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Testing for positive edge responses in a fragmented landscape in the Eastern Tiger (Papilio glaucus) and the Spicebush (P. troilus) swallowtail butterflies

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Biology

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TESTING FOR POSITIVE EDGE RESPONSES IN A FRAGMENTED LANDSCAPE IN THE EASTERN TIGER (*PAPILIO GLAUCUS*) AND THE SPICEBUSH (*P. TROILUS*) SWALLOWTAIL BUTTERFLIES

(Thesis format: Monograph)

by

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Graduate Program in Biology with Environment and Sustainability

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of the requirements for the degree of
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Abstract

Landscape changes such as habitat fragmentation and habitat loss are contributing to a global decline in biodiversity. While habitat fragmentation research has mainly focused on species that avoid edges, or the boundaries between different landcover types (negative edge response), a hypothesized resource distribution model predicts that species that require complementary resources in different landcovers will be most abundant at edges (positive edge response). Adults of Eastern Tiger (*Papilio glaucus*) and Spicebush (*P. troilus*) swallowtail butterflies require forests for oviposition sites and meadows for nectar resources. I examined the relative abundance and flight orientation of both species in relation to the forest/meadow edge to evaluate their edge response. Overall, I found that their distribution and flight behaviour was consistent with the positive edge response model, however there were differences between species and sexes. My results suggest that some degree of forest fragmentation in southernwestern Ontario can actually benefit some native species.

Keywords

Habitat fragmentation, landscape structure, functional connectivity, *Papilio glaucus*, *Papilio troilus*, edge, positive edge response, flight behaviour, flight orientation, relative abundance, resource distribution

Co-Authorship Statement

The work from this thesis was completed under the supervision of Dr. Nusha Keyghobadi and Dr. Daria Koscinski. Nusha, Daria and I designed the study, and formulated the hypotheses and predictions. Both Nusha and Daria helped me interpret the data, and gave valuable feedback and editorial comments. Nusha provided financial support and field equipment. Daria provided background knowledge of the species and study area, contacts of private landowners and conservation groups for potential study sites.

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Chapter 1

1 Introduction

1.1 Habitat loss, habitat fragmentation, and connectivity

Landscape fragmentation involves the loss and division of areas of natural landcover, such as forests, prairies and wetlands, and is increasingly common as a consequence of the expansion of human settlements and economic activities. These landscape changes result in loss and fragmentation of habitat for many species and are major contributing factors to a global decline in biodiversity (Brooks et al. 2002, Fischer and Lindenmayer 2007). *Habitat* is defined by the combination of biotic and abiotic variables that provide the resources necessary for a species' survival and reproduction, and it is where that species is typically found (Taylor et al. 1993, Fahrig 2003, Laurance 2008). Habitat loss refers to the conversion of habitat into inhospitable area called the *matrix* (Taylor et al. 1993, Fahrig 2003). Habitat fragmentation *per se* refers explicitly to the process of breaking up previously contiguous areas of habitat. Fragmentation leads to multiple smaller habitat patches of various sizes and shapes, and in various degrees of isolation from one another, thus creating a more heterogeneous landscape (Fahrig 2003). Although habitat loss and fragmentation are almost always coupled, and occur simultaneously, each is predicted to have distinct effects on the viability of resident populations.

The effects of habitat loss focus on the restricted amount and area of remaining resources, as these constrain the number of individuals and the sizes of the viable populations that can potentially be sustained, both within any given habitat patch and across an entire landscape (Fahrig 1997, Hanski and Ovaskainen 2000, Krauss et al. 2003, Farrow and Broders 2011). Habitat fragmentation *per se* may have a number of effects beyond those of habitat loss, which influence the size, distribution and dynamics of populations, thus making them more vulnerable to extinction (Schultz 1998, Dixo et al. 2009). Two of the most important effects are loss of connectivity among populations, and increased edge effects.

The extent to which individuals of a species can move through a landscape, and the ability of individuals born in different parts of the landscape to interact with each other, reflects the *connectivity* of that landscape. There are two key ways that connectivity can be defined and measured: structural and functional connectivity (Taylor et al. 1993, Tischendorf and Fahrig 2000). *Structural connectivity* reflects the spatial arrangement of landcovers and physical features on the landscape, independent of species that may occur there (Dunning et al. 1992, Taylor et al. 1993). In contrast, the actual or potential ability of individuals to move through a landscape determines the landscape's *functional connectivity* (Tischendorf and Fahrig 2000). Functional connectivity is, therefore, a function of both structural connectivity and the particular behaviours and ecological requirements of the species in question. Habitat fragmentation always results in changes to the structural connectivity of a landscape, but a species' smaller scale routine movements and potentially larger scale dispersal movements in response to structural changes in the landscape will determine the functional connectivity.

When habitat fragmentation reduces functional connectivity, making it more difficult for individuals to traverse the landscape (Ricketts 2001, Boscolo and Metzger 2011), it reduces chances of accessing necessary resources such as food (Mortelliti and Boitani 2007, Blackburn et al. 2011) and mates (Peacock and Smith 1997, Haapakoski and Ylönen 2010, Lange et al. 2013), as well as the opportunity to colonize new areas (Boscolo and Metzger 2011). Furthermore, loss of functional connectivity can lead to more genetically isolated populations (Wells et al. 2009, Dixo et al. 2009) that lose genetic diversity and may experience inbreeding depression (Haikola et al. 2001, Zachos et al. 2007), potentially leading to population declines and greater vulnerability to extripation or even extinction. Many studies suggest corridors or stepping-stones as a conservation strategy to increase connectivity in fragmented landscapes (Haddad 1999, Leidner and Haddad 2011). However, to effectively use such strategies, one must have a solid understanding of movement of individual species, and how each species responds to fragmentation of landcover types across the landscape.

1.2 Edges and edge-effects

When a landscape is subjected to fragmentation of natural landcover types, *edges* or *ecotones*, which are the transitional boundaries between different landcover types that can vary in sharpness (e.g., between forest and meadow, or forest and agricultural field), become more abundant as smaller patches have a higher perimeter to area ratio. Important physical and biological changes occur at these boundaries and create unique conditions that are referred to as *edge-effects* (Saunders et al. 1991, Murcia 1995). For example, the degree to which wind and light attenuation are affected by edges creates a microclimate that differs from that of adjacent landcover types. Edge-effects, in many cases, can be detrimental to species that are strongly associated with the interior of patches of a given landcover, such as forests (Laurance 2008).

For species that depend on resources within the core of landcover patches, edge-effects may limit the area that is actually available or suitable for such species' use within a given patch. In such cases, several fragmented patches may offer less usable habitat than a single, large patch of the same total area. Thus, species richness and abundance has been found to increase with patch size and to decrease with the amount of edge in the landscape (Soga et al. 2012, Youngentob et al. 2012). Furthermore, effects may be evident up to 150 m from the edge and markedly reduce usable habitat for certain species (Murcia 1995).

The abiotic changes characteristic of edge-effects in fragmented landscapes may be beneficial to invasive species (Bartuszevige et al. 2006, Cilliers et al. 2008). The encroachment of invasive species can amplify edge-effects (Watling et al. 2010), and in turn further reduce resource availability and the quality of remaining habitat for native species (Hurst et al. 2013, Lenda et al. 2013).

Not only can edge-effects influence the amount of suitable habitat area and make habitats vulnerable to invasions, edges and edge-effects can also act as physical barriers to movement. Structural differences between two landcover types may deter organisms from moving between one landcover type to another, and across the landscape (Ross et al. 2005). This impediment to species movement can be illustrated most prominently when species exhibit edge avoidance behaviour by turning around and moving away from edges when they encounter them (Ross et al. 2005). Edge-effects can therefore add to the negative impacts of fragmentation on the landscape's functional connectivity for some species.

Overall, increased abundance of edges in a landscape can detrimentally impact many species and for this reason, edge-effects are considered one of the primary negative consequences of landscape fragmentation. However, despite the potential negative effects of edges, the literature suggests that species' response to edges are less predictable than this current paradigm may indicate (Debinski and Holt 2000, Fahrig 2003, Laurance 2008). Indeed, depending on the range of their resource requirements and the spatial overlap of those resources, some species could actually benefit from an increased abundance of edges in the landscape.

1.3 Resource distribution model

A species' distribution in the landscape generally depends on the distribution of their resources (Dunning et al. 1992, Fahrig 2003, Ries et al. 2004) and this could change with landscape alterations, particularly habitat fragmentation. While this concept is fairly intuitive, Ries et al. (2004) describe a formal, predictive model to explain species distributions in heterogeneous landscapes and define mechanisms for their ecological responses to edges.

According to Ries et al. (2004; Figure 1a), a negative edge response occurs when a species is found in highest abundance within one landcover, where it has access to all its necessary resources. These patches define areas of high quality habitat. The same species is found in much lower abundance in adjacent areas, where either resources are absent or the same resources can be found in lower quality or quantity, therefore the distribution of resources is said to be supplementary. These species are unlikely to cross the boundary to move among landcover patches, thus demonstrating a negative edge response (Ries et al. 2004; Figure 1a). In such species, we can expect edge-effects to create conditions that limit movement and reduce the functional connectivity of the landscape. Species that exhibit this behaviour are often *habitat specialists*, with required resources occurring in a

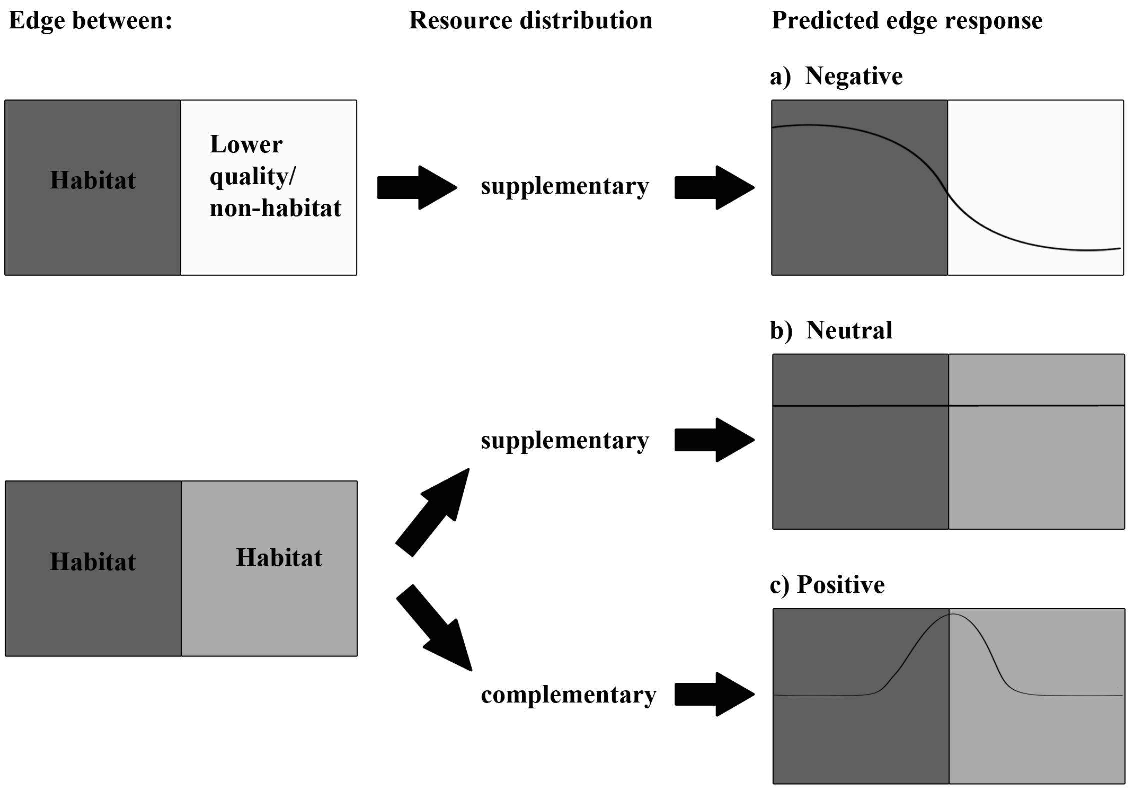

Figure 1. Resource distribution model showing species expected edge response (Adapted from Ries et al. 2004:502). (a) Shows a negative edge response where there is a decline in species abundance from habitat to non-habitat if resources are the same (supplementary), (b) shows a neutral edge response where species abundance does not change if the supplementary resources are provided in adjacent habitats that are of similar quality, and (c) shows a positive edge response where there is higher species abundance at the edge when different resources are in different habitat types (complementary).

narrow range, primarily in one or few landcover types. Studies of habitat fragmentation often focus on assessing habitat specialists that exhibit negative edge responses (Schultz and Crone 2001, Ross et al. 2005, Schtickzelle et al. 2007, Schlossberg and King 2008, Hahn et al. 2011).

A neutral edge response can be predicted by the supplementary distribution of resources between areas of similar quality habitat. Adjacent landcover types may both contain, to a similar degree, the resources required by a particular species, so individuals are equally abundant within the different landcover types as they readily cross the boundary (Ries et al. 2004; Figure 1b). Therefore, edge-effects should have little effect on movement and functional connectivity. Species that exhibit this distribution are often *habitat generalists,* defined as species that have resources in a number of different landcover types, and can therefore occupy and move between them. Studies have demonstrated that habitat fragmentation can result in no effect, or even positive effects, for habitat generalists (Krauss et al. 2003, Hurst et al. 2013).

