right forewing and hindwing of each individual were numbered using permanent black ink (Sharpie™) to allow for any necessary identification after release. After being marked, individuals were stored indoors in hanging mesh nets for approximately 30 min to warm-up, as it can take at least 10 min for *Sympetrum* species to warm-up to ambient air temperatures (Wakeling & Ellington, 1997), and *Leucorrhinia* species may warm similarly to air temperatures (Sformo, 2003). All of the dragonflies became mobile and took flight within these nets before translocations occurred. All individuals that were to be released in the same release area were transported to sites in the mesh net, allowing them to further warm-up to air temperatures. If two release areas were visited in the same day, the second batch of individuals was marked, measured, and allowed to warm-up after we returned from the first release period. During the release of each individual, the mesh bag was attached to a tree under shade so the dragonflies would not overheat. Collections and releases took place between June–October, 2015, when individuals of each species were most abundant (*L. intacta*: June–July, *Sympetrum* hybrids: July–August, *S. vicinum*: August–October). All releases took place within the hours of 10 h30–19 h30, with 80% of releases taking place between 14 h00 and 18 h30.

Individuals were translocated to sites distributed across KSR in which a field was adjacent to a forest edge. A forest area was defined as any continuous line of tree cover where the other side of the forest could not be seen from the edge. A release area (i.e. general location across the reserve where sites were close to one another) contained

2–4 sites for a total of 12 sites across KSR (Fig. 1). Release locations were located 106–414 m away from local ponds, although the presence of ponds did not impact the orientation of dragonflies. To account for any other tendency for dragonflies to orient themselves in a particular direction, such as in response to the sun (Corbet, 1999; Chahl & Mizutani, 2012), sites were set up across KSR such that three sites had forest edge boundaries to the north, three to the south, three to the west, and three to the east.

One individual was released at one of three points (i.e. release locations) at each site (Fig. 1): at 10 m into the field, directly at the forest/field boundary, and 10 m into the forest (e.g. Ross *et al.*, 2005; Schultz *et al.*, 2012). After adults of a single species were collected for one 're-lease replicate' (i.e. 36 individuals), they were released at 36 different locations (forest, edge, and field locations, at each of 12 sites). For each release replicate, the order of release at sites for each release area was randomised, and then, the order of release locations at that site was rando-mised. Only one release replicate was performed at a given time period, and the three replicates for a single spe-cies were performed before conducting the three replicates of the next species. If individuals were collected from dif-ferent source ponds during a 'release replicate', they were pooled together and released randomly across sites and release locations. At each release location, translocated dragonflies were placed on grass or a forb (whichever was available at the site), approximately three feet off the ground and facing parallel to the forest edge. The dragon-flies were then observed for up to 5 min after release for whether they took flight or not. If they took flight, we recorded their initial flight orientation: towards a field or forest matrix, parallel to a forest edge, or up. We also recorded the angle of this flight direction (e.g. Rothermel & Semlitsch, 2002) using a compass and the length of time of their flight. If the landing of the dragonfly was not observed, their flight time was the length of time observed before visual contact was lost. Individuals that flew up were pooled with those that flew parallel to the forest edge, because we assumed both responses were indicative of not having a preference for forest or field environ-ments, even though this may be an oversimplification of

dragonflies' behavioural responses to an ecotone and they may use forest edges for other purposes such as naviga-tion.

