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Butterfly Movement in a Post Agricultural Landscape

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Abstract of the Dissertation

Butterfly Movement in a Post Agricultural Landscape

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A central question in landscape ecology is how organisms move through fragmented landscapes. To explore this I have studied how butterflies behave at habitat borders and how readily they move through matrix (non habitat) vegetation. My work focuses on a guild of fruit feeding nymphalid butterflies and how they react to fragmentation in a post agricultural landscape, with emphasis on the behavior and distribution of the Hackberry Emperor Asterocampa celtis and the Question Mark Polygonia interrogationis. Using a combination of observations at habitat edges and large scale trapping across different vegetation types, I measured nymphalid vegetation preference and how this preference scaled up to landscape level butterfly distribution. I found that butterflies exhibit vegetation bias at a variety of spatial scales and that movements at vegetation borders are indicative of larger scale butterfly distribution. Using mark release recapture studies, I was able to determine that vegetation preference corresponds with the conductance of different matrix vegetation types. I also conducted controlled screen house experiments to isolate the environmental cues that are important for butterfly movement. An analysis of these cues indicated that vegetation structural complexity is likely the most important driver of butterfly vegetation preference. Determining how butterflies identify different vegetation types, how readily they cross habitat edges and how easily they move through non habitat vegetation, has provided valuable insights into how butterflies react to fragmented landscapes.

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CHAPTER 1- INTRODUCTION

Two central goals in landscape ecology are determining the ecological consequences of spatial heterogeneity and how the consequences of spatial heterogeneity vary across different scales (Turner 2005). One important source of spatial heterogeneity is the fragmentation of habitats. Habitats may be fragmented due to natural or anthropogenic causes but in either case, understanding how organisms behave in such landscapes is necessary to evaluate how fragmentation will influence species distribution, abundance and persistence (Hanski et al. 1994; Summerville and Crist 2001; Fahrig 2003; Schtickzelle and Baguette 2003).

An organism's ability to move through a landscape is determined by the conductance of different types of vegetation, defined as the ease by which an organism can move through a given vegetation type, as well as the relative abundance and location of vegetation types within an area (Merriam 1984; Baudry and Merriam 1988; Merriam 1991; Taylor et al. 1993; Fahrig and Merriam 1994; Goodwin and Fahrig 2002). Some types of non-habitat (matrix) vegetation can act as corridors for movement between habitat patches, while others may act as barriers (Ricketts 2001; Bélisle 2005). It has been shown that organisms may choose to avoid particular vegetation types or specific conditions, like low light availability, or structural features of certain vegetation types (Ross et al. 2004). The major behavioral components of matrix conductance are the probability that an organism will cross into non-habitat vegetation (i.e. edge hardness), and how easily they move through matrix vegetation. Edge hardness is likely influenced by the structural contrast between the vegetation types at the edge (Collinge and Palmer 2002). Physical aspects of the matrix, such as foliar height, canopy cover, plant composition and vegetation density, are likely all important in determining species movement probability (Fry and Robson 1994; Desrochers et al. 2003; Keufler and Haddad 2006).

In spite of the clear importance of understanding matrix conductance, we still have little knowledge of the factors that make certain types of matrix vegetation more conducive to movement. Effective measurement of matrix conductance is a critical part of understanding landscape connectivity. Connectivity from a human perspective may not result in connectivity for a species of interest. A promising development is the move towards behavioral-based measures of landscape connectivity (Lima and Zollner 1996; Bélisle 2005). These methods to quantify connectivity can be challenging due to logistical difficulties associated with measuring animal movement. Behavioral based methods also necessitate a consideration of scale; we do not

know whether an organism's preference at small spatial scales corresponds with their distribution in a landscape. We need to ensure that the spatial scales of our studies are dictated by the ecological attributes of the study organism (Addicott et al. 1987; Wiens 1989: Anderson et al. 2010).

Butterflies are well suited to studies of landscape ecology. When one excludes migratory species, butterflies generally move a few hundred meters to a few kilometers in a lifetime, a scale that is tractable and often confined to a single landscape. Further, adult butterflies have short lifespans and are not thought to have a spatial memory; as a result, their movement decisions are generally simpler than those of vertebrates. I studied how a guild of fruit feeding nymphalid butterflies behaved in different vegetation types with emphasis on the behavior of the Hackberry Emperor *Asterocampa celtis* and the Question Mark *Polygonia interrogationis.* Fruit feeding nymphalids are generally associated with late successional structurally complex vegetation. They feed largely on tree sap, rotting fruit, dung and carrion. Their distinctive life history means that they are not likely driven by the floral resources that drive nectar feeding butterfly movement (Brakefield 1982; Murphy et al. 1984; Novotny et al. 1991; Ravenscroft 1994). This research was conducted at the University of Virginia's Blandy Experimental Farm. The combination of lawn, youngfield, shrub and forest vegetation at this 700 acre site provided an ideal setting for measuring butterfly movement.

Several processes are likely affecting the ability of butterflies to navigate a fragmented landscape. To move from one habitat patch to another, butterflies must make the initial decision to leave a habitat patch and cross into matrix vegetation, a decision controlled by the hardness of the edge. Once in the matrix vegetation, butterflies then need to move through this vegetation in order to encounter a new habitat patch. The factors controlling edge hardness and matrix conductance and the degree to which these two phenomena are linked are both poorly understood. To address these gaps in our understanding of butterfly movement decisions, I conducted a series of linked experiments at a variety of spatial scales. My work addressed the following questions.

Chapter 2 - Are the vegetation preferences of fruit feeding nymphalids consistent across multiple spatial scales?

Landscape level trapping of butterflies provided me with basic information about the types of vegetation with which fruit feeding nymphalids were associated. By combining this information with measurements of vegetation structural complexity, I was able to identify whether fruit feeding nymphalids were most commonly associated with structurally complex (shrub, forest) or structurally simple (meadow, lawn) vegetation. I compared these finding with the results of small scale behavioral observations at vegetation borders. These small scale experiments allowed me to assess butterfly movement behavior at the edge between habitat and matrix vegetation. I assessed the importance of structural contrast in determining edge hardness, that is, are edges softer between habitat and structurally similar matrix than between habitat and structurally dissimilar matrix. In comparing the information collected at these two distinct spatial scales, I was able to determine if a butterfly's willingness to cross into a matrix vegetation type corresponded to vegetation preference at a landscape scale.

Chapter 3 - What is the role of structural complexity in determining matrix conductance?

Large scale static trap arrays provided me with information about matrix conductance. By comparing one matrix vegetation type that was structurally similar to habitat vegetation to one that was structurally dissimilar, I was able assess the importance of structural complexity for matrix conductance. In doing this experiment, I explored the use of large static trap arrays as a tool for measuring matrix conductance. This method displayed several promising features. It is suitable for organisms that are not easily to follow on foot either because their movements are difficult to follow or because the landscapes they exist in are difficult to navigate. Further it provided more information about inter-patch movement than traditional mark release recapture methods.

Chapter 4 - What environmental cues do fruit feeding nymphalids use when choosing vegetation types?

The cues driving movement of non-nectar feeding butterflies are poorly understood. I used manipulative experiments in a screenhouse to test the relative importance of host plant availability, vegetation structural complexity and light availability on the behavior of fruit

feeding nymphalids making a movement decision at vegetation borders. By manipulating these cues singly I could begin to evaluate the mechanisms influencing movement observations and distribution patterns observed in Chapter 2 & 3.

Combining information from these manipulative experiments and field observations allowed me to identify whether vegetation preference was consistent across several different spatial scales. Edge crossing behavior and matrix conductance determine the abundance and distribution of butterflies in a landscape, particularly how they are distributed in matrix vegetation. Knowing how butterflies perceive edge hardness and how easily they move once they are in the matrix is critical for understanding how butterflies navigate a fragmented landscape. Measuring vegetation preference at multiple spatial scales and identifying the specific cues that drive these behaviors not only gives us a better understanding of how butterflies use a fragmented landscape, but also informs targeted manipulations of landscapes to increase connectivity.