A positive edge response occurs when a species is most abundant at the edge. This can arise because an ecotone may represent a unique environment that contains some characteristics distinct from both of the adjacent landcovers, and that is particularly suitable for certain species. A positive edge response can also be expected when species have complementary resources which are divided between two different landcover types (e.g., forest and meadow; Ries et al. 2004; Figure 1c). Particular resources can only be found in one or the other landcover type, but each resource is necessary. Individuals must move between adjacent patches of different landcovers to obtain all necessary resources, and are expected to be most abundant at the edges, thus displaying a positive edge response, and are therefore *edge specialists* (Ries et al. 2004; Figure 1c). Edge specialists have been less studied than those species that demonstrate negative or neutral edge responses. Some studies have suggested that edges can increase diversity (insects: Tscharntke et al. 2002, Gavish et al. 2011, Flick et al. 2012; birds: Schlossberg and King 2008, Fonderflick et al. 2013; mammals: Lidicker 1990, Ethier and Fahrig 2011), but there are few empirical examples that have directly used the framework proposed by Ries et al. (2004) to assess species’ distributions and the mechanisms underlying those distributions. To understand the range of potential responses to landscape fragmentation and to be able to manage fragmented landscapes for multiple taxa, it is important to gain a better understanding of the behaviour and movement of species that may respond positively to edges in the landscape (Debinski and Holt 2000, Fahrig 2003, Laurance 2008).

1.4 Behavioural response to landscape structure

Ultimately, species' distributions and responses to changes in structural connectivity depend on fine-scale behavioural responses, particularly how individuals orient themselves and move in relation to specific landscape features, such as edges. Such fine-scale behavioural responses depend on how animals perceive the landscape. For example, many birds rely heavily on sight to capture moving prey (Garamszegi et al. 2002), while insects depend on a combination of olfactory and visual cues to detect mates and host plants (Scott 1974, Carlsson et al. 2011, Ockinger and Van Dyck 2012). Depending on the species, butterflies may detect landscape features from distances between 5 m to 120 m away (Conradt et al. 2000, Ross et al. 2005, Schtickzelle et al. 2007). Generally, larger sensory organs indicate better sensory ability (Rutowski 2000, Nummela et al. 2013). These sensory abilities allow animals to detect and orient towards their resources, in turn influencing their movement through the landscape in order to obtain those resources.

Specific tactics used by animals to obtain their resources can also be important factors in determining patterns of movement across heterogeneous landscapes. For example, some species adopt mate-locating strategies that require extensive movement such as patrolling in butterflies (Scott 1974) or male spiders traveling large distances in search of females (Berger-Tal and Lubin 2011), while others may have more sedentary strategies such as perching behaviour in butterflies (Scott 1974) or mate guarding in birds (Foote et al. 2008). Similarly with foraging, different strategies such as ambushing prey versus active foraging will involve different levels of mobility (McBrayer and Wylie 2009). Therefore, understanding animal behaviour and resource locating strategies can be important in determining patterns of movement.

Given the need for animals to efficiently detect and obtain resources that vary spatially across heterogeneous landscapes, it is not surprising that landscape structural features have been found to strongly influence movement. Animal movement may be impeded or facilitated by various features of the landscape depending on the extent to which they provide necessary resources, are associated with mortality factors, affect the animal's energy expenditures, or constitute a physical barrier to movement (Rayfield et al. 2010). For example, in natural landscapes, Murphy et al. (2010) found that large distances between habitat patches and mountainous topography impede the landscape's functional connectivity for the Columbia spotted frog, *Rana luteiventris*. In contrast for more mobile animals such as some species of birds, relatively large inhospitable areas may act as corridors for movement to avoid predation (Gill et al. 2009). However, as landscapes change, resource distributions will be altered and newly created features, such as edges, are added. These changes to structure have been shown to influence the fine-scale movement patterns of various species, for example agricultural boundaries restricting the movement of the nutterjack toad, *Bufo calamita*, because of low prey abundance found in agricultural fields (Stevens et al. 2006). In addition, various insects exhibit distinctly different movement behaviour in habitat patches compared to intervening areas of matrix. Butterflies have shorter and more exploratory movements, and cover more area within habitat patches (Merckx et al. 2003, Van Dyck and Baguette 2005, Skórka et al. 2013), while in the matrix they tend to fly in straight lines, and spend less time foraging and resting (Schtickzelle et al. 2007, Skórka et al. 2013).

Many studies have investigated animal behavioural responses to landscape structural features and their effect on the species' broad-scales movements. Some studies have experimentally manipulated landscape features in a controlled environment (Stevens et al. 2006). Others use tracking devices to assess animal movements (Ousterhout and Semlitsch 2014), and direct observational studies have also been conducted (Haddad 1999, Conradt et al. 2000, Schultz and Crone 2001, Schtickzelle et al. 2007). These studies allow greater insight to which specific landscape features impede or facilitate movement, the directionality of individual movements, and how species' distributions may change as landscape structure changes.

1.5 Butterflies as a model system

Butterflies are an excellent model system to address many questions in ecology, evolution and animal behaviour. For example, studies on the Glanville fritillary butterfly, *Melitaea cinxia*, and the Edith's checkerspot, *Euphydras editha*, have provided much of the foundational empirical work for metapopulation dynamics (Harrison et al. 1988, Hanski et al. 1995) and provided valuable insight for biological conservation (Ehrlich 1992, Hanski 2011, Ojanen et al. 2013). Furthermore, the use of modern genetic technologies have furthered our understanding of the evolutionary consequences of landscape changes for these species (Hanski and Saccheri 2006, Wells et al. 2009). Their varied patterns of spatial distribution and short generation time make butterflies useful in landscape and spatial ecology (Keyghobadi et al. 2005, Flick et al. 2012, Ockinger and Van Dyck 2012), as well as population ecology and population genetic studies (Nowicki et al. 2005, Baguette and Stevens 2013). They are relatively easy to catch and observe, making them an ideal organism to examine diurnal behaviour (Slamova et al. 2011), mating systems (Scott 1974, Rutowski 1991), flight behaviour and orientation (Haddad 1999, Conradt et al. 2000, Schultz and Crone 2001, Schtickzelle et al. 2007, Skórka et al. 2013).

1.6 Thesis objectives

According to Ries et al.'s (2004) resource distribution model, species that use complementary resources in different landcover types are hypothesized to show positive edge responses (Figure 1c). I use *Papilio glaucus* and *P. troilus* as case studies to test for this positive edge response hypothesis, since both swallowtails use forest species as oviposition sites, but feed on meadow flowers. This would indicate whether these butterflies are indeed edge species, rather than habitat generalists or woodland species as they have previously been considered (Scott 1986, Haddad 1999). I predict that both species will be more abundant at the edge than in the forest or in the meadow. I also predict that when released at points both in the forest and in the meadow, their initial flight orientation as well as their overall flight direction will be directed towards the edge. Furthermore, I will also examine aspects of fine-scale flight behaviour to provide insight into the ecological and behavioural mechanisms underlying their distribution in the landscape.

Chapter 2

2 Materials and Methods

2.1 Study species

The northern edge of *Papilio. glaucus'* range is the southern Great Lakes region of Ontario and the species occurs throughout much of the eastern United States including as far south as Georgia and west to the Great Plains (Scott 1986, Scriber et al. 1991). *Papilio troilus* in Canada reaches only southwestern Ontario, just north of Lake Erie, and its distribution in the eastern United States is similar to that of *P. glaucus* (Scott 1986). Both species over winter as chrysalides and are bivoltine in southwestern Ontario. The flight periods typically last four weeks, with the first flight starting in late May, and the second flight occurring in late August (Scott 1986).

Papilio glaucus females oviposit on deciduous tulip trees (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), and white ash (*Fraxinus americana* L.), which are the larval host species (Scott 1986, Grossmueller and Lederhouse 1987, Scriber et al. 1991), while *P. troilus* uses sassafrass (*Sassafrass albidum* (Nutt.) Nees) and spicebush (*Lindera benzoin* (L.) Blume) (Scott 1986, Nitao et al. 1991). Swallowtails have long probosci and nectar feed on flowers with long corollas (Tiple et al. 2009), such as butterfly milkweed (*Ascelpias tuberosa* L.), common milkweed (*Ascelpias syriaca* L.) and wild lupine (*Lupinus perennis* L.). Other native plants commonly used for nectar, observed during this study, were native wild bergamot (*Monarda fistulosa* L.), hairy beardtongue (*Penstemone hirutus* (L.) Willd), and dwarf blazing-star (*Liatris cylandracea* Michx.). Introduced species used for nectar were dame's rocket (*Hesperis matronalis* L.), purple vetch (*Vicia spp*), clover (*Trifolium spp*) and bouncing bet (*Saponaria officinalis* L.).

2.2 Study area

My study was conducted at the northern limit of both species' distribution in Norfolk County, in southwestern Ontario (UTM: 17N E535866 N4727904; Figure 2).

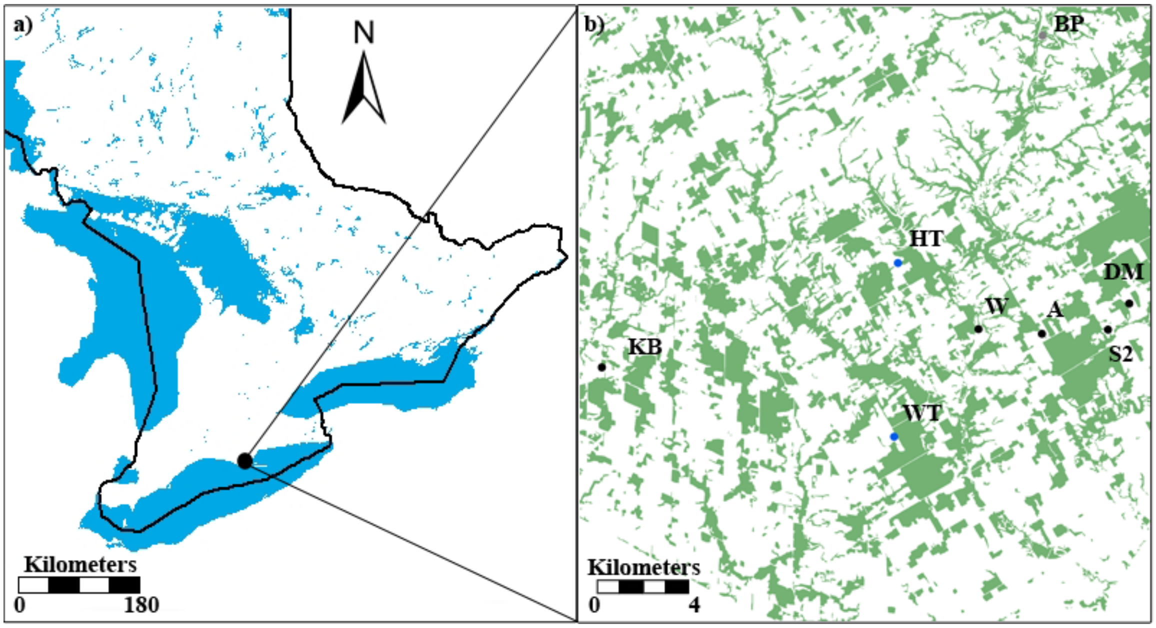

Figure 2. Map of Ontario and location of study in Norfolk County (a) and specific study sites (b) that were used to evaluate relative abundance in 2013 and conduct behaviour trials in 2012. Sites shown in blue were used for both surveying relative abundance and conducting flight behaviour trials, sites in black were used to survey abundance only, and sites in gray were used for behaviour trials only.

Historically, the landscape of southwestern Ontario was a mosaic of mainly deciduous forest with some openings for prairie patches, oak savannah and riparian corridors (Argus 1992, Crins 1997). Fallen trees in the forest or fires would have caused openings for prairie species to colonize. However, the forest has been fragmented and converted into agricultural lands (Argus 1992, Crins 1997) making this area an ideal region to study species' behavioural responses to edges. My objective was to assess how swallowtail adults respond to edges between forest and restored prairies or meadows with native vegetation.

2.3 Field methods

Criteria for choosing appropriate sites for this study were a well-defined forest/meadow boundary, with larval host plants present in the forest and native nectar plants in the adjacent meadows. Temperature and wind speed were recorded at least three times a day (morning, mid-day, afternoon) each time that abundance surveys or behavioural trials were conducted. Data were only collected when the temperature was at least 16 degrees C and the average wind speed was < 9 km/h with gusts no more than of 13 km/h.

2.3.1 Relative abundance

The relative swallowtail abundance in the meadow, at the edge, and in the forest was assessed at seven sites (WT, HT, AN, KB, DM, W, and S2; Figure 2; Table 1), between the late-May to July 2013. To select sites, I created a histogram of the area of contiguous forest patches in Norfolk County using landcover data from Southern Ontario Land Resource Information System, analyzed in ArcGIS v 10.0 (ESRI Corp., Redlands, CA; Figure A.1). There were 3366 forest patches identified in Norfolk County and only forest patches that had a large enough area (>10 ha) for at least two transects were considered for inclusion in the study. Only five forest patches were >300 ha and were considered not to be representative of forest patch size in this area, and were thus excluded. Study sites were then chosen such that the sizes of adjacent forest patches were representative of the range of forest patches found across Norfolk County, as determined by visual inspection of the histogram, and included patches of small (>100 ha), medium (100-200 ha), and large area (200-300 ha; Figure A.2).