A wedge prism (BAF 2, Cruise Master Prisms Inc., Universal Field Supplies) was used to estimate tree stand density (i.e. basal area) at each release location (i.e. forest, field, or forest edge), to test the effects of structural com-plexity on flight time. A spherical densiometer (Model-C, Forest Densiometers, Rapid City, SD, USA) was used to estimate canopy cover at each release location to examine the effects of light availability on the probability of indi-viduals taking flight. Fields had an average of $13 \pm 2\%$ (standard error) canopy cover and a stand density of 0.3 ± 0.2 m^2 ha^{-1} in proximity to release locations, for-ests had $95 \pm 1\%$ canopy cover and a stand density of 32 ± 3 m^2 ha^{-1}, and forest edges had $81 \pm 3\%$ canopy cover and a stand density of 15 ± 2 m^2 ha^{-1}. Wind speed and direction were recorded during releases to account for any influence on flight patterns. An anemometer (Vantage VUE 6250, Davis Instruments, Hayward, CA, USA) was used for part of the study to measure wind speed and direction at a central location among nearby sites in a release area, and a portable weather meter (Kestrel 4500, Nielsen-Kellerman, Minneapolis, MN, USA) was used for the remainder of the study at each release point. The anemometer provided cardinal, ordinal, and secondary intercardinal directions, whereas the portable meter pro-vided 360° compass directions. Each wind direction was converted to a wind bearing (i.e. the direction towards which the wind was moving) to facilitate comparisons with the orientation of the dragonflies' flight. The anemometer measured wind speed and direction at 15-min intervals, so for each release the direction was determined from the clos-est time point to the time of release. Across our releases, wind speeds ranged between 0 and 8 m s^{-1}, with 87% of releases taking place with wind speeds of 0–2.2 m s^{-1}.

Statistical analyses

We tested the probability of dragonflies taking flight in response to release location, species identity, head width,
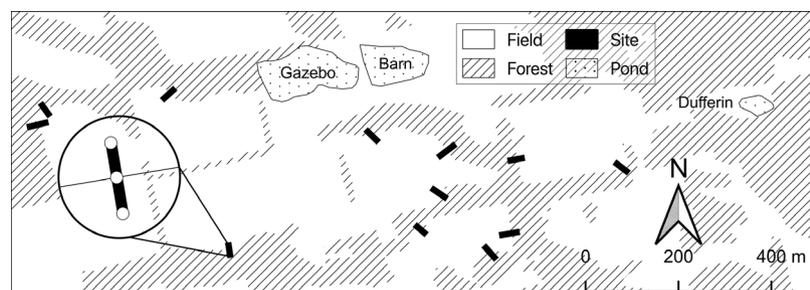
Fig. 1. Dragonflies were released at three release locations (white circles in inset; forest, field, and forest edge) at each of 12 sites, with three replicates per species for three species at the Koffler Scientific Reserve. Local source ponds are also indicated (Gazebo, Barn, and Dufferin Ponds).

and their interactions, using a generalised linear model (GLM) with binomial errors. We removed interaction terms and main effects sequentially and compared models using the anova function in R with a chi-square test and used least-square means (package: emmeans; Lenth, 2018) to compare the effects of specific release locations and species identities on movement. We determined *P*-values using the Anova function (car package; Fox & Weisberg, 2011) with a type III Wald chi-square test. We also used a generalised linear mixed-effects model (GLMM) that incorporated site as a random effect, but that could not test the interaction between location and species due to a lack of convergence at this level of complexity. This analysis was excluded from our results as the main effects of location and species on movement did not substantially differ in comparison with a GLM with no random effects. To see whether canopy cover affected dragonfly activity within forested release locations, we tested the effect of canopy cover on the probability of individuals taking flight using a GLM with quasibinomial errors due to overdispersion.

To test whether dragonflies preferentially flew towards one of the matrix environments (field or forest), we compared their orientations using a GLMM (glmer function in lme4 package; Bates *et al.*, 2015). Orientation (i.e. flying towards field or forest), and its separate interactions with species identity and release location (i.e. forest, field, and forest edge), were used as predictor variables, and count data were used as the response variable, with a Poisson error distribution. Site was included as a random effect. We determined *P*-values using the Anova function with a type III Wald chi-square test. Least-square means were used to compare the effect of specific release locations on dragonfly orientation. We assumed that individuals moving parallel to the forest edge or flying up after release had no preference for a matrix environment.