CHAPTER 2: Butterfly movement and vegetation preference at multiple spatial scales

INTRODUCTION

Habitat fragmentation, which may influence species distribution and abundance (Hanski et al. 1994; Summerville and Crist 2001; Fahrig 2003; Schtickzelle and Baguette 2003; Cane et al. 2006), is increasingly prevalent as humans require more space for agriculture, housing and commerce. When fragmentation occurs, many species are forced from continuous habitat into landscapes where suitable habitat is intermixed with human modified vegetation. Vegetation that lacks the combination of microclimatic conditions and resources to support a given species is referred to as matrix. Matrix conductance is the ability of an organism to move through different types of matrix vegetation, such as open grass or crops. Organisms tend to move through matrix vegetation that is structurally similar to their habitat (Ricketts 2001). The conductance of different types of matrix vegetation, and the relative abundance, location and spatial relationships of matrix types and habitat determine the functional connectivity of a landscape (Merriam 1984; Baudry and Merriam 1988; Merriam 1991; Taylor 1993; Fahrig and Merriam 1994; Goodwin and Fahrig 2002). Increasingly, landscape connectivity is evaluated using behavioral observations and experiments in realistic landscapes (Lima and Zollner 1996; Bélisle 2005). While this organism-centric behavioral approach has provided insights into what causes organisms to make decisions in different landscape contexts, it is not clear if these small scale decisions made by individuals correspond to larger patterns of organism abundance and distribution in a landscape. Scaling up individual behavioral decisions to evaluate the causes of landscape-level patterns of species abundance and distribution remains a challenge in landscape ecology. Here I evaluate if the behavior of several fruit-feeding nymphalid butterflies at borders between habitat and different types of matrix corresponds to landscape-level abundance patterns across a post agricultural landscape.

In behavioral landscape ecology it is useful to consider two types of connectivity: structural connectivity of landscapes, the degree to which features in the landscape are physically linked, and the functional connectivity of a landscape, the ease with which organisms can move between habitat patches (Bélisle 2005). Most approaches to manipulating landscape connectivity have focused on structural connectivity. For example, habitat corridors may be created to link suitable habitats in order to facilitate animal movement (Haddad 1999; Haddad 2000; Tewksbury

et al. 2002). However, changing structural connectivity may be ineffective if the organism does not perceive these changes. Behavioral information on the perception of the landscape from the perspective of the organisms making movement decisions is required to ensure such structural changes result in functional connectivity.

Butterflies are an excellent target group for studying functional connectivity of landscapes because most species move within a limited geographic area and make relatively simple and consistent decisions (Hanski et al. 1996; Haddad 1999; Ricketts 2001). Butterflies tend to move between a few hundred meters to a few kilometers a day and their estimated perceptual range is between thirty and a few hundred meters (Cant et al. 2005; Schtickzelle 2007). These distances make studying butterfly movement tractable because movements occur within a single landscape. At this scale, a researcher can reasonably evaluate how a mosaic of habitat patches and matrix types influences butterfly behavior. Butterflies are also useful study organisms because their decision making appears to be simpler than that of many other organisms, such as birds and mammals, which are often used in landscape behavioral ecology. While butterfly behaviors are relatively more consistent and less complicated than other organisms, experimental work shows that butterflies can distinguish between different types of matrix vegetation (Roland et al. 2000; Ricketts 2001; Leimar et al. 2003; Ross et al. 2005). How the organism perceives the border between habitat and matrix is a critical, but poorly understood factor that influences whether an organism moves into the matrix.

I conducted a variety of experiments to determine vegetation preference at a series of different vegetation borders. If the borders between habitat and matrix vegetation are soft, that is they are readily crossed, then more butterflies will enter the matrix vegetation. Borders between habitat and matrix vegetation that is structurally similar will likely be softer and pose less of a barrier to movement. Therefore, I expected that butterflies would be more likely to move into vegetation types that are structurally similar to their natural habitat. The butterfly species evaluated in this paper are generally associated with wooded or shrubby structurally complex vegetation (Glassberg 1993); therefore I expected that they would prefer late successional matrix vegetation to open vegetation like lawns and youngfields. Emigration rates out of habitat patches and into the matrix are at least partially determined by encounter rates with habitat edges (Conradt and Roper 2006). They are also largely driven by an individual's willingness to cross that edge once it is encountered. To quantify the large scale consequences of the decisions being

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made at edges, I evaluated how vegetation preference at specific types of borders corresponded to landscape level butterfly distribution. I expected that preference at vegetation borders would correspond to nymphalid abundance across different vegetation types.

METHODS

STUDY SITE AND SPECIES

I conducted this research at Blandy Experimental Farm and E. Orland White Arboretum, a 280-hectare site, located in Clarke County, Virginia. The field site has a variety of vegetation types including lawn, pasture, hay and alfalfa fields, youngfields (meadows), shrubs and a variety of forested areas. The arboretum also has diverse vegetation including monotypic groves of *Ginkgo biloba*, and Lebanon cedar *Cedrus libani,* as well as flower gardens. The combination of these vegetation types in a relatively small area means that variation occurs on the order of a few hundred meters to a few kilometers, a scale that is meaningful to butterfly movement (Haddad 2000, Fahrig and Paloheimo 1988, Schultz 1998).

There are eleven species of fruit feeding nymphalid butterflies at Blandy Experimental Farm. The most common species are the Hackberry Emperor (*Asterocampa celtis*) and the Question Mark (*Polygonia interrogationis*). The adult wingspan of Hackberry Emperors is between 3.5 and 6.3 cm with females larger than the males (Clark and Clark 1951). Hackberry Emperors feed on fruit, dung, carrion and tree sap. Their range encompasses much of the central and eastern United States and parts of Mexico (Clark and Clark 1951; Langlois and Langolis 1964). Hackberry Emperors are most often found in close proximity to the hackberry or sugarberry *Celtis spp.,* which serves as its larval host plant. The Question Mark has a wingspan between 5.75 and 7.6 cm with females larger than males. Like the Hackberry Emperor, Question Mark adults feed on carrion, dung, rotting fruit and tree sap though they may occasionally visit flowers. The larval host plants include members of the Ulmaceae including American elm and red elm; a variety of hackberry *Celtis* species; and members of the nettle family Urticaceae including false nettle, *Boehmeria*; hop, *Humulus* and nettle, *Urticau* (Glassberg 1993).

I designated shrub vegetation as the primary habitat for both species based on maximum abundances found in this vegetation during the butterfly inventory (see below). Further, both species use the Hackberry *C. occidentalis* as larval host plants and these trees are most abundant in this vegetation type.

VEGETATION CLASSIFICATION

I delineated four different vegetation types at Blandy. These vegetation types are structurally distinct and thus easily identified in the field. They were characterized based on canopy height, understory density and successional age into lawn, youngfield, shrub and forest. My classifications were in agreement with previous Geographic Information System maps created for the site. Lawn was defined as frequently mowed vegetation with minimal vertical structure; it may include a few widely spaced trees. Youngfield vegetation was approximately 0.5 to 1.5 meter tall, with occasional widely spaced shrubs. The successional age of youngfield varied somewhat but was not more than 15 years old. In some cases succession in this vegetation type was prevented via periodic burning or mowing. Shrub vegetation was 15-20 year old abandoned fields dominated by shrubs. The dominant vegetation is between one and three meters tall, it may include small patches of grass and trees. Late successional vegetation more than 90 years old with a canopy generally greater than 20 meters high was designated forest. The understory in forest is more open than in shrub vegetation.

To quantify the structural complexity of the vegetation types, I used a Trimble hand held Geographic Positioning System to determine the bounds of each vegetation type. I selected ten random points within each of three replicate patches of four vegetation types for a total of 120 points. A 5m pole marked every quarter meter was placed vertically at that random point. I then recorded the number of times a stem or leaf came in contact with the pole within each one-quarter meter section.