Each site had between 2-6 transects spaced at least 20 m apart for a total of 22 transects for this study (Figure 3). Each transect was 240 m x 5 m and extended 120 m into the meadow and 120 m into the forest (Figure 3), with the exception of two transects that were 110 m in the direction of the meadow due to restricted length of the meadow at sites KB and W (Figure 2; Table 1). Transects were divided into nine different sections (A-I; Figure 3; Fonderflick et al. 2013) to allow more fine-scale recording of the location where each butterfly was seen. Sections varied in length to reflect the relative amount of habitat; sections were longer further into the forest or meadow and shorter near the edge.

Table 1. Location in Universal Transverse Mecator (UTM) of sites used for relative abundance surveys of swallowtail butterflies in Norfolk County, Ontario in 2013. Numbers of each species recorded at each site are shown.

Site Abbreviation	Site	Easting	Northing	$N_{P.\ glacus}$	$N_{P.\ troilus}$
WT	Wilson	535094	4721111	150	55
HT	Hepburn	536179	4726535	58	32
AN	Anderson	540685	4724847	26	6
KB	Boothby	524705	4723556	35	11
DM	DeMaere	543943	4725806	33	3
W	Weeden	538419	4725368	25	9
S2	Soenen2	543050	4724946	27	8

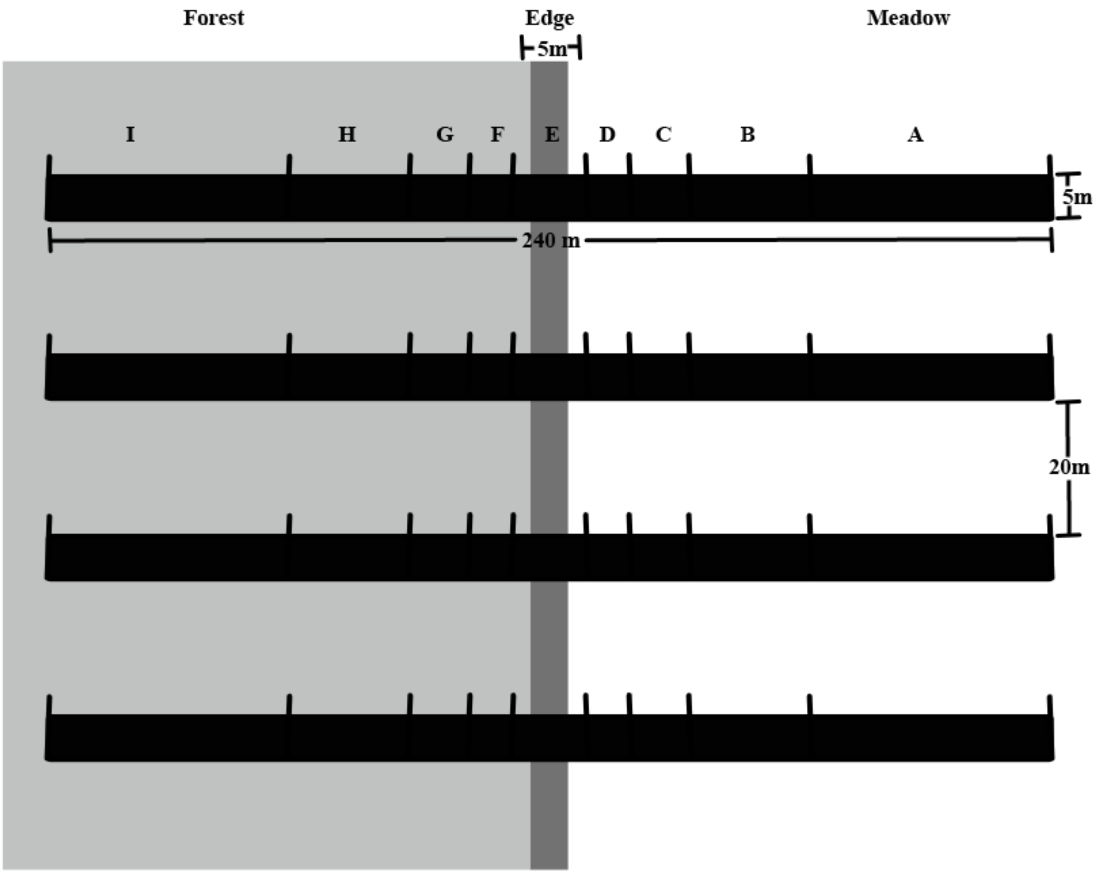

Figure 3. Sample site with transects used to survey relative abundance of swallowtail butterflies during May-July 2013 using the Pollard walk method. Black lines represent four transects (5m x 240m) that are divided into nine sections (A-I) that span the forest, edge, and meadow.

Swallowtail abundance was quantified using an approach similar to the method of a Pollard walk using transect counts (Pollard 1977). Two observers each walked along a separate transect at a slow and steady pace that took between 14-16 minutes. The same two observers surveyed all of the transects. Observers recorded any butterflies seen that were certain to be *P. glaucus* and *P. troilus* flying within the transects and the specific section in which they were seen. Observers were unable to record the sex of the butterflies by sight. If the same butterfly was definitely seen repeatedly during the same observation period, it was only recorded once. However, if there was any doubt about the identity of an individual butterfly, then it was recorded as a new observation, as per the Pollard walk method (Pollard 1977). Sites were surveyed regularly at different time periods of the day: morning (10:00 – 12:00), mid-day (12:30 – 14:30) and afternoon (15:00 – 17:00). Counts of butterflies recorded within each section were summed across the total number of times each transect was visited.

The portions of each transect that were in the meadow and at the edge were also surveyed to quantify the abundance of plants that are commonly used as nectar sources. The number of individual plants was recorded within each section of each transect. The presence of larval host plants for each species within the adjacent forest up to 120 m from the edge was also confirmed at each site.

2.3.2 Flight behaviour trials

Three sites (WT, HT, and BP; Figure 2; Table 2) were chosen for flight behaviour trials. In addition to having the aforementioned site criteria, each of these sites had areas within 1 km where many butterflies could easily be caught to avoid translocating individuals over longer distances.

Trials were conducted during the flight period from mid-May to mid-July 2012. Butterflies engage in various activities and behaviours throughout the day such as basking, feeding, male patrolling, and female egg-laying (Slamova et al. 2011). To capture these diurnal patterns, trials were conducted during the hours of 9:30 – 18:30 and the time of day the trial took place was recorded.

Table 2. Location in Universal Transverse Mecator (UTM)s of sites in Norfolk County, Ontario used for behaviour trials, where responses of swallowtail butterflies to forest/meadow edges were assessed in 2012. Number of trials conducted for males and females caught for each species at each site are shown.

				P. glaucus		*P. troilus*	
Site Abbreviation	**Site**	**Easting**	**Northing**	**N_{males}**	**$N_{females}$**	**N_{males}**	**$N_{females}$**
WT	Wilson	535094	4721111	156	89	86	63
HT	Hepburn	536179	4726535	77	22	66	16
BP	Brian	540868	4735379	13	15	0	0

At each site, butterflies were netted, uniquely marked with permanent marker, and cooled (>10 minutes and < 2 hours) before their release at the trial location. Cooling was done using a standard procedure where butterflies are carefully placed in a glassine envelope and kept in a cooler with ice packs (similar to Schultz 1998). This ensured that the butterfly was calm when they were placed on the ground to be released. The flight behaviour of captured and released butterflies has been shown to not differ from their natural movement behaviour in some species (Schultz 1998, Kuefler and Haddad 2006; Skorka et al. 2013).

Butterflies were released at specific distances from the edge, in the meadow (10 m, 30 m, 60 m) and in the forest (10 m, 60 m). Each individual butterfly was also oriented in one of four different directions (towards, away, right or left relative to the forest edge) when placed on the ground at their initial release point, to ensure mean flight direction was not influenced by their initial placement. After release, each butterfly was followed for a maximum of 30 minutes or until they flew out of sight. Butterflies were lost from sight more quickly in the forest and more often once they entered the adjacent habitat, however at a minimum, the last point where the butterfly was seen was recorded. Locations of resting points were recorded using a high-accuracy GPS (Trimble GeoXH 2005) with an accuracy of up to 1 m in the field and 2 m in the forest. Behaviour at each resting point was recorded (resting, feeding, basking), flights between resting points were timed using a stopwatch, and distances and angles between resting points were determined from the GPS data after importing into ArcGIS v 10.0. Alighting points were counted only if the individual remained at the location for > 3 seconds, so that butterflies came to a complete rest. A trial was terminated if a butterfly rested and did not fly for >15 minutes. To ensure minimal disturbance to each butterfly's flight behaviour, its flight and alighting points were monitored from approximately 2 m away. Two people were required to track a butterfly's flight. One person focused on following the butterfly, while the other person flagged and referenced the exact spot of each alighting point once the butterfly left that spot. Trials ended if obvious disturbances were observed (e.g., if an observer unintentionally disrupted the butterfly's flight), which occurred three times.

2.4 Statistical analysis

2.4.1 Relative abundance

Spatial autocorrelation analysis was performed using multivariate Mantel correlograms as implemented by the R package vegan v 2.0-10 (J. Oksanen, F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R. B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, and H. Wagner, available at http://vegan.r-forge.r-project.org). I used spatial autocorrelation to assess whether the number of butterflies seen in one section of a transect was significantly correlated with the number seen in any other section (Fonderflick et al. 2013). For each section of each transect, I calculated the average density of butterflies per visit to account for the number of times each transect was surveyed and the different lengths of each section. I obtained the average density of butterflies per visit by dividing the summed count of butterflies across visits by the number of visits and the length of each section. A separate correlogram was examined for each transect. If the correlation for at least one distance class was significant, the entire correlogram was considered significant (Fonderflick et al. 2013).

I used a generalized linear mixed model (GLMM) approach to assess landscape and ecological factors affecting the distribution of swallowtails along the transects using the R package lme4 v 1.0-5 (D. Bates, M. Maechler, B. Bolker, S. Walker, available at http://lme4.r-forge.r-project.org). Since data were collected as counts of butterflies, I used the Poisson distribution in the GLMM. Abundance of butterflies was analyzed separately for the meadow and forest, and for each species, for a total of four GLMMs. The main fixed effect of interest in my GLMMs was the distance to the edge, measured at the mid point of each section. Other effects in the model were: number of nectar plants in each section (meadow only), time of day (morning, mid-day, and afternoon), number of surveys conducted for each transect, and the length of each section, since sections were not of equal length. Nested random effects included transects within sites, to account for the variation among different transects and sites. Butterflies engage in different activities during the day, and thus their spatial distribution relative to the edge may change throughout the day. Therefore, the interaction between time of day and distance to the edge was also included as a fixed effect in the model.

I followed a multimodel inference approach to determine the relative importance of each factor (Burnham and Anderson 2002) using the R package MuMin v 1.9.13 (K. Barton, available at http://mumin.r-forge.r-project.org). A set of candidate models was generated and ranked based on the second-order Akaike information criterion value (AICc), which accounts for sample sizes relative to the number of parameters (Burnham and Anderson 2002). Separate sets of candidate models were generated for the meadow and the forest, and for each species, for a total of 4 sets of models. The top model in each set has the lowest AIC_c value, and other candidate models were only considered if they had ΔAIC_c less than 4, where ΔAIC_c indicates the difference between the AIC_c value for model i and the AIC_c value for the best model (Burnham and Anderson 2002). Akaike weights (w_i) of each model i were then used to obtain the probability that model i is the best model given the data we sampled (Burnham and Anderson 2002). Inferences could be made conditionally on a selected best model if $w \geq 0.90$ (Burnham and Anderson 2002).

Since no single best model was obtained based on Akaike weights, I used model averaging of the top models ($\Delta AIC_c < 4$) to determine the relative importance of each factor and parameter estimations. I used $w+(i)$, which sums the w_i of each model that contains predictor variable i over the total, to obtain the relative importance of each predictor (Burnham and Anderson 2002). In addition, I used the R package AICcmodavg v 1.35 (M.J. Mazerolle, available at http://cran.r-project.org/package=AICcmodavg) to obtain the parameter estimate $\hat{\bar{\beta}}_J$, where $\hat{\bar{\beta}}_J$ is the linear regression coefficient associated with a predictor variable and is averaged across all models that include that predictor variable (Burnham and Anderson 2002).

2.4.2 Flight behaviour trials

The alighting points referenced for each butterfly flight path and imported into ArcGIS v 10.0 were used to assess turning angles, as well as the initial and final divergence angles. A turning angle is defined as the angle between two lines of the flight path, where the intersection of these lines is the alighting point of the butterfly. The trigonometric sine and cosine functions were applied to the turning angles for each flight path to assess directionality and flight persistence, respectively. Only flight paths that had one or more turning angles could be used for this analysis. The mean sine of turning angles indicates that there is a right turning bias if values are positive and significantly different from zero, and it indicates a left turning bias if values are negative and significantly different from zero (Turchin et al. 1991). Most insects show no directional bias in their turns, and therefore the mean sine of the turning angles is typically symmetrical around zero (Kareiva and Shigesada 1983; Turchin 1991). Mean cosines of turning angles indicate the degree of persistence in the flight path—the extent to which the individual continues movement in a particular direction. If the mean cosine of turning angles is not significantly different from zero, this indicates that the direction of each move is not correlated with the previous movement and that the flight path is random. Mean cosine values that are positive and significantly different from zero indicate a forward persistence, and values that are negative and significantly different from zero indicate reversal movements (Turchin et al. 1991). The Wilcoxon signed-rank test was used to determine if the mean sine and cosine of flight paths were significantly different from zero. All calculations were done separately for each species, release point and sex.