Differences in the flight time of those individuals that took flight were tested against release location and species identity, using a GLMM with gamma errors and a log link. Site was included as a random effect. We determined *P*-values using the Anova function with a type III Wald chi-square test and used least-square means to compare the effects of specific release locations and species identities on flight times. We also used a GLM that incorporated wing length as a main effect; however, wing length did not impact flight times. Wing length was excluded from our results due to a lack of convergence when site was included as a random effect. We also tested the effect

of tree density within forested release locations on flight time using a GLM with gamma errors and a log link, to see whether increased structural complexity affected the dragonflies' flight capabilities.

Kruskal–Wallis rank sum tests with post hoc Nemenyi tests (PMCMR package; Pohlert, 2014) were used to compare head widths and wing lengths separately among species. Moore's test for paired angles (Pewsey *et al.*, 2013) was used to test whether the compass direction of dragonfly flight corresponded to wind direction, separately for wind directions measured by the anemometer and the portable meter. We also compared wind speed to the absolute difference between wind and dragonfly flight directions, to test whether greater wind speeds made flight directions more similar to wind directions, using Spearman's correlation. The probability of individuals taking flight in response to wind speed and time of day was tested using a GLM with binomial errors. Wind speed was taken as the average between anemometer and portable meter measurements when available, whereas time of day was calculated as decimal time using the TIMEVALUE function in Excel. All analyses were performed in R (version 3.4.4; R Core Team, 2018).

Results

Overall, there were mixed effects of release location and species identity on the flight responses of dragonflies to forest and field matrix environments. Of the 324 individuals released, across species, 111 flew towards the field, 58 flew towards the forest, 77 did not fly towards either matrix environment, 61 did not take flight, and 17 disappeared immediately after taking flight. Responses, however, differed among species (see Table 1).

Both release location and species identity affected the movement of adult dragonflies (Fig. 2). Specifically, the proportion of individuals taking flight was species-specific ($\chi_2^2 = 30$, $P < 0.001$), and there was an interaction between their release location and species identity ($\chi_4^2 = 10$, $P = 0.037$). Release location alone did not affect movement ($\chi_2^2 = 3.2$, $P = 0.20$). When movement was averaged across release location, *L. intacta* individuals were less likely to move than *Sympetrum* hybrids ($z = -3.9$, $P < 0.001$). *Leucorrhinia intacta* individuals were less likely to move than *Sympetrum* hybrids at forest edges ($z = -2.9$, $P = 0.010$) but equally likely to move in comparison to both *Sympetrum* spp. in forests ($z = -2.2$, $P = 0.067$ in both cases).

Table 1. Species-specific behaviours of dragonflies once released, including individuals flying towards field and forest matrix environments, not flying towards either matrix environment (i.e. flying parallel to the forest edge or up), not taking flight, and disappearing after release.

Species	To field	To forest	No preference	No flight	Disappeared
Sympetrum hybrid	38	22	26	12	10
Sympetrum vicinum	43	21	29	10	5
Leucorrhinia intacta	30	15	22	39	2
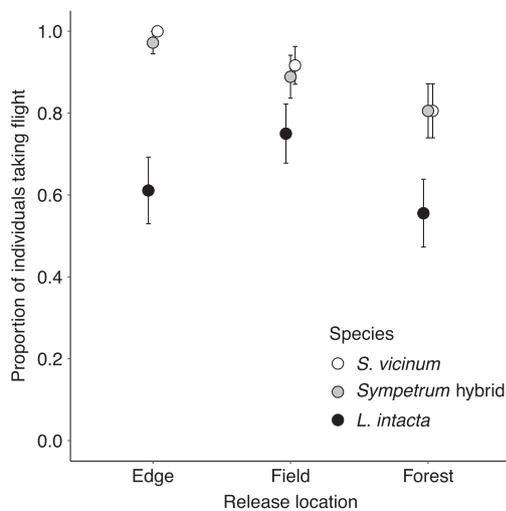
Fig. 2. Proportion (± SE) of *Sympetrum vicinum*, *Sympetrum* hybrid, and *Leucorrhinia intacta* individuals that took flight when released at edges, in fields, and in forests. *Leucorrhinia intacta* individuals moved less than *Sympetrum* hybrids when released at edges ($P = 0.010$) but did not differ from either *Sympetrum* species when released in forests ($P = 0.067$). Within a single species, individuals were equally likely to take flight across release locations.