BUTTERFLY INVENTORY

To determine the distribution of fruit feeding nymphalids across vegetation types, butterflies were trapped for a total of eleven days during the months of July and August 2006. Trapping was conducted on days with temperatures greater than 24 degrees Celsius without rain or heavy cloud cover. Van-Someren Rydon traps (cylindrical mesh traps with a wooden platform for bait suspended below) were placed throughout the landscape (DeVries 1987). Two traps were placed in three replicate patches of five vegetation types: lawn, youngfield, shrub, forest and horticultural plantings. A total of 30 traps were used. Sites for traps were selected in two ways. In dense vegetation, which included forest and shrub, a random number generator was used to designate distances along existing pedestrian and horse trails, a second random number was used

to designate left or right of the trail and a third number was then used to measure a distance off the trail. In vegetation with a sparse understory, polygons of the vegetation patch were generated in a GIS and random points were then generated within these polygons. These points were located using a Trimble handheld GPS. Traps were baited with a mix of ripe bananas and rum. The traps were checked every twenty-four hours. Trapped butterflies were removed and their species and sex recorded. To ensure that individuals were not counted multiple times, butterflies were marked on the outer part of their right hind wing with indelible marker.

EDGE CIRCLES

To determine how readily fruit feeding nymphalids crossed into various types of matrix vegetation I employed edge circle experiments following Schultz (1998).Vegetation edges were located via examination of aerial photographs and extensive ground searches. Edges were chosen that had a clear border that was fairly straight for at least 20 meters. At each edge, I erected 5 meter radius edge circles and marked them using flags in low vegetation and a combination of driveway markers and flagging in tall vegetation. During 2006, four different vegetation borders were chosen: youngfield to lawn, youngfield to forest, forest to shrub, and shrub to youngfield. I set up three replicate circles at each vegetation border for a total of 12 circles. I varied the proportion of the two types of vegetation in a given edge circle such that a circle contained either equal proportions of each vegetation type, 75% of one type and 25% of the second or 25% of the first type and 75% of the second (Figure 1). This was done to assess whether the vegetation in which the trial originated affected butterfly vegetation choice. After completing one choice trial at the 12 different sites, the circles were shifted to the next configuration of vegetation types; the positions that formerly had a circle like that in figure 1A were changed so that they had a circle like that in figure 1B. Circles like those in figure 1B were changed to figure 1C and so on. In total I conducted 36 trials.

Trials were conducted on sunny days with temperatures between 28 and 36 Celsius and were suspended when wind speed exceeded 2 meters/second. For each trial, butterflies were captured in Van-Someran Rydon traps. They were placed in small Dixie cups and chilled in a cooler with ice packs for ten minutes to minimize agitated dispersal (Southwood 1966). I released butterflies at the center of the edge circles (see Figure 1) and noted the vegetation composition of the release point to determine whether the initial vegetation encountered had an

influence on the initial route taken by the butterfly. I also noted the vegetation type that each butterfly was flying through at the time it left the circle. I expected that butterflies with no vegetation bias would leave the circle with an incidence proportional to the amount of the perimeter of the circle contained within that habitat. For example, if fifty percent of the perimeter is in vegetation type 1 and fifty percent of the perimeter is in vegetation type 2, approximately fifty percent of butterflies departing the circle would leave via vegetation 1, assuming that there is no biased movement. If individuals prefer vegetation type 1 one might expect a significantly higher proportion of individuals to depart in the direction of vegetation type 1.

In 2006 I determined that the origin of trials did not influence vegetation choice; therefore all experiments done after 2006 had edge circles with centers at vegetation borders as shown in Figure 1A. During the summer of 2007 and 2008, I focused on three replicates of the shrub-youngfield vegetation border, as the largest difference in vegetation preference was recorded there in 2006. All butterfly capture, handling and data collection was unchanged from that of 2006.

STATISTICAL ANALYSIS

To evaluate the structural characteristics of the different vegetation types I used non-metric multi-dimensional scaling (NMS) and a Shannon index. The NMS allowed me to explore how vegetation structure varied across vegetation types. I used the autopilot "slow and thorough" mode with random starting configurations, 500 runs, and Sorensen (Bray-Curtis) distance as the dissimilarity measure (McCune and Grace 2002). NMS is an iterative ordination method that attempts to place n samples on k axes so that the rank order of the distances between samples agrees with the rank order of the original distances in the data matrix. Stress is the departure from monotonicity in the relationship between the dissimilarity (distance) in the original n-dimensional space versus the distance in the reduced dimensional ordination space (McCune and Grace 2002). I used NMS because it avoids the assumption of linear relationships among the variables and is well suited for data with many zeros. This is a common problem in ordinations of heterogeneous communities which I also experiences since vegetation structure differed greatly from one vegetation class to another. To test for differences among the vegetation types in terms of vegetation structure, I used a non-parametric multi-response permutation procedure (MRPP; Mielke and Berry 2001), which is a non-parametric method for testing for differences

among groups (McCune and Grace 2002). I used PC-ORD software to run both the MRPP and NMS (McCune and Mefford 1999)

By treating the presence or absence of vegetation at different heights like the presence or absence of species in a given area, I was able to use a Shannon diversity index to provide an estimate of the structural complexity of a given vegetation type. I then compared sites located across the different vegetation classes (lawn, youngfield, shrub, forest). To determine if the diversity of vegetation structure differed between vegetation classes, I compared the Shannon diversity values using paired t-tests.

To determine if butterflies were distributed randomly across different vegetation types, I completed a chi-square test following the methods of Sokal and Rohlf (2000). Expected values were generated by totaling the number of individuals captured and dividing them equally across all vegetation types. I also used chi-square tests to determine if individuals of a given species chose randomly in edge circle trials and if the results of the edge circle tests corresponded to abundance patterns in the different vegetation types. Expected values for the latter were generated using the relative abundances of individuals in different vegetation types from the butterfly inventory. Edge circle data were then tested against these predictions. The large sample size and independence of these two data sets allowed me to treat the inventory data as independent, creating a hypothesis extrinsic to the edge circle data. In the test designed to determine if there was a correspondence between the edge circle preference and vegetation occupancy, I did not include data from the youngfield-lawn edge circles. I chose to exclude these data because butterflies in the youngfield and lawn vegetation trial that chose lawn almost universally landed in mature trees scattered within this vegetation type. Since butterflies almost never landed on the actual grass and routinely flew into trees, I felt that the initial vegetation classification didn't fully capture the complexity of lawn vegetation.

RESULTS

VEGETATION STRUCTURE

Analysis of vegetation structure identified three distinct vegetation types (Figure 2). They revealed that lawn and youngfield vegetation were distinct from each other and each was also distinct from shrub and forest vegetation which were grouped into a single structurally complex class by this analysis. The NMS, used to compare the structural diversity of different vegetation

types, corroborated these results. The three dimensional ordination had a final stress of 17.2 (Figure 3); a stress level below 20 is considered to give appropriate confidence to the results of this analysis (McCune and Grace 2002). The NMS axes one through three explained 21%, 25% and 33% of the variation, respectively. As NMS is traditionally used to compare community composition, to use this method to compare vegetation structural complexity, the presence or absence of vegetation at different vegetation sampling heights were treated like the presence or absence of species. In the resulting NMS plot, the distance between two points in the ordination represents the relative dissimilarity in their structure compositions (Lee et al. 2005). The ordination showed that lawn vegetation was most associated with structure between 0-0.25 meters, youngfield vegetation had the majority of its complexity between 0.5 and 2.25 meters and forest vegetation had the peak of complexity between 3 and 5 meters. Shrub vegetation showed overlap with both youngfield and forest vegetation, it was most associated with structural complexity between 1.5 and 4.5 meters. The MRPP showed that all vegetation types differed significantly in terms of structure (Table 1).