A divergence angle is defined as the angle between the shortest straight line to the edge from a release point, and a straight line from the same release point to some other point in the flight path (Conradt et al. 2000; Figure 4). The initial divergence angle of a flight path (β) is the angle between the shortest line to the edge and the line to the location of the butterfly at 5 m radius from the release point, and is used to assess the initial orientation of the swallowtails' flight path (Conradt et al. 2000; Figure 4). The final divergence angle of a flight path (α) is the angle between the shortest line to the edge and the line to the point where the butterfly was last recorded and is used to assess the overall flight path direction (Conradt et al. 2000; Figure 4).

To analyze divergence angles, I employed circular statistics using the R package circular v 0.4-7 (U. Lund and C. Agostinelli, available at https://r-forge.r-project.org/projects/circular/). Distributions of angles were tested to fit the von Mises distribution, which is equivalent to a normal distribution for circular data (Zar 2010). The Rayleigh test of uniformity was used to test if the initial and final divergence angles were uniformly distributed around a circle or if there was significant directionality, where zero

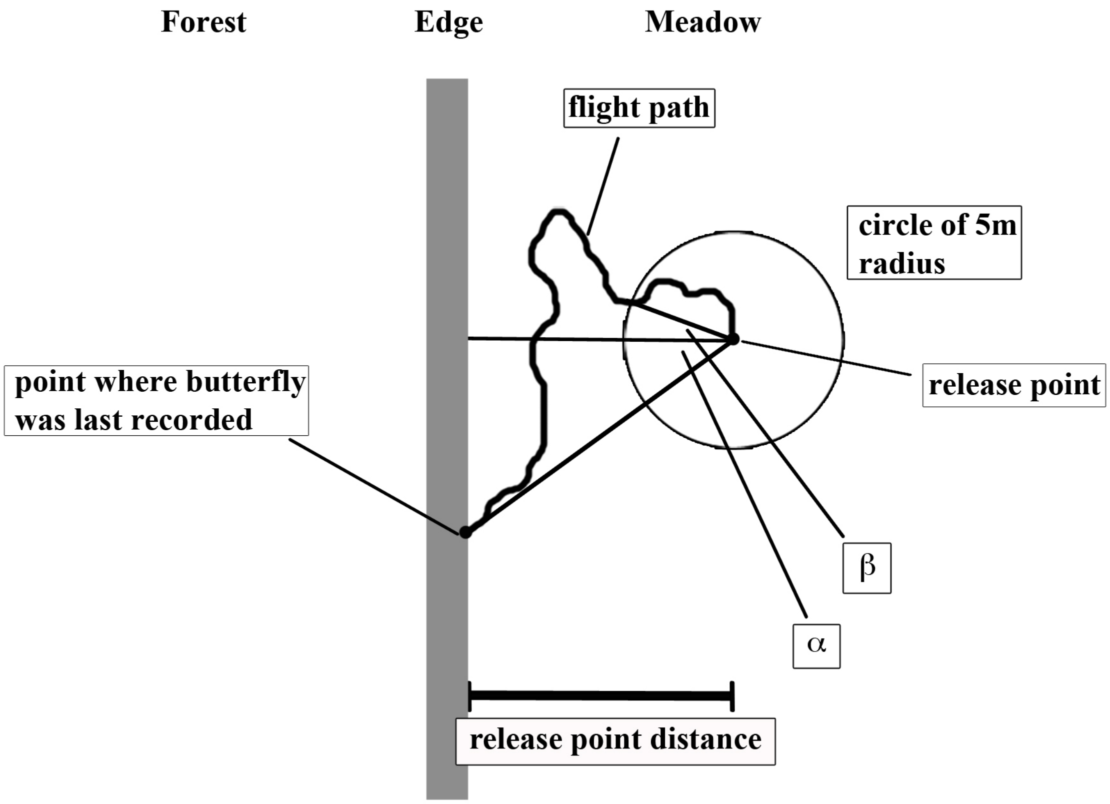

Figure 4. Sample flight path showing how initial (β) and final (α) divergence angles were measured from flight paths that were obtained during May-July 2012 (Adapted from Conradt et al. 2000:1506). The initial divergence angle β is the angle between the shortest straight line to the edge from the release point, and the straight line to the location of the butterfly at 5 m distance from the release point. The final divergence angle α is the angle between the shortest straight line to the edge from the release point and the straight line to where the butterfly was last recorded.

degrees represents the direction of the shortest straight line towards the forest/meadow boundary. For data that did not fit the von Mises distribution, non-parametric methods were used to determine the mean direction, and confidence intervals (Fisher 1993). If the confidence interval for the mean direction was between ±90°, then we fail to reject the hypothesis that the mean direction was towards the edge (Fisher 1993).

All statistical analyses were conducted using R version 3.0.2 (R Development Core Team 2012; R Foundation for Statistical Computing, Vienna).

Chapter 3

3 Results

3.1 Relative abundance

A summary of the abundance data for each species is shown in Table 3. Accounting for the different lengths of transect sections and the number of visits, out of the three time periods and 22 transects, there were only three significant correlograms for *P. glaucus* and three for *P. troilus*. As only 4.5% of all correlograms tested were significant, which can be expected by chance given a Type I error rate of 0.05, there was no evidence for significant spatial autocorrelation in butterfly counts among sections of individual transects.

Model selection results for *P. glaucus* indicated that relative abundance was associated with a number of variables (Table 4), but distance to the edge was consistently an important predictor in determining their relative abundance, in both the forest and the meadow ($w_+(i)$=1.00 and $w_+(i)$=1.00, respectively; Table 5). Our parameter estimates suggest a negative relationship between distance to the edge and relative abundance of butterflies, thus abundance increases with proximity to the edge (Table 5). As expected, the section length also had a strong effect in both the forest and in the meadow ($w_+(i)$ = 1.00 and $w_+(i)$=1.00, respectively; Table 5). The mean density of *P. glaucus* also showed that they are clearly more abundant at the edge at all time periods of the day (Figure 5).

Model selection results for *P. troilus*, showed that relative abundance was associated with a number of variables (Table 4). In the meadow, the number of observer visits to the transects was a good predictor of butterfly counts ($w_+(i)$= 0.67; Table 5), while distance to the edge was not ($w_+(i)$ = 0.28; Table 5). However, distance to the edge was important in the forest ($w_+(i)$ =0.92; Table 5), as was as the length of each section ($w_+(i)$=0.90; Table 5), and time of day ($w_+(i)$=0.69; Table 5). The interaction between time of day and distance to the edge ($w_+(i)$=0.62; Table 5) was also important in the forest.

Table 3: Summary of butterfly abundance relative to the edge data from 2013 in Norfolk County. Counts recorded of *P. glaucus* and *P. troilus* at each time period of the day (morning, mid-day, and afternoon), in each habitat type (meadow, edge, and forest), and in each section of the transect (A-I) are shown.

		Habitat type								
		Meadow				Edge	Forest			
		Transect sections								
Species	Time of day	A	B	C	D	E	F	G	H	I
P. glaucus	Morning	17	11	6	6	39	3	4	5	8
	Mid-day	7	17	6	10	51	2	0	4	16
	Afternoon	22	13	15	10	57	3	1	1	20
P. troilus	Morning	6	4	4	7	9	0	1	3	5
	Mid-day	4	3	4	5	4	1	2	12	7
	Afternoon	4	5	2	2	3	0	1	10	16

Table 4. Summary of model selection results for relative abundance for both *P. glaucus* and *P. troilus* in meadow and forest habitat types at the seven selected sites in Norfolk County during May-July 2013. Only models with $\Delta_i AIC_c < 4$ are shown, and are ranked by AIC_c. Factors included are distance to the edge (dis), section length (sl), time period (tim), number of visits (vis), and plant count (pl), which is only included in models assessing the meadow. Addition symbols indicate additive effects and colons indicate interactions. Log likelihood (logLik), second order Akaike information criterion (AIC_c), $\Delta_i AIC_c$, and Akaike weights (w_i) were derived from generalized linear mixed-model

Model	logLik	AIC_c	$\Delta_i AIC_c$	w_i	Model	logLik	AIC_c	$\Delta_i AIC_c$	w_i
MEADOW					FOREST				
P. glaucus									
dis+sl	-380.16	770.50	0.00	0.15	dis+sl	-275.06	560.30	0.00	0.51
dis+sl+tim+dis:tim	-376.19	770.95	0.45	0.12	dis+vis+sl	-274.89	562.05	1.75	0.21
dis+vis+sl	-379.49	771.24	0.74	0.10	dis+sl+tim	-274.05	562.45	2.15	0.17
dis+sl+tim	-378.50	771.35	0.85	0.10					
dis+pl+sl	-379.60	771.45	0.95	0.09					
dis+pl+sl+tim+dis:tim	-375.54	771.77	1.26	0.08					
dis+vis+sl+tim+dis:tim	-375.63	771.96	1.45	0.07					
dis+vis+pl+sl	-378.91	772.16	1.66	0.07					
dis+pl+sl+tim	-377.94	772.32	1.82	0.06					
dis+vis+sl+tim	-377.94	772.33	1.82	0.06					
dis+vis+pl+sl+tim+dis:tim	-374.95	772.73	2.22	0.05					
dis+vis+pl+sl+tim	-377.35	773.27	2.76	0.04					
P. troilus									
vis	-167.87	343.87	0.00	0.12	dis+sl+tim+dis:tim	-182.27	383.11	0.00	0.31
vis+pl	-167.34	344.87	1.00	0.07	dis+sl	-187.24	384.67	1.56	0.14

tim	-167.56	345.31	1.44	0.06	dis+vis+sl+tim+dis:tim	-182.14	384.97	1.86	0.12
vis+tim	-166.57	345.39	1.52	0.06	dis+tim+dis:tim	-184.57	385.58	2.47	0.09
int	-169.82	345.71	1.84	0.05	sl	-188.97	386.06	2.95	0.07
dis+vis	-167.86	345.90	2.03	0.04	dis+sl+tim	-186.11	386.56	3.45	0.05
vis+sl	-167.87	345.93	2.06	0.04	dis+vis+sl	-187.24	386.74	3.63	0.05
dis+vis+pl	-166.98	346.21	2.34	0.04					
pl+tim	-166.99	346.23	2.36	0.04					
vis+pl+tim	-166.03	346.41	2.54	0.03					
vis+pl+sl	-167.14	346.55	2.68	0.03					
pl	-169.28	346.68	2.81	0.03					
dis+vis+sl	-167.24	346.74	2.87	0.03					
dis+vis+pl+sl	-166.25	346.84	2.97	0.03					
dis+tim	-167.55	347.35	3.48	0.02					
sl+tim	-167.56	347.38	3.51	0.02					
dis+vis+tim	-166.55	347.45	3.58	0.02					
vis+sl+tim	-166.57	347.48	3.61	0.02					
dis+pl+tim	-166.61	347.58	3.71	0.02					
dis	-169.80	347.73	3.86	0.02					
sl	-169.82	347.76	3.89	0.02					
dis+vis+pl+tim	-165.67	347.80	3.93	0.02					

Table 5: The effect of distance to the edge and other factors on the relative abundance of both *P. glaucus* and *P. troilus* in the meadow and forest in Norfolk County during May-July 2013, as determined by model-averaging. Factors included are distance to the edge (dis), section length (sl), time period (tim), number of visits (vis), and plant count (pl). Colons indicate interaction effects. Model-averaged Akaike weights ($w_+(i)$), parameter estimates ($\hat{\hat{\beta}}_J$), and standard errors (SE) are derived from generalized linear mixed-models and model selection.