Head width did not significantly affect movement ($z_{323} = -0.96$, $P = 0.36$) and was not retained in the model. For those individuals released in the forest, increased canopy cover did not affect the probability of taking flight ($t_{107} = -0.091$, $P = 0.93$).

Across all species and of the adult dragonflies that took flight towards one of the two matrix environments (169/324 individuals), individuals oriented themselves more towards fields than forests ($\chi^2_1 = 13$, $P < 0.001$; Fig. 3). The release location of individuals (i.e. forest, field, or at the forest edge), however, also interacted with the orientation of dragonflies ($\chi^2_4 = 14$, $P = 0.0061$). When released at the edge, individuals flew more often towards the field than the forest ($z = 4.2$, $P < 0.001$); however, there were no differences in orientation when individuals were released in the field ($z = 1.9$, $P = 0.42$) or in the forest ($z = 0.70$, $P = 0.98$). Species identity did not affect the number of dragonflies moving towards fields or forests ($\chi^2_4 = 3.8$, $P = 0.44$) and was not retained in the model.

Of the individuals that took flight, species identity and its interaction with release location had significant effects on flight time ($\chi^2_2 = 57$ and $\chi^2_4 = 26$, respectively; $P < 0.001$ in both cases), whereas release location alone did not ($\chi^2_2 = 2.2$, $P = 0.34$; Fig. 4). The interaction between release location and flight time seemed to be driven by the responses of *S. vicinum* individuals, which had shorter flight times in forests than at forest edges or in fields ($z = 6.5$ and $z = 5.7$, respectively; $P < 0.001$ in both cases). In fields and at forest edges, *S. vicinum* individuals also had longer flight times than *L. intacta* and *Sympetrum* hybrids ($P < 0.001$ for all pairwise comparisons),
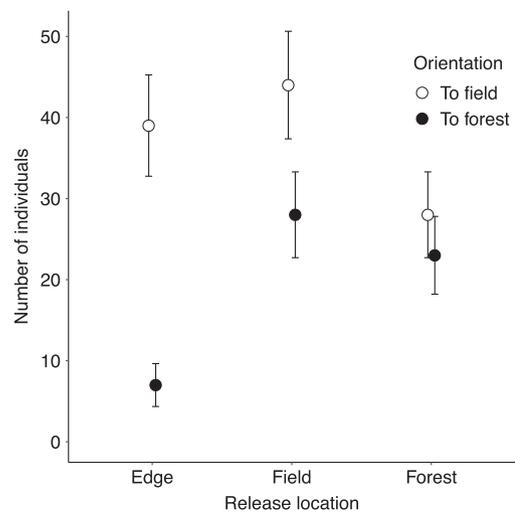
Fig. 3. Number of dragonfly individuals (± square root of count) flying towards forests and fields, when released at edges, in fields, and in forests. More individuals flew towards fields than forests when released at forest edges ($P < 0.001$), but not when released in fields ($P = 0.42$) or forests ($P = 0.98$).

whereas in the forest, all three species had similar flight times ($P > 0.53$ for all pairwise comparisons). Of those individuals that took flight in forests, increased tree density (i.e. a more complex and cluttered environment) did not affect flight time ($t_{67} = 1.8$, $P = 0.070$).