BUTTERFLY INVENTORY

I completed a total of 11 trapping days during which time I captured 281 butterflies representing 11 species (Table 2). The distribution of fruit feeding nymphalids was not random across the different vegetation types; they were more common in the shrub than any other vegetation type, somewhat less abundant in the forest vegetation and least abundant in the youngfield and lawn vegetation types (Figure 4).

EDGE CIRCLES

Data from 2006 showed that fruit feeding nymphalids did not choose to move towards one vegetation type over the other at the shrub-forest, youngfield-lawn or youngfield-forest vegetation borders (Table 3). Fruit feeding nymphalids did not behave randomly at the shrub youngfield vegetation border, biasing their movement in the direction of the shrub ($X^2=36.14>\chi^2_{0.00025[11]}= 34.98$; Table 3). This relationship was consistent for the two most common species of fruit feeding nymphalids in 2007; Hackberry Emperors and Question Marks both showed a preference for shrub over youngfield vegetation ($X^2=20.65> \chi^2_{0.001[5]} =20.51$ and $X^2=27.80> \chi^2_{0.0001[5]} =25.74$, respectively). When data from the summers of 2006-2008 were combined, it

showed that nearly twice as many nymphalids chose shrub vegetation over youngfield vegetation ($\chi^2_{[25]}$= 77.28, p<<0.001; Table 4). Similar relationships are seen when the two species were examined separately indicating that neither species is driving the pattern alone (Table 4)

Butterfly preference in edge circle experiments did not deviate significantly from the distribution of butterflies in the inventory across different vegetation types ($\chi^2_{[5]}$= 10.63, p=0.06). Butterflies preferentially chose vegetation that was more structurally complex.

DISCUSSION

It is likely that no one factor controls butterfly vegetation preference. Boundary shape and contrast likely play an important role in determining edge hardness (Collinge and Palmer 2002). Physical aspects of the boundary that contribute to that contrast such as foliar height, canopy cover, plant composition and vegetation density are also important to consider, as are factors that may cause edge avoiding behaviors such as food availability, conspecific attraction and predator avoidance (Fry and Robson 1994; Desrochers et al 2003; Keufler and Haddad 2006). Processes that may explain animal responses to habitat edges are not only varied, but they usually occur at distinct spatial scales (Desrochers et al. 2003). By examining butterfly behavior and distribution at multiple scales I can better evaluate vegetation preference. Further, using a combination of invasive and passive methodologies decreases the likelihood that my results are artifacts of the butterfly handling process. By integrating trapping data with experimental measurements of butterfly preference at edges we can move towards a mechanistic understanding of how butterfly movement scales up to butterfly distribution across landscapes.

Both the Hackberry Emperor and the Question Mark flew more often toward shrub vegetation than youngfield vegetation in edge circle experiments indicating that butterflies are able to assess vegetation and make movement decisions accordingly. This result adds to a growing literature showing that butterflies can perceive habitat edges and alter their movements in response to them. For instance, previous work has shown that butterflies altered turn angles and step length based on proximity to habitat edges (Schultz and Crone 2001), made U-turns near edges to avoid unsuitable vegetation (Schtickzelle and Baguette 2003) and chose habitat vegetation over matrix vegetation at edges (Schultz 1998).

Vegetation structure likely plays an important role in determining butterfly choices (Stamps et al. 1987; Fry and Robson 1994; Haynes and Cronin 2003). To understand vegetation

preference and how butterflies make movement decisions at habitat matrix edges, I examined the structural complexity of a variety of vegetation types available to my study species. Based on the structural similarity between youngfield and lawn and their dissimilarity from shrub and forest vegetation, we would expect a hard edge between shrub and youngfield and youngfield and forest vegetation and a soft edge between youngfield and lawn and shrub and forest vegetation. Butterflies showed non-random movement patterns at the edge between shrub and youngfield vegetation indicating that they perceived it as a somewhat hard edge. While they chose the forest vegetation more frequently than the lawn vegetation at the other predicted hard edge, this relationship was not significant. This may be driven by the presence of isolated trees in the lawn, as butterflies were often observed landing in these trees soon after choosing lawn vegetation. As expected, butterflies did not distinguish between either of the soft edges between youngfield and lawn or shrub and forest. It is possible that there are other factors in addition to structure driving butterfly vegetation preference.

The patterns from this study are consistent with the findings of previous studies. Edge hardness has been found to increase with vegetation contrast for a variety of butterflies. Landscape context was important in determining the rate of patch emigration in the butterfly *Melitaea cinxa*. This open habitat species crossed more readily into non-habitat vegetation that was similar to its youngfield habitat and rarely crossed into forest vegetation (Kuussaari et al. 1996). In another study, several species of satyrine butterflies were shown to spend more time in non-habitat vegetation that was structurally similar to habitat vegetation. All of the butterflies studied exited release plots less quickly if they were located in unburned bottomland forests. This non-habitat vegetation type is structurally similar to the butterflies' ecotone habitat. (Keufler and Haddad 2006). It is possible that there are other factors in addition to structure driving butterfly vegetation preference. While habitat specialists respond to a variety of boundaries, generalists may only respond to high contrast boundaries (Duelli et al. 1990; Ries and Debinski 2001) Likewise, butterfly vagility may affect edge perception with larger, more vagile species perceiving edges as softer than smaller species (Lidicker 1998).

A variety of studies have also shown increased edge responses related to increases in matrix contrast in other taxa. This behavior has been demonstrated in ground dwelling beetles (Collinge and Palmer 2002), plant hoppers (Haynes and Cronin 2003), and bush crickets (Diekötter et al. 2007). The pattern is not limited to insects. Shrubland birds were shown to have

stronger responses to edges of mature eucalyptus plantations than to lower contrast young oak plantations (Reino et al. 2009). Stevens et al. (2006) demonstrated that natterjack toads used a combination of edge contrast and ease of movement in matrix substrate to determine edge crossing probability and Desrochers et al. (2003) demonstrated that flying squirrels responded differently to edges depending on the structure of nearby matrix habitat.

While it is likely that large scale patterns of animal distribution are determined by mechanisms acting at local scales, the degree to which butterfly behavior at vegetation borders scales up to overall vegetation preference is unknown (Kuefler and Haddad 2006). There is some evidence that butterflies engage in foray loops, leaving habitat vegetation and traveling into the matrix only to return soon after (Conradt and Roper 2006). If this is the case then measures of vegetation preference examined at vegetation borders might not be indicative of vegetation preference (Schultz 1998). Several studies have found relationships between local movement patterns and larger scale dispersal behaviors (Dennis 2004; Levey et al. 2005; Conradt and Roper 2006; Kuefler and Haddad 2006). What had not yet been determined is the relationship between these local movements and large scale vegetation preference. A formal inventory of fruit feeding nymphalid butterflies allowed me to confirm a pattern that had not been previously quantified; that these butterflies are closely tied to later successional, structurally complex vegetation. By comparing these inventory data to the edge circle data designed to measure vegetation preference, I determined that vegetation preference at the 5-10 meter scale was representative of vegetation preference at the landscape level. These small scale decisions being made at vegetation borders likely play a key role in determining the distribution of these species in a landscape.

Understanding the movement of organisms in non-habitat vegetation has important conservation implications. An ever increasing amount of habitat fragmentation means that species that inhabited previously contiguous habitat are now forced to exist as metapopulations. Metapopulation persistence is dependent on recurrent colonization, a certain rate of movement between patches is necessary for population persistence (Hanski and Zhang 1993). Even in spatially segregated populations where traditional metapopulations dynamics do not apply, where populations are able to persist rather than blinking on and off, inter-population movement is still important for gene flow. One important part of understanding movement is determining the ease with which species move into non-habitat vegetation. This study allowed me to quantify

the hardness of various vegetation borders; this information combined with relative rates of movement in different vegetation types will allow a better measure of the connectivity of a landscape. I was also able to demonstrate that butterfly vegetation preference is consistent across scales. While edge circles can not replace inventory trapping when making conservation decisions they may be a good method for approximating the relative abundance of butterflies in different vegetation types. Our study suggests that edge circles and inventory trapping illustrate similar patterns of vegetation preference. Given that edge circles are less labor intensive and require a smaller study area than traditional large scale inventory trapping, edge-circles have great potential to be used as a rapid assessment method for determining butterfly vegetation preference.