	Meadow			Forest		
Variables	$w_+(i)$	$\hat{\hat{\beta}}_J$	SE	$w_+(i)$	$\hat{\hat{\beta}}_J$	SE
P. glaucus						
dis	1.000	-0.130	0.012	1.000	-0.264	0.022
sl	1.000	0.211	0.022	1.000	0.452	0.039
tim	0.584	-	-	0.194	-	-
vis	0.393	-0.108	0.097	0.237	-0.057	0.098
pl	0.390	0.003	0.003	-	-	-
dis:tim	0.325	-	-	-	-	-
P. troilus						
dis	0.282	-0.013	0.021	0.916	-0.052	0.028
sl	0.229	0.014	0.033	0.893	0.097	0.051
tim	0.370			0.687	-	-
vis	0.673	0.271	0.150	0.206	0.068	0.177
pl	0.372	0.005	44.000	-	-	-
dis:tim	-	-	-	0.621	-	-

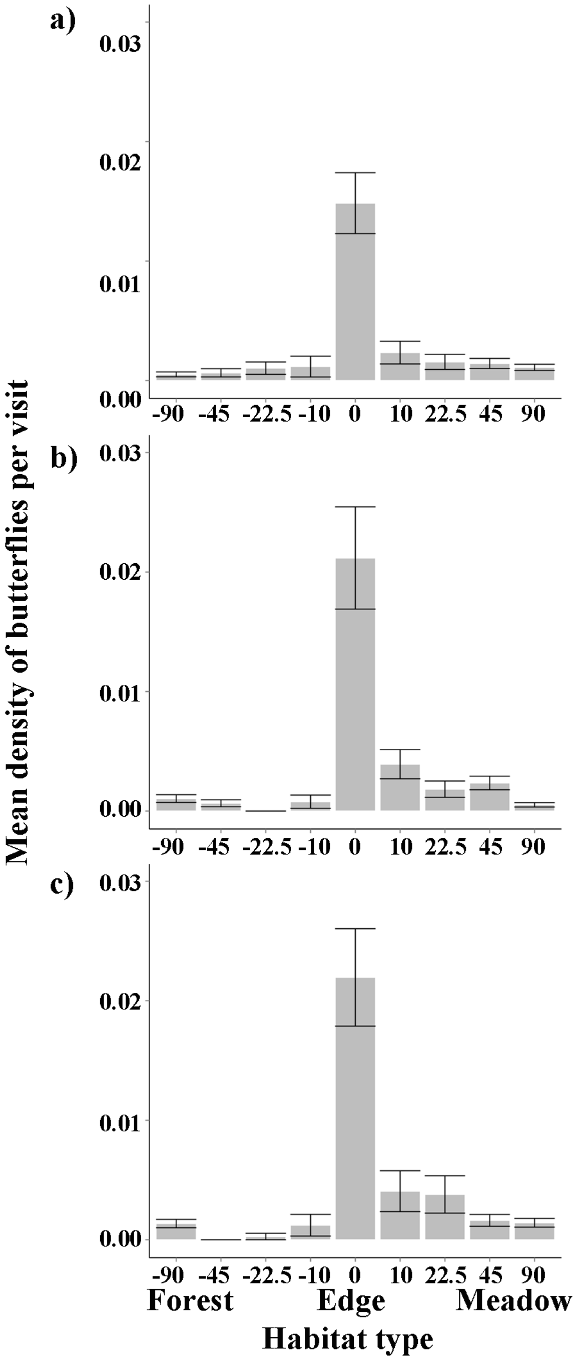

Figure 5. Mean density of *P. glaucus* per visit, in each habitat type: forest, edge, and meadow in Norfolk County during May-July 2013, separately for the (a) morning (10:00-12:00), (b) mid-day (12:30-14:30), and (c) afternoon (15:00-17:00). Standard error bars are shown. The distance to the edge in meters, measured by the mid-point in each section, is also shown. Mean density was calculated as the number of butterflies observed in each section (A-I), divided by section length and averaged over the total number of visits.

Although distance to the edge only emerged as an important predictor in our GLMM for *P. troilus* in the forest, and not in the meadow, the trend in Figure 6 suggests that there was higher mean density of *P. troilus* at or near the edge compared to other locations in both the meadow and the forest. However, this pattern of higher relative abundance at the edge was much less pronounced in *P. troilus* than it was in *P. glaucus*. Figure 6 also indicates that for *P. troilus* in the forest, the interaction between time of day and distance to the edge occurs because in the morning, *P. troilus* is most abundant at the edge and few individuals are seen in the forest. However, during mid-day and afternoon, *P. troilus* becomes proportionately less abundant at the edge and more individuals are seen in the forest, particularly at 45 m (Figure 6).

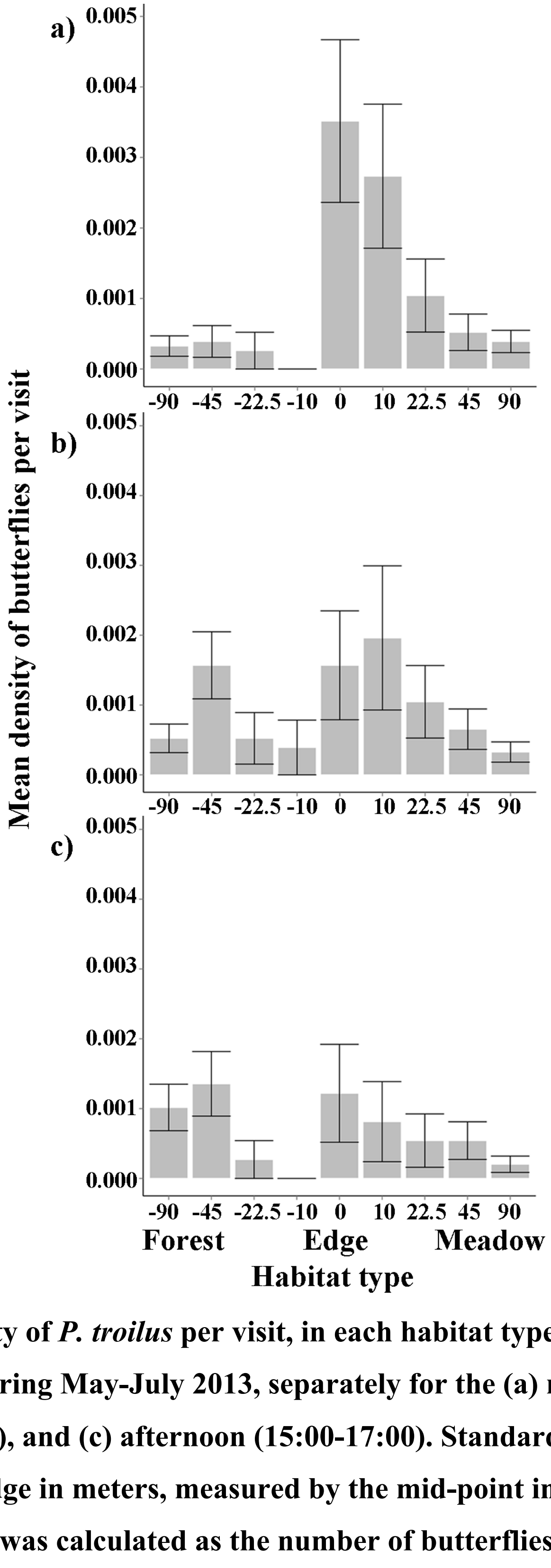

Figure 6. Mean density of *P. troilus* per visit, in each habitat type: forest, edge, and meadow in Norfolk County during May-July 2013, separately for the (a) morning (10:00-12:00), (b) mid-day (12:30-14:30), and (c) afternoon (15:00-17:00). Standard error bars are shown. The distance to the edge in meters, measured by the mid-point in each section, is also shown. Mean density was calculated as the number of butterflies observed in each section (A-I), divided by section length and averaged over the total number of visits.

3.2 Flight behaviour trials

At all release points in both the meadow and in the forest, the mean sines of turning angles, for both species and sexes, were not significantly different from zero. This indicates that there was no left or right turning bias exhibited by either species (Table 6).

Both males and females of *P. glaucus* at 60 m into the forest did not have a mean cosine that differed significantly from zero (males: mean cos=0.22, p=0.81 and females: mean cos= 0.28, p=0.50; Table 6), meaning that they exhibited more random flight behaviour deep in the forest. Male *P. glaucus* also exhibited random flight behaviour at 10 m into the forest (mean cos=0.20, p=0.15, Table 6), but females showed forward persistence (mean cos=0.41, p=0.02, Table 6). At all other release distances mean cosines for *P. glaucus* were significantly greater than zero and indicated a forward persistent flight (Table 6).

Similarly, for *P. troilus* released at 60 m in the forest, both males and females exhibited more random flight behaviour (males: mean cos=-0.09, p=1.00 and females: mean cos=0.47, p=0.25; Table 6). For male *P. troilus* at 10 m into the forest, the mean cosine was also not significantly different from zero (mean cos=-0.20, p=0.30, Table 6), also showing random flight behaviour. At all other release points, mean cosines were positive and significantly different from zero, showing a persistent forward flight for both males and females (Table 6).

Divergence angles for *P. glaucus* did not fit the von Mises distribution, thus non-parametric confidence intervals were calculated for the mean direction of initial and final divergence angles at each release distance, for each sex. Ninety-five percent confidence intervals were used at all distances, except at the 10 m release point in the meadow for females. In this case 80% confidence intervals were used (Table 7) because the standard errors were so large that using an $\alpha = 0.025$ resulted in a number >1, and thus it was mathematically impossible to calculate the inverse sine in order to obtain the confidence intervals in angles.

At a release point of 60 m into the forest, the mean direction of both male and female *P. glaucus* initial divergence angles was further towards the forest interior (males: mean=123.63, CI= 111.81-135.44 and females: mean=109.45, CI=93.39-125.51; Table 7). The initial divergence angles for females had wider confidence intervals than those for males, particularly at 10 m in

Table 6. Trigonometric cosine and sine functions were used to evaluate flight persistence and turning bias, respectively. Mean cosine and mean sine are shown for *P. glaucus* and *P. troilus*, males and females, and at all release points in the forest and the meadow in Norfolk County during May-July 2012. The Wilcoxon signed rank test was used to test if means significantly differed from zero. Shown are the number of trials included (N), the mean cosine/sine (Mean), the standard error (± SE), the test statistic (V), and the p-value (P). Positive mean cosines that are significantly different from zero are bolded and indicate a forward persistent flight.

			cos θ				sin θ			
Distance	Sex	N	Mean	± SE	V	P	Mean	± SE	V	P
P. glaucus										
FOREST										
60m	M	5	0.22	0.47	9	0.81	0.16	0.80	14	0.13
	F	2	0.28	0.18	3	0.50	0.94	0.05	3	0.50
10m	M	20	0.20	0.15	144	0.15	0.19	0.16	136	0.26
	F	18	0.41	0.14	139	**0.02**	-0.28	0.15	28	0.13
MEADOW										
10m	M	20	0.62	0.12	191	**<0.01**	0.03	0.13	111	0.84
	F	48	0.55	0.09	994	**<0.01**	0.07	0.08	604	0.49
30m	M	41	0.43	0.10	713	**<0.01**	0.01	0.10	366	0.95
	F	22	0.63	0.10	242	**<0.01**	0.06	0.14	123	0.51
60m	M	71	0.53	0.06	2304	**<0.01**	0.06	0.08	1289	0.48
	F	42	0.53	0.09	774	**<0.01**	0.03	0.10	408	0.81
P. troilus										
FOREST										
60m	M	5	-0.09	0.42	7	1.00	-0.11	0.26	6	0.81
	F	4	0.47	0.19	9	0.25	-0.02	0.47	5	1.00
10m	M	14	-0.20	0.19	35	0.30	0.07	0.20	61	0.63
	F	16	0.57	0.17	109	**0.03**	-0.02	0.12	68	1.00
MEADOW										
10m	M	53	0.65	0.07	1328	**<0.01**	-0.04	0.07	610	0.47
	F	20	0.42	0.13	168	**0.02**	0.06	0.16	113	0.78
30m	M	55	0.53	0.08	1331	**<0.01**	-0.03	0.08	639	0.83
	F	25	0.56	0.10	299	**<0.01**	-0.08	0.13	131	0.60
60m	M	51	0.68	0.05	1309	**<0.01**	0.08	0.09	756	0.39
	F	18	0.51	0.13	149	**<0.01**	-0.05	0.16	76	0.70

Table 7. Non-parametric confidence intervals (CI.Low and CI.High), mean direction, and standard errors (SE) of both male and female *P. glaucus*, at all release points in the forest and meadow in Norfolk County during May-July 2012. The number of trials conducted is also shown (N). Asterisks indicate that 80% confidence intervals were used at the 10 m release point in the meadow, while 95% confidence intervals were used for all other release points. Bolded values indicate significant directionality towards the edge.

Distance	Sex	N	Mean direction	SE	CI.Low	CI.High
Initial divergence angle (initial orientation)						
FOREST						
60m	M	39	123.63	0.10	111.81	135.44
	F	19	109.45	0.14	93.39	125.51
10m	M	43	71.96	0.13	**56.69**	**87.23**
	F	20	52.01	0.18	**31.15**	**72.87**
MEADOW						
10m	M	43	-14.15	0.22	**-39.18**	**10.88**
	F	20	-55.92	0.68	-117.31*	5.48*
30m	M	44	-18.29	0.16	**-36.46**	**-0.12**
	F	21	-35.45	0.25	**-65.17**	**-5.73**
60m	M	44	-30.06	0.17	**-49.04**	**-11.08**
	F	19	-47.63	0.24	**-76.22**	**-19.04**
Final divergence angle (overall flight direction)						
FOREST						
60m	M	39	120.95	0.11	108.59	133.30
	F	19	107.74	0.15	91.07	124.41
10m	M	43	61.24	0.14	**45.45**	**77.02**
	F	20	36.63	0.17	**17.12**	**56.14**
MEADOW						
10m	M	43	-14.11	0.22	**-39.58**	**11.36**
	F	20	-53.72	0.77	-136.49*	29.05*
30m	M	44	-21.68	0.18	**-52.09**	**-11.26**
	F	21	-40.61	0.26	**-71.83**	**-9.39**
60m	M	44	-25.03	0.18	**-45.31**	**-4.75**
	F	19	-43.16	0.28	**-76.18**	**-10.13**

the meadow, where direction of females was not significantly towards the edge (females: mean=-55.92, CI=-117.31-5.48; Figure 7a; Table 7). However, at all other release distances, both in the forest and in the meadow, the mean direction of butterfly initial divergence angles was significantly towards the edge (Figure 7a; Table 7).