Overall, *L. intacta* had greater head widths ($\chi^2_2 = 218$, $P < 0.001$) and wing lengths ($\chi^2_2 = 134$, $P < 0.001$) than both *Sympetrum* species (Table 2). Wind direction did not correspond with the flight direction of dragonflies (i.e.
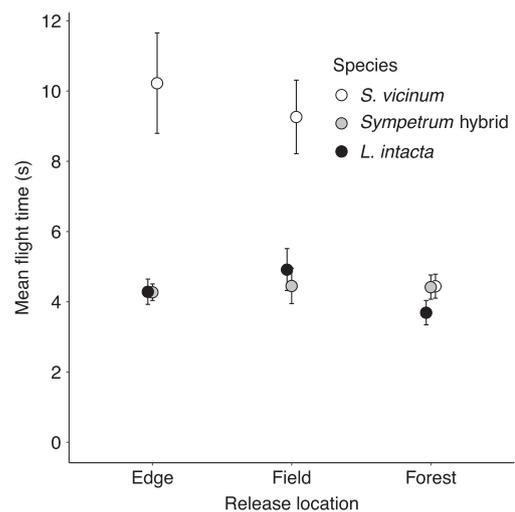
Fig. 4. Mean flight times (s; ± SE) of those *Sympetrum vicinum*, *Sympetrum* hybrids, and *Leucorrhinia intacta* individuals that took flight. At forest edges and in fields, *S. vicinum* individuals had the longest flight times ($P < 0.001$); however, all species had similar flight times when released in forests ($P > 0.53$ in all cases).

Table 2. Morphological characteristics of the three dragonfly species used during releases.

Species	Median head width (mm) and (interquartile range)	Median wing length (mm) and (interquartile range)
Sympetrum hybrid[a]	4.91 (0.19)	23.63 (0.99)
Sympetrum vicinum[a]	4.98 (0.21)	23.82 (1.22)
Leucorrhinia intacta[b]	5.60 (0.22)	25.18 (1.03)

Shared letters indicate similarity in characteristics ($P > 0.05$).

they were significantly dissimilar), either using the cup anemometer ($R = 2.3$, $P < 0.001$) or using the portable wind meter ($R = 1.4$, $P = 0.005$). Increasing wind speeds did not result in wind direction controlling the direction of dragonfly flight ($P = 0.14$, $P = 0.11$). Individuals tended to take flight less often with increasing wind speed ($z_{272} = -3.3$, $P < 0.001$). Time of day also affected the probability of individuals taking flight ($z_{272} = -2.2$, $P = 0.027$), with individuals being less likely to move in the late afternoon and early evening.

Discussion

The dragonfly species in our study showed preferences for open field environments compared to forest environments; however, their movements were affected by where individuals were released. Dragonflies flew more often towards fields than forests when released at the forest edge boundary, when both land cover types were visible and readily accessible (Fig. 3). This difference, however, disappeared when individuals were released in fields and forests. Their responses when released in fields and forests may be due to a lack of perception of the ecotonal boundary (e.g. Ross *et al.*, 2005) or its associated risks. This may be especially likely for dragonflies released in forests as the cluttered conditions of these environments would reduce or eliminate their ability to perceive open fields outside the forest. Species showed markedly different movement and flight behaviours, exhibiting differential responses to matrix conditions. *Leucorrhinia intacta* individuals were less likely to move than *Sympetrum* individuals at forest edges and in forests (Fig. 2), and only *S. vicinum* individuals showed a reduction in flight times in forests (Fig. 4). Whether differences in taking flight and subsequent flight times were due to body size, body temperature, or differences in monthly air temperatures among species' release dates was not discerned. In addition, the results of flight times should be interpreted with caution. The total flight time of individuals was more difficult to track within forest environments as they landed less than in field environments, and visual contact was lost more readily. This pattern was largely driven by the two *Sympetrum* species, since most *L. intacta* individuals were observed to land. The differences in colouration between *Leucorrhinia* and *Sympetrum* species (i.e. black and red, respectively) may

also have affected our ability to see them land in either field or forest environments. These results support previous observational studies that suggested that dragonflies prefer to fly through fields and other open environments to reach aquatic habitats (Chin & Taylor, 2009), but also indicate the importance of understanding species-specific movement behaviour.