Table 1: Multi-response permutation procedure results for vegetation type (Lawn, Youngfield, Shrub, Forest) based on differences in structural complexity.

Vegetation types	*T*	*A*	*P*
Lawn vs. Youngfield	-32.479	0.368	<0.001
Lawn vs. Shrub	-26.905	0.258	<0.001
Lawn vs. Forest	-29.303	0.298	<0.001
Youngfield vs. Shrub	-10.610	0.084	<0.001
Youngfield vs. Forest	-21.297	0.165	<0.001
Shrub vs. Forest	-20.826	0.166	<0.001

T is the test statistic representing the separation between the groups (vegetation types). More negative values of *T* signify stronger separation; McCune and Grace 2002). *A* describes within-group homogeneity as compared to random expectation, independent of sample size (McCune and Grace 2002).

Table 2: Butterflies of the family Nymphalidae caught in baited traps during the summer of 2006

Species	Common Name	Subfamily	Number captured
Asterocampa celtis	Hackberry Emperor	Apaturinae	128
Asterocampa clyton	Tawny Emperor	Apaturinae	16
Polygonia interrogationis	Question Mark	Nymphalinae	86
Polygonia comma	Eastern Comma	Nymphalinae	25
Vanessa atalanta	Red Admiral	Nymphalinae	5
Nymphalis antiopia	Mourning Cloak	Nymphalinae	1
Limenitis arthemis	Red Spotted Purple	Limenitidinae	9
Limenitis archippus	Viceroy	Limenitidinae	1
Cercyonis pegala	Common Wood Nymph	Satyrinae	1
Enodia anthedon	Northern Pearly Eye	Satyrinae	7
Libytheana carinenta	American Snout	Libytheunae	2

Table 3: Vegetation choice of fruit feeding nymphalid butterflies as measured by edge circles during summer 2007

EDGE (A-B)	Chose A	Chose B	X^2	df	p
Shrub-Youngfield	29	9	13.46	5	**p=0.02**
Shrub-Forest	9	11	4.10	5	p=0.54
Youngfield-Lawn	14	20	1.07	5	p=0.96
Youngfield-Forest	10	22	5.57	5	P=0.35

Table 4: Nymphalid vegetation preference as measured by edge circles for the summers of 2006-2008

	Shrub	Youngfield	X^2	df	p
Nymphalids	218	120	77.28	25	p<<0.001
Asterocampa celtis	165	83	62.21	13	p<<0.001
Polygonia interrogationis	30	8	34.87	13	p<<0.001
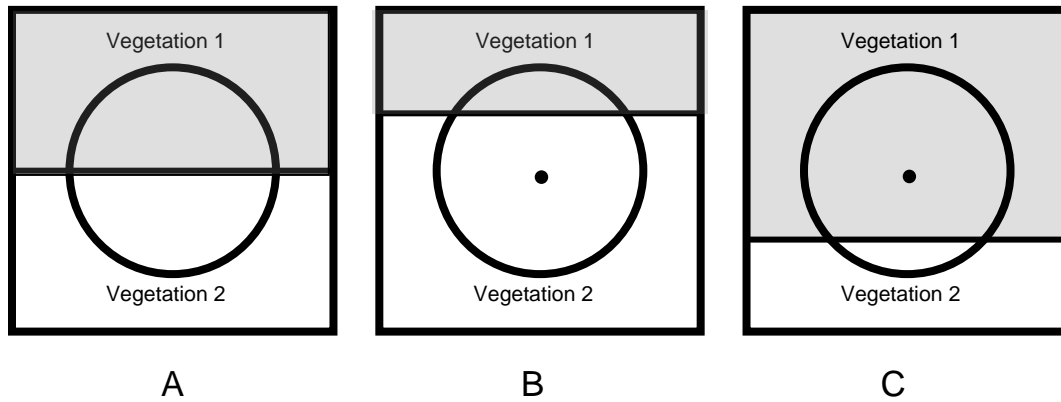
Figure 1: Three different possible starting states for replicate edge circles. **A**. 50% of the perimeter of the circle is located within Vegetation 1 and 50% of the circle is located within Vegetation 2. **B**. 25% of the circle's perimeter is located within Vegetation 1 and 75% of the perimeter is located within Vegetation 2. **C**. 75% of the circle's perimeter is located within Vegetation 1 and 25% of the circle is located within Vegetation 2. Adapted from Schultz 1998.

Shannon diversity of structure

H'

3
2.5
2
1.5
1
0.5
0

A   B   C   C

Lawn   Youngfield   Shrub   Forest
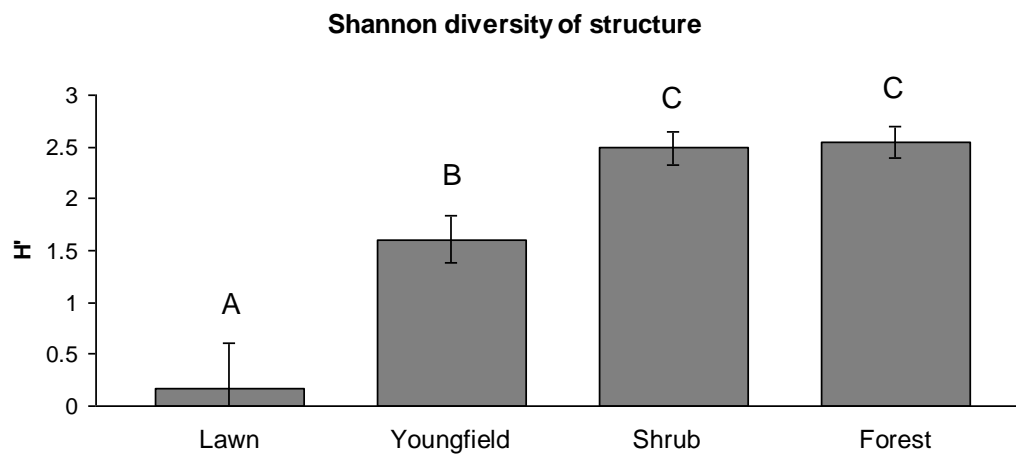
Figure 2: Graph showing the difference in structural complexity of vegetation types. Lawn is different from youngfield ($t_{[112]} = 2.98$, $0.02 < p < 0.05$), shrub ($t_{[91]} = 5.12$, $p < 0.001$) and forest ($t_{[89]} = 5.26$, $p < 0.001$). Youngfield is also different from shrub ($t_{[319]} = 3.17$, $p < 0.01$) and forest ($t_{[297]} = 9.26$, $p << 0.001$). Shrub and forest have equal structural complexity.
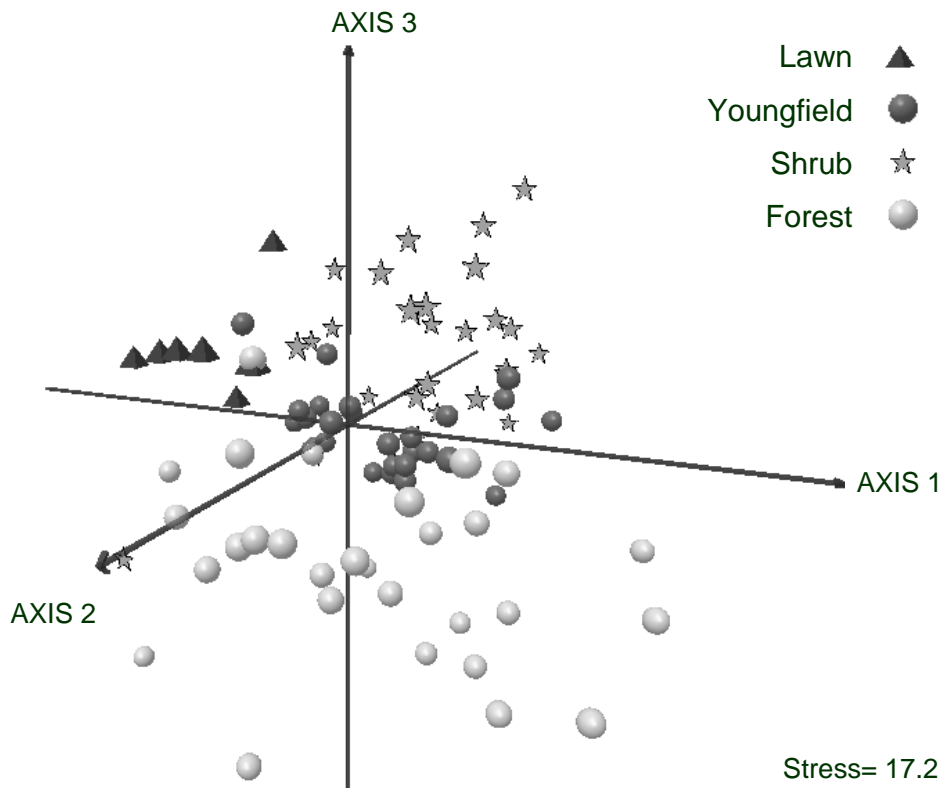
Figure 3: Non-metric multi-dimensional scaling ordination of points within vegetation types. Each vegetation type is represented by a unique shape as shown in the legend. MRPP confirms that these four vegetation types are structurally distinct ($p \ll 0.001$).