Similarly, the mean direction of both male and female *P. glaucus* final divergence angles were directed towards the edge, with the exception of those individuals released at 60 m in the forest, (males: mean=120.95, CI=108.59-133.30 and females: mean=107.74, CI=91.07-124.41; Figure 7b; Table 7) and females released at 10 m in the meadow (females: mean= -53.72, CI=-136.49-29.05; Figure 7b; Table 7). Females consistently had wider confidence intervals in their final divergence angles in the meadow than males (Figure 7b; Table 7).

Both initial and final divergence angles for *P. troilus* fit the von Mises distribution. Thus the Rayleigh test of uniformity was performed to assess whether significant directionality was present in both their initial orientation (Table 8).

From release points in the forest, the initial divergence angles of both male and female *P. troilus* did not fit a uniform circular distribution and indicated significant directionality in the initial flight orientation. At 60 m in the forest, the mean initial divergence angle for both sexes indicated a flight direction neither towards nor away from the edge, but rather parallel to the edge (male 60 m: $p<0.01$, mean=98.03, CI=65.53-127.07 and female: 60 m: $p<0.01$, mean=94.33, CI=61.38-128.94; Figure 8a; Table 8). At the 10 m release point in the forest, male mean initial divergence angle was also parallel to the edge ($p<0.01$, mean=97.61, CI=71.34-121.27; Figure 8a; Table 8), while female mean initial divergence angle indicated flight direction towards the edge ($p <0.01$, mean=56.98, CI=34.40-88.55; Figure 8a; Table 8). From release points in the meadow, only the initial divergence angles for males released at 10 m and 30 m did not fit a uniform circular distribution, indicating significant directionality in the initial flight orientation. Males released at these points had mean initial divergence angles in the direction of the edge (10 m: $p<0.01$, mean=-43.89 CI=-82.58- -7.92 and 30 m: $p<0.01$, mean=17.01, CI=-10.40-49.40; Figure 8a; Table 8). For males released at 60 m in the meadow, and for females released at all distances in the meadow, the initial divergence angles did not deviate from a uniform circular distribution, indicating no significant directionality in the initial flight

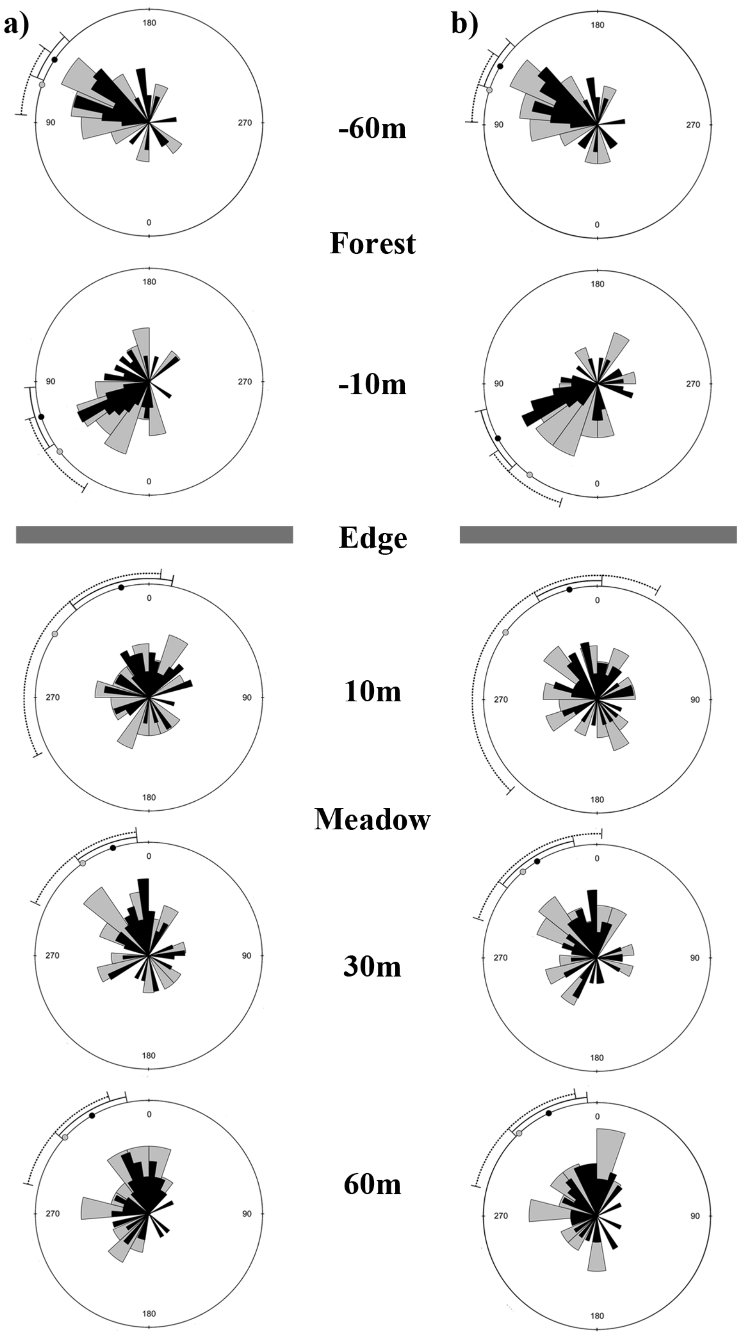

Figure 7. Rose diagrams show the distribution of (a) initial and (b) final divergence angles relative to the edge from all release points in the forest and meadow for *P. glaucus.* Data were collected at three selected sites in Norfolk County during May-July 2012. Points on the circle are the mean directions bounded by non-parametric confidence intervals. Females are represented by gray and dotted lines, and black and solid lines represent males.

Table 8. Mean direction and parametric confidence intervals (CI.Low and CI.High) of initial and final divergence angles for both male and female *P. troilus*, at all release points in the meadow and forest in Norfolk County during May-July 2012. Numbers of trials conducted are also shown (N). Data fit the von Mises distribution and the Rayleigh test was performed: dispersion (r) and significance of directionality (P) are shown. Bolded values indicate significant directionality (i.e., deviation from a uniform, circular distribution).

Distance	Sex	N	Mean direction	CI. Low	CI. High	r	P
Initial divergence angle (initial orientation)							
FOREST							
60m	M	28	98.03	65.53	127.07	0.46	**0.00**
	F	14	94.33	61.38	128.94	0.61	**0.00**
10m	M	26	97.61	71.34	121.27	0.54	**0.00**
	F	13	56.98	34.40	88.55	0.68	**0.00**
MEADOW							
10m	M	26	-43.89	-82.58	-7.92	0.42	**0.01**
	F	13	39.32	-12.93	116.22	0.39	0.14
30m	M	29	17.01	-10.40	49.40	0.50	**0.00**
	F	13	-43.18	-145.67	57.40	0.27	0.40
60m	M	28	-37.66	-140.46	25.53	0.21	0.31
	F	10	-59.57	-131.45	5.74	0.37	0.27
Final divergence angle (overall flight direction)							
FOREST							
60m	M		98.03	65.53	127.07	0.41	**0.01**
	F		94.33	61.38	128.94	0.59	**0.01**
10m	M		97.61	71.34	121.27	0.51	**0.00**
	F		56.98	34.40	88.55	0.64	**0.00**
MEADOW							
10m	M		-43.89	-82.58	-7.92	0.28	0.13
	F		101.52	-12.93	116.22	0.20	0.61
30m	M		17.01	-10.40	49.40	0.61	**0.00**
	F		-43.18	-145.67	57.40	0.20	0.61
60m	M		-37.66	-140.46	25.53	0.29	0.10
	F		-59.57	-131.45	5.74	0.28	0.48

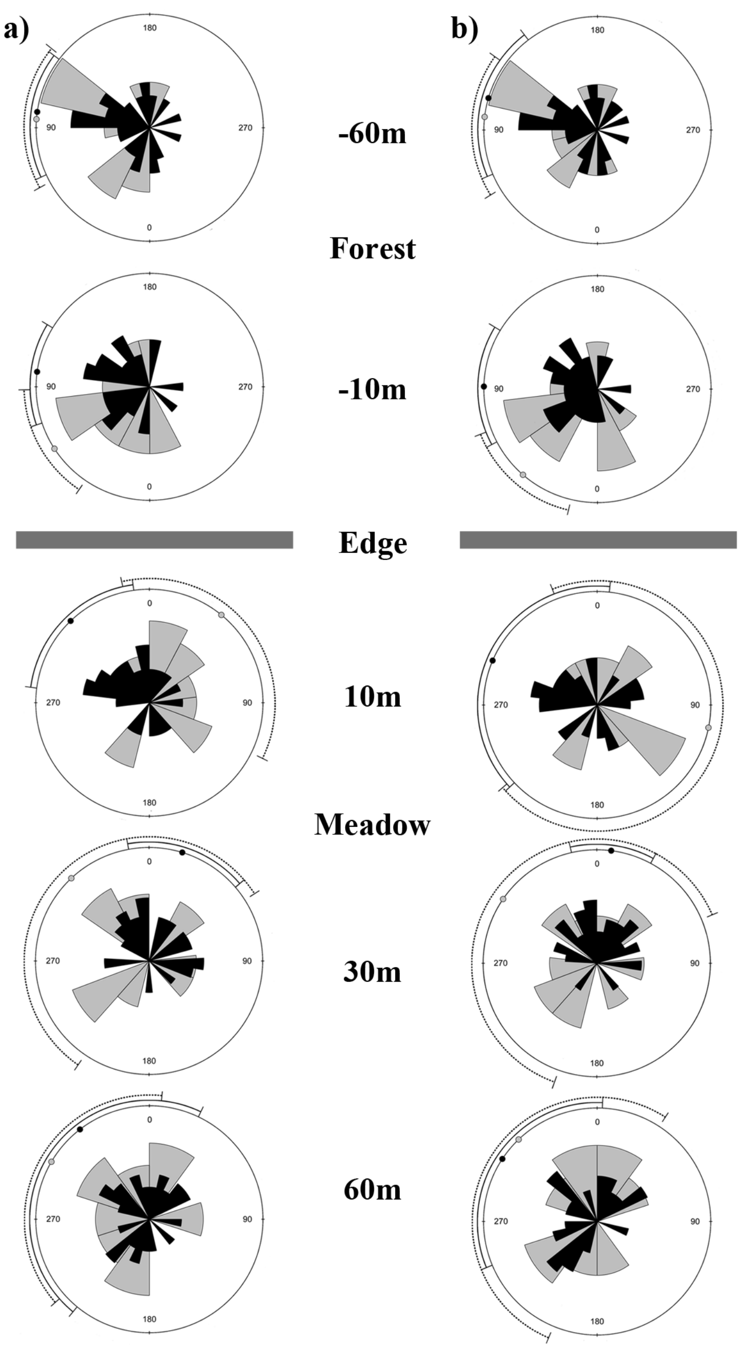

Figure 8. Rose diagrams show the distribution of (a) initial and (b) final divergence angles relative to the edge from all release points in the forest and in the meadow for *P. troilus.* Data were collected at three selected sites in Norfolk County during May-July 2012. Points on the circle are the mean directions bounded by parametric confidence intervals. Females are represented by gray and dotted lines, and black and solid lines represent males.

orientation (male: p=0.31 and females: p=0.14 - 0.40; Table 8). In these cases, the mean initial divergence angles did show a trend of being oriented towards the edge, however they were associated with very high variability and wide confidence intervals (Figure 8a; Table 8).

From release points in the forest, the final divergence angles of both male and female *P. troilus* also did not fit a uniform circular distribution, indicating significant directionality in the overall flight path (male: 60 m: p<0.01, 10 m: p<0.01 and female: 60 m: p<0.01, 10 m: p<0.01; Figure 8b; Table 8). The mean final divergence angle at the 60 m release point in the forest for both sexes (males: mean=98.03, CI=65.53-127.07 and females: mean=94.33, CI=61.38-128.94; Figure 8b; Table 8), and at 10 m in the forest for the males was close to 90° (mean=97.61, CI=71.34-121.27), suggesting an overall flight direction neither towards nor away from the edge, but parallel to the edge. From the 10 m release point in the forest, females did show an overall flight direction towards the edge (p<0.01, mean=56.98, CI=34.40-88.55; Figure 8b; Table 8). In the meadow, only the final divergence angles for males released at 30 m deviated significantly from a uniform circular distribution, with the mean values indicating an overall flight path directed towards the edge (p<0.01, mean=17.01 CI=-10.40- -49.40; Figure 8b; Table 8). For males released at 10 m and 60 m in the meadow, and females released at all distances in the meadow, the final divergence angles did not deviate from a uniform circular distribution, indicating no significant directionality in the overall flight orientation (males: p= 0.10 - 0.13 and females: p= 0.48 - 0.61; Table 8). While males released at 10 m and 60 m in the meadow, and females released at 30 m and 60 m in the meadow, did have mean final divergence angles oriented towards the edge, these were associated with very high variability and wide confidence intervals (Figure 8b; Table 8).