Forests may therefore act as a partial boundary for local movements rather than a complete structural boundary: providing refuge to dragonflies in between foraging attempts or overnight at small scales (Corbet, 1999), but deterring large-scale dispersal to reproductive habitats (Chin & Taylor, 2009). It is not known whether forests have other effects on dragonfly movement and survival. In tropical regions, forests play a key role in the survival of the adults of many dragonfly species, providing refuge, food, and occasionally sites for reproduction (Paulson, 2006). In temperate regions, many damselfly species (Zygoptera) use forests. Although damselflies do not tend to move as great a distance as dragonflies, forests and forest ecotones can provide resources and refuges for some damselfly species, motivating them to move away from bodies of water (Jonsen & Taylor, 2000; Taylor, 2006; Harabiš, 2016). Less is known, however, about the effects of forests on dragonfly movement and survival in temperate regions. Fields, forests, and the ecotone between them may support different predator communities and may vary in predation risk. This risk may also vary seasonally, potentially leading to differential risks to dragonflies and effects on their movement behaviour both spatially across a heterogeneous landscape and temporally (Brown, 1999; Haynes & Cronin, 2006). These potential differences in habitat use show the importance of assessing individual responses to environmental conditions across scales. Dragonflies may also fly over forests to avoid such a boundary; however, the height of flight of many dragonfly species has not been documented, and they may still prefer to fly over open environments to improve their chances of detecting reproductive habitats during long-distance dispersal. We observed 15% of individuals flying directly up after release, and a number of individuals that did not fly up immediately gained altitude while flying, both behaviours potentially giving them a better vantage point for further movement. Although larger-bodied dragonfly taxa (e.g. Aeshnidae) have been observed to fly higher than the tree canopy (French & McCauley, personal observation), many smaller-bodied dragonfly taxa likely fly lower than tree height (e.g. <2 m for some Libellulidae spp.; Remsburg *et al.*, 2008; Soluk *et al.*, 2011).

Our results showed that the adults of dragonfly species that have varying associations with forests at both the larval and adult stages have clear preferences for orienting towards open environments, but show differences in movement abilities between open and closed environments. We used these more forest-tolerant species to provide conservative estimates of overall dragonfly responses to forest cover; we would expect that species that are specialised to open environments might show stronger preferences for open

matrix environments. Dragonflies may differ in how they respond to canopy or forest cover depending on species-specific traits. For example, species with a shorter adult stage may prefer more open environments, whereas those with a longer adult stage may prefer more closed environments (Kadoya *et al.*, 2008). Previous studies, each using a single dragonfly species to test for landscape effects on movement, have found that adults may move more readily through open environments (*Libellula depressa* in Angelibert & Giani, 2003; *Leucorrhinia hudsonica* in Chin & Taylor, 2009). Adult dragonflies, however, may also show plasticity in their behavioural responses to forest boundaries. Such behaviour has been observed in the Fender's blue butterfly (*Icaricia icarioides fenderi*, Lepidoptera), which generally prefers to move through open environments but will cross a forest boundary when the forest contains the host plant for its larvae (Schultz *et al.*, 2012). The behavioural responses of adult dragonflies to an ecotonal boundary may be species-specific, however, which may drive species-specific distributions of dragonfly larvae across a gradient of pond canopy cover and landscape forest cover (McCauley *et al.*, 2008). Such differential responses among species have been observed in two congeneric Nymphalidae spp. (Lepidoptera), where their likelihood of entering a forest may depend on a species-specific perceptual range or ability to evaluate the risk of crossing the boundary (Stasek *et al.*, 2008).

There is little information on how adult dragonflies move in response to open versus closed land cover types in more forested temperate regions. The landscape in our study had approximately 49% field cover and 51% forest cover. In a previous study with more variable landscape cover (i.e. either >40% forest cover or >40% open cover between a release point and wetlands), dragonflies appeared to move through open landscapes at greater distances (500–1400 m) but traversed forested landscapes at shorter distances (125 m; Chin & Taylor, 2009). At the Edwin S. George Reserve in Michigan, which has approximately 70% forested land cover (based on maps by Howard, 1998), forests do not seem to pose a barrier to dragonfly movement, as dragonfly larvae are found in ponds across the reserve (see McCauley, 2006; McCauley *et al.*, 2008). In the latter example, however, there may be influences of historical land use (i.e. agriculture) on present larval dragonfly distributions that may supersede adult movement responses to the current landscape.