Nymphalid Distribution
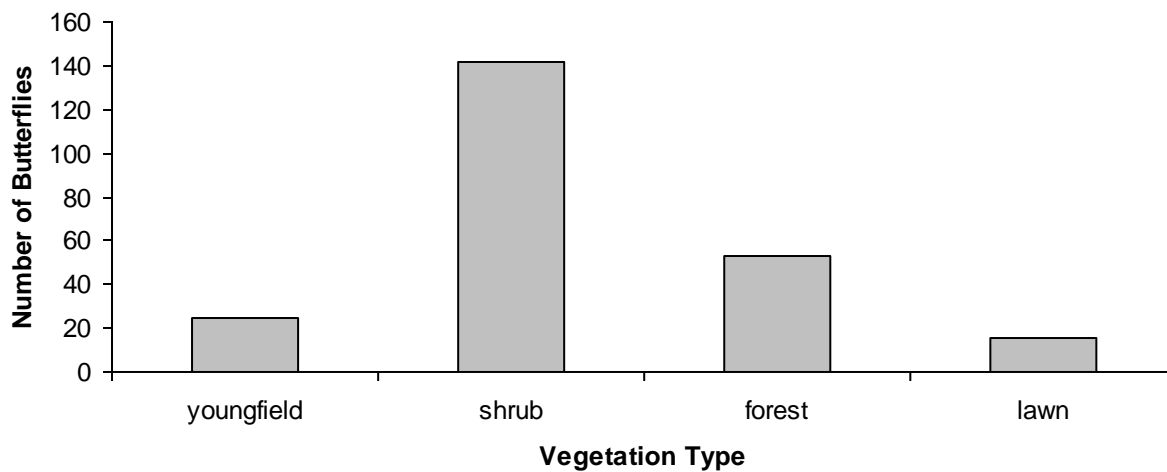
Figure 4: Nymphalid butterflies captured between 15th of July and 15th of August 2006 and their distribution across four vegetation types. Butterflies were not distributed randomly across all vegetation types $\chi^2_{[3]}= 168.31$, p<<0.001

CHAPTER 3: Measuring matrix conductance for fruit feeding nymphalids

INTRODUCTION

Human-induced habitat alteration has forced many organisms into fragmented landscapes. Determining how organisms behave in such landscapes is necessary to evaluate how fragmentation will influence species distribution, abundance and persistence (Hanski et al. 1994; Summerville and Crist 2001; Fahrig 2003; Schtickzelle and Baguette 2003; Cane et al. 2006). Functional connectivity, that is, the ease with which organisms move through a landscape, is determined by the conductance of different types of vegetation and the relative abundance and location of vegetation types within a landscape (Merriam 1984; Baudry and Merriam 1988; Merriam 1991; Taylor 1993; Fahrig and Merriam 1994; Goodwin and Fahrig 2002). Some types of matrix vegetation can act as corridors for movement between habitat patches, while others may act as barriers (Ricketts 2001; Bélisle 2005). We know that organisms tend to prefer matrix types that are structurally similar to their natural habitat (Kuussaari et al. 1996; Collinge and Palmer 2002; Desrochers et al. 2003; Haynes and Cronin 2003; Keufler and Haddad 2006; Stevens et al. 2006; Diekötter et al. 2007; Reino et al. 2009). However, we do not know what level of structural similarity is biologically meaningful for a particular organism.

The major behavioral components of matrix conductance are the probability that an organism will cross into non-habitat vegetation (i.e., edge hardness), and how easily they will subsequently move through this vegetation. Edge hardness is likely influenced by the structural contrast between the vegetation types at the edge (Collinge and Palmer 2002, Chapter 2). Physical aspects of the matrix such as foliar height, canopy cover, plant composition and vegetation density are likely all important in determining species movement probability (Fry and Robson 1994; Desrochers et al 2003; Keufler and Haddad 2006). However, despite understanding what features make certain matrix vegetation types attractive for movement, conductance has proven difficult to measure for many organisms. Further, while behavioral-based measures of landscape connectivity are increasingly used (Lima and Zollner 1996; Bélisle 2005), there are challenges to measuring connectivity due to logistical difficulties associated with measuring animal movement.

Two general categories of methods are used to quantify matrix conductance. Individual based methods, where single organisms are followed by an observer, and mark release recapture (MRR) methods, in which individuals or groups of individuals are marked in one habitat patch

and recaptured in another location within that patch, another habitat patch, or in the matrix. Both of these methods have benefits and challenges. Individual based methods require that the landscapes are open enough to facilitate visual tracking of an organism and that organisms move in such a way that they can be easily followed. As a result, these studies are often conducted in small to moderately sized landscapes on a restricted number of individuals (Leimar et al. 2003; Schooley and Wiens 2004). Mark release recapture (MRR) methods overcome several of the challenges of the individual based methods in that they can be used for animals and landscapes of all sizes, and often afford a larger sample size of individual movements. Despite these benefits, MRR studies are often plagued by low recapture rates. Further, it is generally not possible to record the path between the release point and the capture point. This may not influence conductance measurements when target habitat patches are embedded in a homogenous matrix vegetation (Joly et al. 2001; Haynes and Cronin 2003; Schooley and Wiens 2004) or when an individual's movements are restricted to a certain path, such as following riparian corridors or mountain ridges (Roland et al. 2000). However, in heterogeneous landscapes comprised of multiple types of matrix, MRR studies may miss important details of animal movement because animals may move preferentially through one matrix type. One possible method that overcomes many of the shortcomings of both of these methods is harmonic radar, allowing researchers to record detailed movement paths (Riley et al. 1996; Riley & Smith 2002). It has been used to successfully track a variety of insects including bees (Osborne et al. 1999; Capaldi et al. 2000; Riley et al. 2003), beetles (Wallin & Ekbom 1988), moths (Riley et al. 1998) and butterflies (Roland et al. 1996; Cant et al. 2005). However, these methods are costly, have somewhat limited perceptual range and are not suitable for species moving through dense vegetation. Here, I evaluate the potential of static trap arrays to measure matrix conductance for a guild of fruit feeding nymphalid butterflies living in a post agricultural landscape.