Chapter 4

4 Discussion

My work demonstrates that both swallowtail butterfly species, *P. glaucus* and *P. troilus*, are more abundant at or close to the edge relative to the forest and the meadow. This pattern is consistent with the predictive model of ecological responses to habitat edges that Ries et al. (2004) proposed, where species exhibit a positive edge response when complementary resources are required in two different landcover types. This is especially important for species that require different landcover types during different stages of development to complete their life cycle, such as insects and frogs (Pope et al. 2000). While many butterfly species can access both nectar sources and the larval host plants in one landcover type (Shultz and Crone 2001, Ross et al. 2005), adult *P. glaucus* and *P. troilus* must be able to access forests for oviposition sites and meadows for nectar sources. As expected, these swallowtail species are more abundant at the edge, which can provide them access to both of these resources. My study corroborates other studies looking at multiple species of insects (Ries and Sisk 2008), birds (Fonderflick et al. 2013), and mammals (Lidicker 1990) that found that the abundance of individuals in the landscape corresponds to the distribution of their resources. In the GLMMs, distance to the edge emerged as an important predictor of abundance for *P. glaucus* in both the meadow and the forest, and for *P. troilus* in the forest, suggesting that forest/meadow edges are important structural features determining the distribution of these swallowtail butterfly populations across the landscape. The occurrence of such species that have complementary resources may explain why higher species richness is sometimes observed in more heterogeneous landscapes, where edge density is high (Tscharntke et al. 2002, Rossi and van Halder 2010, Ethier and Fahrig 2011, Flick et al. 2012, Di Napoli and Caceres 2012). Furthermore, because they require forest/meadow edges to persist, my results suggest that some degree of forest fragmentation in southwestern Ontario, which would increase the amount of edge in the landscape, may actually benefit these swallowtail butterfly populations.

An underlying mechanism for the spatial pattern that I specifically examined is ecological flows; the movement of individuals from one resource patch to another (Ries et al. 2004). Overall, I found that the flight behaviour of both *P. glaucus* and *P. troilus* indicated a forward persistent movement, particularly within the meadow. By tracking individual butterflies and assessing turning angles, I also found that both species can initially orient their flight, and have an overall flight path directed towards the edge from release points in both the forest and in the meadow. Both species exhibited more random flight behaviour within the forest, which is not surprising since the vegetation height and density may limit their visual perception. It is clear that the edge is not a barrier to movement for these butterflies, in contrast to many other species (Shultz and Crone 2001, Ross et al. 2005). These results support the hypothesis of a preference for the edge and provide an underlying process that explains both species' spatial patterns of abundance as other butterflies also exhibit non-random movement and direct their flight towards a desired location (Conradt et al. 2000, Schtickzelle et al. 2007).

4.1 Species-specific differences

Other studies that have considered the edge response model of Ries et al. (2004) to explain patterns of species distribution, have not taken into account species-specific differences and additional factors that may alter the resulting patterns of spatial distribution relative to edges (Ries and Sisk 2008, Fonderflick et al. 2013). Even though both *P. glaucus* and *P. troilus* have complementary resources in the meadow and in the forest, and both demonstrated the general pattern and mechanism associated with positive edge responses, distinct species-specific differences nonetheless exist. *Papilio glaucus* showed a very clear and strong pattern of edge association, with noticeably higher density at the edge and strongly directed movement towards the edge. *Papilio troilus* exhibited a gradual increase in abundance to the edge, proportionally higher abundance in the forest later in the day, and also showed more variability in the direction of their initial orientation and overall flight path. Given that both species have the same pattern of complementary resources distribution between forest and meadow areas, it is clear that additional factors must also contribute to species distribution patterns relative to edges in the landscape. The observed differences between these two swallowtail species in patterns of abundance and movement behaviours could reflect differences in how their respective resources are distributed at a fine-scale, as well as differences in their behavioural ecology and life history traits.

Ries et al. (2004) describe that resource mapping is the most common mechanism to explain species' distributions. However, depending on how a species' resources are distributed at a fine-scale, including within a particular type of landcover, this could also determine how they move in order to obtain those resources and what their spatial patterns of distribution will be. Studies have shown that animal movements are correlated with resource availability, and movement patterns shift as resource availability changes (Schultz and Crone 2001, Fryxell et al. 2005, Khamcha et al. 2011). In my study, both swallowtail species use the same nectar sources in the meadow, but oviposit on different plants in the forest. One possible reason for species-specific differences in flight patterns and abundances is that these swallowtails may have evolved under conditions that require specific flight behaviours to help locate forest resources. *Papilio glaucus*' main larval host plant, *L. tulipifera,* is a tall deciduous tree where oviposition sites are near the canopy. Therefore, more direct flights may be suitable to reach these sites with less complex vegetation structure to obstruct their flight path and *P. glaucus'* visual acuity may be better in lighter conditions (Land 1997). In contrast, the host plants for *P. troilus* are the understory shrub, *L. benzoin*, and understory tree species*, S. albidum*. *Lindera benzoin* is found patchily in the interior forest (Cipollini et al. 1994, Matlack 1994) and *S. albidum* is abundant and often seen at forest edges. Since these larval host plants are in the understory, it may be necessary for *P. troilus* to exhibit more flight agility to navigate through complex forest vegetation in order to locate suitable oviposition sites. The distribution of larval host plants in the canopy versus in the understory of the forest may explain the clear flight directionality that *P. glaucus* demonstrates, but not *P. troilus*.

In addition to resource distribution, other aspects of a species' ecology and life history traits can affect their movement and spatial patterns of abundance. Another potential hypothesis for the differences I observed in movement and abundance patterns of *P. glaucus* and *P. troilus* is related to movement behaviour in ectotherms and their ability to thermoregulate. Studies have shown that heating rates differ between different coloured morphs or species, and this corresponds with different types of behaviour and habitat requirements (Watt 1968, Van Dyck and Matthysen 1998). *Papilio troilus* have darker colouration in wings and thorax than *P. glaucus,* and thus are expected to heat up at a faster rate (Watt 1968, Van Dyck and Matthysen 1998), have more flight activity such as larger displacements, and more manoeuvrability and faster take off (Roland 1982, 2006, Samejima and Tsubaki 2010). These flight characteristics associated with body temperature may help explain the flight behaviour I observed in the field and the directionality of their flight path. *Papilio glaucus* tended glide and have more direct movements through the landscape, while *P. troilus* were observed to be faster fliers, harder to catch, and to have more erratic flight behaviour. The increased flight activity and agility *P. troilus* exhibited may have lead to the more random flight behaviour and less directionality that was observed in the initial orientation and overall direction of their flight paths.

In addition to fine-scale resource distribution and thermal control of flight behaviour, the potential for observer bias in estimating spatial patterns of the abundance of these two swallowtail species should also be considered. Overall there were proportionally fewer butterflies of both species seen in the forest than in the meadow. This may have been because less sunlight in the forest and more complex vegetation structure could make it more difficult for the observer to record them. Also, the consistently lower proportion of *P. glaucus* recorded in the forest may be because the canopy of its larval host plant, *L. tulipifera,* is often not easily seen from the ground. Thus, *P. glaucus* could be in the forest more often than my results would suggest, but they may be less visible searching for mates or for oviposition locations on leaves near the canopy. In contrast, the larval host plants for *P. troilus* are found in the understory or close to the edge (Cipollini et al. 1994, Matlack 1994, Gram and Sork 1999). The smaller vegetation structure of these larval host plants may explain why proportionally higher counts of butterflies were recorded in the forest for *P. troilus* than for *P. glaucus*; *P. troilus* may be more visible to the observer on the ground while they search for oviposition sites and mates. The distribution of butterflies is also likely to change with respect to the edge and time of day because in the morning butterflies will bask at the edge or in the meadow, but later in the day when temperatures are at their peak, they may seek shade, mates, and oviposition sites. This could explain the observed change in the distribution of *P. troilus* which became more abundant in the forest later in the day, but such a pattern may be masked in *P. glaucus* due to taller and larger larval host plants. Nonetheless, while there is some potential for observer bias in recording butterfly abundance in the forest, the clear trend for flight that is oriented towards the edge from release points in both meadow and forest, particularly in *P. glaucus*, suggests that the greater abundance of individuals recorded at the edge cannot be entirely an artefact of a reduced ability to observe these butterflies in the forest.

4.2 Detecting the edge from the forest

Further into the forest both species did not initially orient their flight or direct their overall flight path towards the edge, and exhibited random flight behaviour. The lack of directionality and random flight behaviour deep in the forest may be interpreted as either that individuals perceive their surrounding environment as a preferable location and have low motivation to leave the area to locate the edge or meadow, or simply that individuals have more difficulty locating and orienting towards the edge.

Olfactory cues help butterflies perceive their environment and even help them navigate through the landscape. Ockinger and Dyck (2012) found that by experimentally removing some butterflies' antennae, thus limiting their olfactory senses, they were less likely to locate their habitat, whereas butterflies with antennae intact oriented towards their habitat more quickly and more often. Pheromones and chemical compounds may be detected to help locate mates (Pivnick et al. 1992), and distinguish and locate suitable oviposition sites (Heinz and Feeny 2005, Carlsson et al. 2011). For both swallowtail species deep in the forest, they may be sensing these resources that are in close proximity, instead of the edge, and thus choosing to remain in the forest. Although olfactory cues have been shown to be important for other species, without further experimental evidence it is difficult to discern the role for these swallowtail species.

Visual cues also play an important role in detecting landscape features, particularly for diurnal insects. Butterfly eyes operate as apposition compound eyes, similar to other diurnal insects (Land 1997). Larger butterflies, such as swallowtails, are found to have larger eyes suggesting that overall they have higher visual sensitivity, larger fields of vision, and higher acuity (Rutowski 2000). However, lower light levels in forests, can affect visual acuity and reduce the ability to detect contrast (Land 1997), thus it may be more difficult for these swallowtails to detect favourable landscape features, such as edges, from locations within the forest.

Solar radiation and air temperature can be increased at edges compared to interior forest, and wind characteristics change as the vegetation type changes in the landscape (Saunders et al. 1991). Wikström et al. (2009) showed that these abiotic factors can influence butterfly behaviour and may act as a signal that the edge can provide access to a nearby meadow with nectar sources. These abiotic cues likely become more difficult to perceive deeper in the forest, providing the butterflies with fewer signals that would allow them to efficiently detect and orient towards the edge. When butterflies were released closer to the edge from the forest, with the exception of male *P. troilus*, they did exhibit a forward persistent flight behaviour and initially oriented and had an overall flight path directed towards the edge. These observations support the hypothesis that even from points within the forest, these swallowtail butterflies are motivated to orient towards the edge, and therefore their lack of edge-orientation behaviour deeper in the forest may be a result of insufficient cues to detect the edge.

At release points in the forest, the butterflies' movements may also have been motivated by the attraction to light. At the 60 m release point, butterflies often flew in an upward movement towards the canopy while at the 10 m release point they were more likely to fly towards the edge. It is possible that this orientation to the edge was primarily in response to greater light levels at the edge rather than gaining access to food resources.

4.3 Detecting the edge from the meadow

Close to the edge, from release points in the meadow, *P. troilus* exhibited more variability in their initial flight orientation and even moreso in their overall flight direction than *P. glaucus*. Conradt et al. (2000) found similar behaviours in the butterfly *Maniola jurtina* and suggested that it may be due to low motivation to direct their flight towards the habitat at very close distances, since habitat was so easily accessible at those points (i.e., they perceive that they have arrived at their desired location and begin to undertake less directional activities). I suggest that *P. troilus* may demonstrate more variability in flight behaviours close to the edge, particularly in their overall flight direction, due to a combination of observed species-specific difference in their flight behaviour as previously mentioned and ease of access to resources that the edge provides. That is, close to the edge they are at the optimal or desired location and engage in less directional movements and behaviours.

The perceptual range among butterfly species can vary substantially. For example, *Parnassius smintheus* can detect forest up to 5 m from the edge (Ross et al. 2005), *Proclossiana eunomia* can perceive habitat up to 30 m away (Schtickzelle et al. 2007), and *M. jurtina* exhibit homing behaviour as far as 125 m away from their habitat (Conradt et al. 2000). Further from the edge in the meadow, *P. glaucus* showed directed flight towards the edge suggesting that it can detect the edge from up to 60 m away. *Papilio troilus*, however, shows strong directionality at 30 m from the edge but more variability in direction at 60 m. The variation in directionality from such distances could indicate species-specific differences in perceptual ranges for *P. glaucus* and *P. troilus*, however, further examination is necessary to specifically test each species' visual acuity. Previous studies have indicated that size of the species' sensory organs can generally predict their sensory abilities (Rutowski 2000, Nummela et al. 2013), and since these swallowtail species are similar in size, this suggests that species-specific differences in perceptual range may not be the case.

Informative data about butterfly flight behaviour can be obtained from their flight paths, and methods very similar to those I used have been practiced to study flight behaviour in a large number of other butterfly species, as well as other flying insects (Ross et al. 2005, Skórka et al. 2013). Nonetheless, the flight paths recorded in this manner, by connecting alighting points with straight lines, are somewhat coarse in resolution and fine-scale details of flight paths may become overlooked. More detailed data on turning angles, for example, may have revealed additional insights into flight behaviour. However, considering that I was primarily interested in behaviours relating to orientation toward the edge at a scale of tens of meters, the resolution of the flight paths I recorded was in line with the scale of the phenomenon I was interested in studying. Also, in comparison to many other butterfly species that are highly erratic fliers (i.e. Lycaenida or Nymphalidae; Scott 1986), these swallowtail butterflies often fly in more linear paths and therefore, finer details of their flight may not be highly relevant to resource acquisition or habitat selection. Furthermore, the resolution of the flight paths that I used allowed me to obtain a large number of flight paths for butterflies at each release point and thereby gain a more representative overview of their flight behaviour.