Our study demonstrates the effects of different matrix types on small-scale animal movement. One species in our study, *S. vicinum*, had shorter flight times in forests than fields. The structural simplicity of a field versus a forest may therefore play an important role in promoting movement in the landscape for dragonflies. Structurally complex or cluttered environments can have large impacts on movement, particularly for flying organisms. For example, complex environments can slow down flight in a bumblebee species (*Bombus impatiens*, Hymenoptera), especially for larger-bodied individuals (Crall *et al.*, 2015). More complex environments can also affect foraging in larger bat

species, as they are less able to manoeuvre or detect prey in denser environments (Patriquin & Barclay, 2003; Schnitzler *et al.*, 2003) and may be injured by running into these structures (Stockwell, 2001). Environmental complexity, however, can also provide benefits to many species. For some species moving through terrestrial environments, structural complexity can help to minimise risk for individuals by limiting their exposure to adverse conditions or predators (e.g. Rothermel & Semlitsch, 2002), while also providing access to resources (McElhinny *et al.*, 2005).

On a landscape level, the presence of ecotones or other less prominent features in a landscape may affect how individuals move. Some species of butterfly (e.g. *Lycaena helle*; Fischer *et al.*, 1999) and bumblebee (e.g. *Bombus* spp.; Cranmer *et al.*, 2012) use ecotonal edges as a linear feature to direct movement, and dragonflies may also use landmarks in the landscape to direct their flight (Eason & Switzer, 2006). The extent to which dragonflies use linear features to navigate, and how this affects their risk of moving through terrestrial environments, is largely unexplored.

Given the behavioural preferences for open matrix environments that we observed here and from results in other studies (i.e. Chin & Taylor, 2009; damselflies in Keller & Holderegger, 2013; French & McCauley, unpublished data), it is likely that the presence of open matrix environments such as fields improves the chances of a dispersing dragonfly finding an aquatic habitat or quickens their detection of these habitats (e.g. Stamps *et al.*, 2005). Open environments may therefore improve functional connectivity for these species in the landscape, particularly at larger scales. Future work on these topics will provide insight into how features in the landscape affect connectivity for dragonflies and other flying insects, and how a mosaic of forests and fields in the landscape might be important for adult dragonflies and other semi-aquatic taxa, at multiple scales of habitat use and selection. In addition, when assessing habitat connectivity for restoration or conservation purposes, incorporating the responses of multiple species to the landscape may be ideal (e.g. Ricketts, 2001), although more difficult to accomplish.

Conclusions

Forest regrowth is occurring in some regions around the world (Hansen *et al.*, 2013), particularly across mid-latitudinal North America following the abandonment of agricultural fields (Foster *et al.*, 1998, 2003). Our results, taken with those of previous studies, suggest that some dragonfly species show a marked preference for moving in open terrestrial environments. Consequently, increased forest cover may negatively affect connectivity among aquatic environments for dragonflies, potentially decreasing the movement of animals among ponds, and as a result reducing genetic, species, and functional diversity among populations, communities, and ecosystems (Crooks & Sanjayan, 2006; Dixo *et al.*, 2009; Staddon *et al.*, 2010). This is not, however, a

general response across taxa, and our results should not, therefore, be interpreted to mean that forest removal is an effective tool to facilitate connectivity among ponds for all dragonflies, particularly since dragonflies use forest edges for roosting (Corbet, 1999; Timofeev, 2016), or for other pond-dwelling species. Understanding individuals' responses to ecotonal boundaries is vital to predict their success in moving across changing landscapes to colonise habitats.

Acknowledgements

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