Butterflies are an excellent target group for studying matrix conductance and functional connectivity of landscapes because most species move within a limited geographic area and make relatively simple and consistent decisions (Hanski et al. 1996; Haddad 1999; Ricketts 2001). They tend to move between a few hundred meters to a few kilometers a day and their estimated perceptual range is between thirty and a few hundred meters (Cant et al. 2005; Schtickzelle 2007). These distances make studying butterfly movement tractable because movements occur within a single landscape. At this scale, a researcher can reasonably evaluate

how a mosaic of habitat patches and matrix types influences butterfly behavior. Butterflies are also useful study organisms because decision making in butterflies is perceived to be simpler than that of many other organisms, such as birds and mammals, which are often used in landscape behavioral ecology. While butterfly behaviors are relatively more consistent and less complicated than other organisms, experimental work shows that butterflies can distinguish between different types of matrix vegetation (Roland et al. 2000; Ricketts 2001; Leimar et al. 2003; Ross et al. 2005).

Given the limitations of individual based methods and mark release recapture (MRR) studies, and the fact that the butterflies of interest in this study were associated with dense vegetation making harmonic radar impractical, I explored the use of trapping arrays as a method to quantify matrix conductance (Fig 1). I modified the methods of Turchin and Thoeny (1993) by centering trap arrays at the borders between matrix and habitat vegetation. This method has several key benefits. It allows for the larger sample size associated with MRR studies, but the design of the arrays also means that we have increased resolution when monitoring movement. Further, both initial captures and recaptures provide valuable information on matrix conductance. The butterfly species evaluated in this paper are generally associated with wooded or shrubby structurally complex vegetation (Glassberg 1993). I expected that butterflies would be more likely to move into vegetation types that are structurally similar to their natural habitat. I therefore predicted that they would be found more often and be recaptured further from the release point in late successional matrix vegetation.

METHODS

STUDY SITE AND SPECIES

This research was conducted at Blandy Experimental Farm and E. Orland White Arboretum, a 280-hectare site, located in Clarke County Virginia. The variety of vegetation types, including, lawn, youngfields, shrub and forest, occurring in a relatively small area means that habitat variation occurs on the order of a few hundred meters to a few kilometers, a scale that is meaningful to butterfly movement (Haddad 2000; Fahrig and Paloheimo 1988; Schultz 1998).

There are eleven species of fruit feeding nymphalid butterflies at Blandy Experimental Farm, the two most common species, the Hackberry Emperor (*Asterocampa celtis*) and the

Question Mark (*Polygonia interrogationis*), make up about 75 percent of the individuals commonly captured. For a description of their natural history please see Chapter 2. Other butterflies include the Eastern Comma (*Polygonia comma*), Tawny Emperor (*Asterocampa clyton*), Red Spotted Purple (*Limenitis arthemis*), Red Admiral (*Vanessa atalanta*), Mourning Cloak (*Nymphalis antiopia*), Viceroy (*Limenitis archippus*), American Snout (*Libytheana carinenta*), Northern Pearly Eye (*Enodia anthedon*) and Common Wood Nymph (*Cercyonis pegala*).

      I designated shrub vegetation as the primary habitat for fruit feeding nymphalids based on the fact that they were found more than twice as often in this vegetation type as in forest vegetation and four to five times as often than in youngfield or lawn vegetation (Chapter 2). Further, the two most common species, the Hackberry Emperor and The Question Mark both use the common hackberry, *Celtis occidentalis,* as larval host plants and these trees are most abundant in shrub vegetation.

VEGETATION CLASSIFICATION

      I delineated four different vegetation types at Blandy. They were characterized as forest, shrub, youngfield and lawn based on understory density, canopy height and successional age. I quantified and compared the structural complexity of these vegetation types in two ways, I used a Shannon diversity index to compare the amount of structural diversity among vegetation types and non metric multi-dimensional scaling (NMS) to determine how that structural complexity was distributed within a vegetation type. I also used a Multi Response Permutation Procedure (MRPP) to determine if the distribution of structural complexity differed among the vegetation types. A Shannon diversity index revealed that the structural complexity of lawn and youngfield vegetation differed and that both had different levels of structural complexity from shrub and forest vegetation, which formed a single structurally complex group (Chapter 2). Non metric multi-dimensional scaling showed that the structural complexity was distributed differently within each of these vegetation types. This pattern was confirmed statistically using a multi response permutation procedure (MRPP) (McCune and Grace 2002; Lee et al 2005; Chapter 2). My classifications were in agreement with previous Geographic Information System maps created for the site. Late successional vegetation more than 90 years old, with a canopy generally greater than 20 meters high was designated forest. Shrub vegetation was composed of 15-20 year

old abandoned fields dominated by shrubs. The dominant vegetation was generally between one and three meters tall. Shrub vegetation also often has small patches of grass and occasional trees. The successional age of youngfield varied somewhat but was not more than 15 years old, it was primarily composed of grasses and forbs. In some cases succession in youngfield was prevented via periodic burning or mowing. Lawn was defined as frequently mowed vegetation with minimal vertical structure with occasional widely spaced trees.

TRAP ARRAYS

Matrix conductance was determined using experimental trap arrays centered on vegetation borders following the design of Turchin and Thoeny (1993) (Figure 1). A central focal point was located at a vegetation border and concentric rings of traps radiated into the two vegetation types being considered in a given trial. Concentric rings were located at 25, 50, 100, 150, 200 and 250 meters from the focal point. The rings at 25 meters and 50 meters had two and four traps, respectively, while the remaining four rings had eight traps each for a total of 38 traps. By decreasing the trapping effort close to the release point, this design minimizes the chance that butterflies that would have traveled to the edges of the array will be captured close to the release point. Butterflies were captured in Van Someren-Rydon traps, cylindrical nylon mesh traps baited with rotting bananas and rum.

Sites for trap arrays were selected that had relatively straight borders between vegetation types for 500m, the diameter of a single trap array. The diameter represented the largest circle that could be contained within the chosen areas without encompassing a third vegetation type (Figure 1). Two vegetation comparisons were chosen, one that maximized structural complexity contrast, shrub-youngfield and one with minimal structural complexity contrast, shrub-forest. In both cases, shrub vegetation was included in the comparison as it was the habitat vegetation of the Hackberry Emperor and Question Mark, the two most common fruit feeding nymphalids at the site. Traps were checked every 24 hours, between the hours of 07:00 and 13:00. At this time, all insects were removed from the traps and the bait was replaced. On rainy mornings, trapping was delayed. If rain continued beyond 13:00, trapping was suspended until the following morning. I recorded the sex and species of all butterflies captured in the traps. Individuals were marked on the underside of their hind-wing with fine tipped indelible markers (Southwood 1966; Sparrow et al. 1994). Different color markers were used for the two different vegetation types

under consideration. Butterflies collected in the traps were released en masse at the center of the trap array on the afternoon of capture between the hours of 13:00 and 14:30 hours. All individuals subsequently recaptured were recorded, marked a second time and released as before. The shrub-youngfield trap array was monitored for 11 days during the summer of 2007 and 15 days during the summer of 2008 wile the shrub-forest trap array was monitored for 15 days during the summer of 2008 and 15 days during the summer of 2009.

INITIAL CAPTURES

To determine how butterflies were initially distributed with respect to the habitat-matrix edge, I used a Chi Square test to compare the number of butterflies captured within 50 meters of the edge, between 100 and 150 meters from the edge and between 200 and 250 meters from the edge.

RECAPTURES

I used a Chi Square test to determine if butterflies were recaptured in equal numbers at similar distances from the release point in habitat and matrix vegetation. Since the trap array data could not be transformed to meet ANOVA assumptions, I used the Wilcoxon two sample test to analyze how far butterflies moved in the different vegetation types. Finally, I compared how many butterflies were recaptured at different distances from the edge in the forest and youngfield matrix. Since these two matrix types were in two different trap arrays, with different butterfly densities, I standardized the sample size by scaling the relative preference at each trap to the sample size of the array with fewer captures to make the comparison possible. I also used the Wilcoxon two sample test to determine how far butterflies moved from the release point in the two matrix vegetation types.