4.4 Differences between the sexes

My results demonstrated distinct differences in flight behaviours and orientation between males and females within both species. Females generally showed more variability in their initial orientation and overall direction of flight paths compared to males, particularly in the meadow. Differences in flight behaviour between sexes may depend on the species' mating system (Wickman 1992). *Papilio glaucus* and *P. troilus* are classified as being patrollers, rather than perchers in their mate location behaviour (Brower 1959, Scott 1986). Males of patrolling species fly around continuously searching for females, whereas in species that are perchers, males sit and wait to intercept females which are the more mobile sex (Scott 1974). The patrolling strategy of males of these swallowtail species may explain their less variable flight behaviour relative to females.

Another possible explanation for more variable directionality of females in the meadow is that females may spend more time nectar feeding to regain the energy spent locating suitable oviposition sites. Dickins et al. (2013) highlight the complexity of finding a suitable oviposition location, which can depend on factors at multiple scales, including the site and individual plant. Oviposition site location is extremely important since it can influence the survival of offspring to adulthood (Rausher 1979), and a butterfly's ability to find suitable sites can depend on direct contact with the plant (Heinz and Feeny 2005). Thus, oviposition that optimizes fitness can require much flight activity and a large expenditure of energy. Furthermore, these swallowtail species lay their eggs singly (Scott 1986), which further increases the flight distances covered and energy expended. Since females are likely expending more energy than males because of their oviposition activity, they must nectar feed more often. Therefore, in the meadow their directionality may be more variable as they engage in longer and more extensive searches for nectar.

While the females of both species need to find larval host plants in the forest, males may also have an incentive to go into the forest to find virgin females to mate with. Males have been shown to prefer unmated females (Klein and Araújo 2010) and spermatophore size decreases with successive copulations (Caballero-Mendieta and Cordero 2013). Thus it has been suggested that males will have the highest fitness gains when they mate with a virgin female, and that their best chance to encounter one is at their pupation sites in the forest (Rutowski 1991, Ide 2004). While female swallowtails may exhibit less directional flight behaviour further away from the edge within the forest because they are actively searching for oviposition locations, males may similarly be searching out pupation sites within the forest for newly emerged virgin females to mate with (Schultz and Crone 2001).

4.5 Future directions

I examined butterfly abundance and flight behaviour at well-defined boundaries. This is useful in identifying the specific effects of sharp boundaries. It may also be more representative of behaviours that are relevant in the current landscape, highlighting how the increased prevalence of sharp edges due to landscape changes influence the distribution and behaviour of resident species. Future studies can expand on this work by examining how more natural and gradual types of edges, such as less sharp ecotones or riparian corridors, can influence the distribution and flight behaviour of these swallowtail butterflies and may give insight to how these species behaved historically. Kuefler and Haddad (2006) showed that natural ecotone habitats can be important and that vegetation cover of these areas can facilitate movement of butterflies. In addition, other studies have shown that boundaries between different urban landcover types can result in different edge responses (Brearley et al. 2012, Nowicki et al. 2013). Thus, it could also be important to examine patterns of distribution and flight behaviour of swallowtail butterflies at sites that represent contemporary landscapes with hedgerows or roadsides. Studying swallowtail distribution and flight behaviour in areas that have different types of edges can provide insight into what natural and modern landscape features are important for movement and inform land management plans.

Future studies could also test the response of these swallowtail species to edges between a wider range of, and various combinations of, landcover types including anthropogenic landcovers, such as agriculture and forest edges, or agriculture and meadow edges. The quantity or type of resources may vary in these different landcover types and such studies help identify how landscape change and current landcovers have influenced the species' distribution and behaviour and how this will affect the populations in the future. Finally, it may also be useful to examine edges that face in different directions, as edge aspect may influence important abiotic factors such as light attenuation or wind exposure (Dignan and Bren 2003).

Habitat fragmentation has been suggested to have evolutionary consequences on flight and movement for butterflies. Ockinger and Van Dyck (2012) showed that *Pararge aegeria* originating from fragmented habitats are more effective at navigating through a fragmented landscape than those originating from intact habitats, and suggest that searching strategies become adapted to minimize flying costs. Several other studies show changes in morphology of butterflies such as wing colour, wing loading, and flight muscles, in fragmented landscapes, which presumably reflect selection on dispersal traits (Davis et al. 2012, Kalarus et al. 2013, Rauhamäki et al. 2014). If southernwestern Ontario was historically mostly covered by deciduous forest, it is plausible that both swallowtail butterfly species may have been less abundant and that the increase in edges due to landscape fragmentation has helped expand both their density and geographic range. It is also possible that they have already undergone evolutionary change and my results may reflect the effects of adaptations to landscape changes that have occurred over the past two centuries. Future studies could compare distribution patterns and movement of these butterflies in southernwestern Ontario to areas with greater forest cover, such as conserved tracts of forest in the eastern United States. Areas that have experienced less forest fragmentation and loss can give insight to the swallowtails' dispersal capabilities and evolutionary potential to adapt to changing landscapes. Comparison of morphological features, particularly flight-related morphology, between historical samples and contemporary butterflies could also yield some insight into potential evolutionary changes in flight behaviours of these butterflies.

4.6 Conclusion

The results from my study support the model of positive edge response proposed by Ries et al. (2004), while highlighting that species-specific differences in other ecologically important traits, for example resource distributions and thermoregulatory ability, can modify these edge responses. Other specialist species are often associated with one landcover type and are highly sensitive to landscape changes affecting their habitat. In contrast, I have shown that the swallowtail butterflies, *P. glaucus* and *P. troilus*, which use complementary resources in different habitat types, are frequently found in the forest and in the meadow, but most often at or near the edge. Furthermore, I have shown that, in general, these species orient their flight towards forest/meadow edges. This suggests that these swallowtail species benefit from the occurrence of forest/meadow edges, and thus may be considered edge species rather than the generalists or woodland species they have been previously labeled (Scott 1986; Haddad 1999). My results suggest that some degree of forest fragmentation can actually benefit certain native species in contrast to the current paradigm that the creation of edges in landscapes causes only negative effects. Most importantly, my study highlights the need to understand mechanisms for fine-scale behaviour, species-specific movements, and species’ distribution to gain a better understanding of their habitat requirements and potential responses to landscape change.

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Appendices

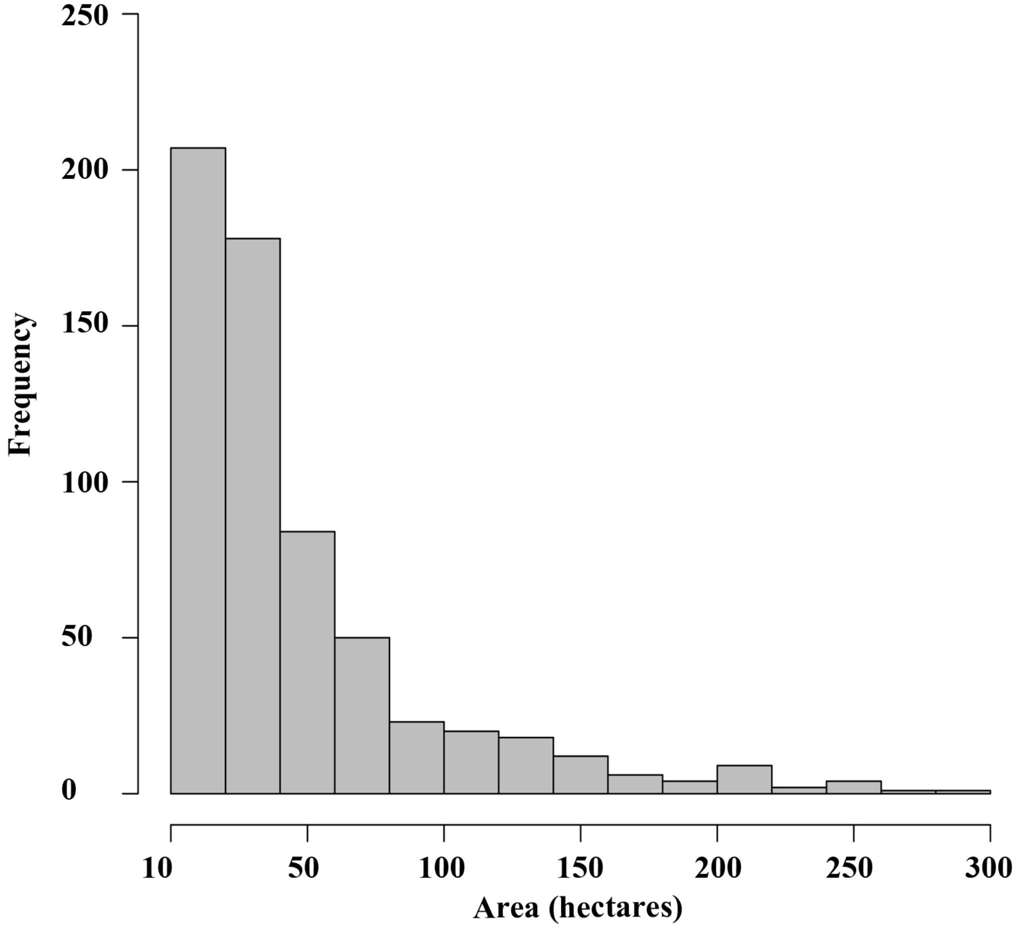

Figure A.1: Frequency distribution of all forest patches by area (hectares) in Norfolk County that were considered for relative abundance data collection during May-July 2013.

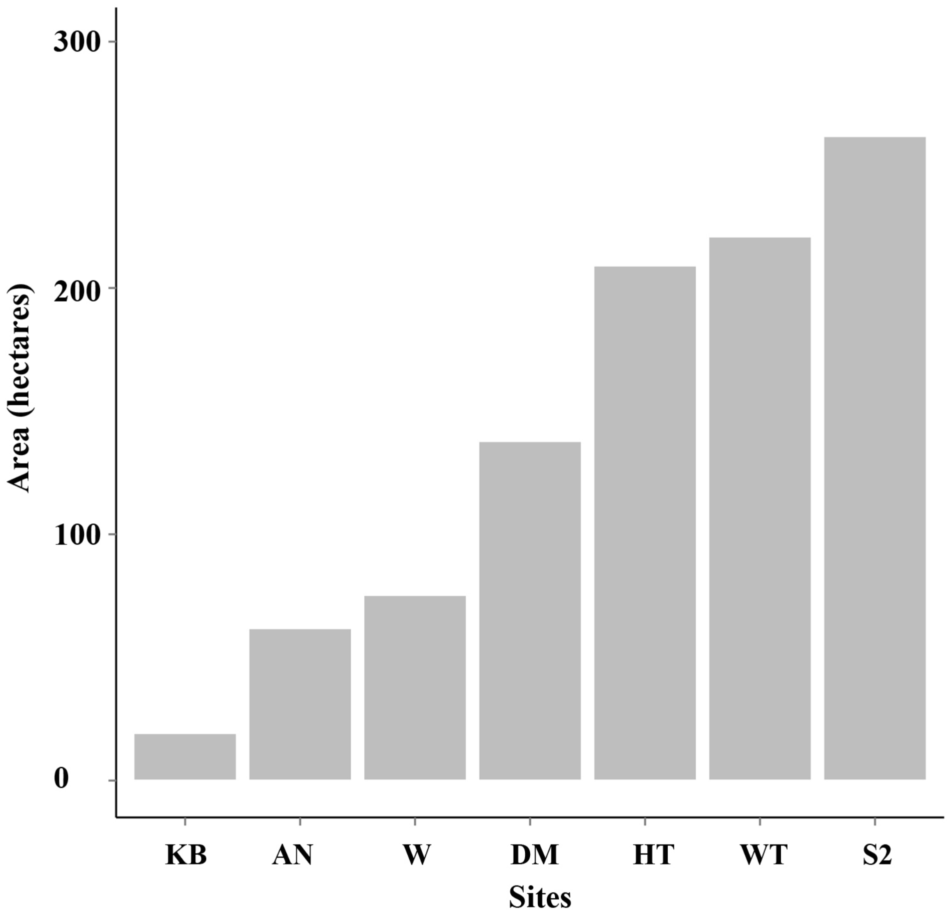

Figure A.2: Area in hectares of forest patches that were chosen study sites in Norfolk County used for relative abundance data collection during May-July 2013. The study sites KB (Boothby), AN (Anderson), and W (Weeden) were categorized as having small forest patch area (<100 ha), DM (DeMaere) was categorized as medium (100-200 ha), and HT (Hepburn Tract), WT (Wilson Tract), and S2 (Soenen2) were large (200-300 ha).

Curriculum Vitae

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Environment and Sustainability Research Forum. University of Western Ontario, ON (poster presentation) – 2014

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*Biology Graduate Research Forum.*_University of Western Ontario, ON (poster presentation) – 2013

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Ontario Ecology, Ethology and Evolution Conference. University of Western Ontario, ON (oral presentation) – 2013

10th Annual Earth Day Colloquium. University of Western Ontario, ON (oral presentation) – 2013