RESULTS

INITIAL CAPTURES

Initial trap array capture data from 2007, 2008 and 2009 demonstrated that fruit feeding nymphalids were not distributed randomly across the shrub-youngfield vegetation interface or the shrub-forest vegetation interface. I captured a total of 335 individuals in the youngfield vegetation and 1511 individuals in the shrub vegetation (Figure 2). There were similar numbers

of butterflies captured in the shrub and youngfield vegetation 50-100 meters from the border. In contrast, butterflies were captured more frequently in shrub vegetation both within 25 meters of the border and between 200 to 250 meters from the border (Table 1). Fruit feeding nymphalids also showed differential distribution across the shrub forest vegetation interface with 143 individuals captured in the forest vegetation and 290 individuals captured in the shrub vegetation. They consistently preferred shrub vegetation across all of the distances from the border considered in this study (Table 2).

RECAPTURES

Recapture data from 2007, 2008 and 2009 agreed with the pattern demonstrated by the initial capture data. Fruit feeding nymphalids did not move equally through habitat and matrix vegetation. Of the 1846 butterflies released at the border between youngfield and shrub vegetation, 268 were recaptured. Nearly three times as many butterflies were recaptured in the shrub (196) versus the youngfield vegetation (75) (Figure 3). There were no differences in the number of individuals recaptured within 25 meters; however, more butterflies were recaptured in the shrub vegetation when comparing locations 50 to 200 meters from the border (Table 3). Individuals were recaptured on average 121.1 meters from the release point in shrub vegetation, significantly farther than in the youngfield vegetation where they were captured 92.0 meters from the release point ($t_{s[\infty]}$=3.03 p<0.001). Fruit feeding nymphalids also showed differential movement in shrub versus forest vegetation. Of 433 butterflies released at the shrub-forest vegetation border, 260 were recaptured with 84 recaptured in the forest and 176 recaptured in the shrub (Figure 3). Butterflies were recaptured more often in shrub vegetation than in youngfield vegetation within 150 meters of the border. Similar numbers of butterflies were captured in both vegetation types at distances greater than 150 meters (Table 4). Even though fewer individuals were recaptured in the shrub vegetation, the average distance traveled was longer ($t_{s[\infty]}$=3.93 p<0.001) with an average distance of 153.3 meters in the shrub and 113.9 meters in the forest vegetation. Finally, when the two matrix types were compared to each other, fruit feeding nymphalids moved further in shrub vegetation (113.9 meters) than in youngfield vegetation (92 meters) ($t_{s[\infty]}$=2.20 p=0.03). Individuals were more likely to be recaptured close to the border in youngfield vegetation and farther from the border in forest vegetation (Table 5; Figure 4).

DISCUSSION

Vegetation structure likely plays an important role in determining the permeability of edges between habitat and matrix vegetation, as well as matrix conductance (Stamps et al. 1987; Fry and Robson 1994; Haynes and Cronin 2003). The trap arrays used in this study demonstrated, as predicted, that fruit feeding nymphalids were found more often in and moved farther in matrix vegetation that was structurally similar to habitat vegetation. Based on the structural similarity between shrub and forest vegetation and their dissimilarity from youngfield and lawn vegetation, I expected forest vegetation to have high conductance and youngfield to have low conductance. These predictions were verified by the results of this study. Fruit feeding nymphalids were more numerous in the forest matrix than they were in the youngfield matrix, they were initially captured deeper in forest matrix and when they were released at the border between matrix and habitat vegetation, they moved farther into the forest matrix than into the youngfield matrix.

The patterns of matrix conductance found in this study are consistent with several studies that have identified the ability of butterflies to perceive discontinuities in vegetation and alter their movements in response (Schultz 1998; Schultz and Crone 2001; Schtickzelle and Baguette 2003). While only a handful of butterfly studies have measured matrix conductance directly, many have addressed butterfly behavior at habitat-matrix borders and quantified butterfly abundance in different types of matrix vegetation. Both of these processes are closely related to matrix conductance. For example, Ross et. al (2004) found that butterflies flew less frequently, shorter distances and at lower rates in matrix vegetation. In a mark, release, recapture study of four butterfly taxa (Satyrinae, Meliaeini, Pierinae, Polyommatini) Ricketts (2001) found that willow matrix had a conductance three to twelve times higher than conifer matrix (Ricketts 2001). In addition, perception of matrix vegetation has been found to differ across and within butterfly species. The same landscape may be perceived differently by similar species (With and Crist 1995; Turner et al. 2001), with, in some cases, larger, more vagile species having higher propensity to cross edges and higher rates of movement in matrix habitat (Stasek et al. 2008). Within species, variation in willingness to cross open areas may also exist, with open habitat dwelling populations crossing open matrix more readily than the forest dwelling populations (Leimar et al. 2003).

The results from my study also support several others demonstrating preferences for structural similarity between habitat and the matrix being utilized. For instance, the open habitat butterfly, *Melitaea cinxa*, was found to cross more readily into non-habitat vegetation that was structurally similar to its youngfield habitat, and rarely into forest vegetation (Kuussaari et al. 1996). Further, several species of satyrine butterflies were found to spend more time in non-habitat vegetation structurally similar to their habitat vegetation (Keufler and Haddad 2006).

The importance of matrix structure and its effects on conductance are of course not limited to butterflies, or even invertebrates. Both matrix type and species identity were found to affect movement rate between habitat patches of leafy spurge in flea beatles, with *Aphthona nigriscutis* demonstrating a high movement rate in grass matrix (low structural contrast to habitat) and a low movement rate in shrub matrix (high structural contrast to habitat), while its congener *A. lacertosa* had low interpatch movement rates in both shrub and grass matrix (Jonsen et al 2001). Plant hoppers, *Prokelisia crocea*, also move between patches at a rate of five-times higher in the low structural contrast matrix than in the high structural contrast matrix (Haynes and Cronin 2003). In addition, between patch movement in cactus bugs, *Chelinidea vittiger*, has been shown to be negatively correlated with matrix structure, with greater matrix structure decreasing mean step length, directionality and net displacement (Schooley and Wiens 2004). Finally, even vertebrates demonstrate differential willingness to move through matrix vegetation. Stevens et al. (2006) demonstrated that natterjack toads used a combination of edge contrast and ease of movement in matrix substrate to determine edge crossing probability, and Castellon and Seiving (2006) demonstrated that low structural contrast shrub matrix and wooded corridors were similarly good at encouraging movement between forest patches for the Chucao Tapaculo (*Scelorchilus rubecula*) an understory bird.

In this study, I found that trap arrays effectively quantify conductance, allowing me to differentiate butterfly movement rates in different vegetation types, and demonstrate the importance of vegetation structure in determining matrix conductance for a group of fruit feeding nymphalid butterflies. The trap array method outlined in this paper combines strengths of both individual-based and MRR methods, and even offers advantages over some MRR methods. For instance, detailed behavioral information (e.g., parameters of interest such as directionality of movement, or movement along features of interest such as riparian corridors) can be captured by altering the array design, location or number. These trap arrays can be deployed and monitored

daily, with each trap providing information about the position of dozens of individuals. Further, this method can be used on animals that are not easily followed and are too small to permit radio telemetry. While this will not replace individual-based methods for finer scale behavioral information, it is a valuable tool for assessing the habitat preferences and movement of any animal that can be captured in a baited trap.

For many species the matrix constitutes unsuitable and potentially hostile habitat (Arendt 2004), but it is rarely a complete barrier to dispersal. Distinct habitat types within the matrix, defined by vegetative and other structural features, may be differentially permeable to a variety of species (Roland et al. 2000; Ricketts 2001; Ries & Debinski 2001; Rodriguez et al. 2001; Jonsen et al. 2001; Schooley and Wiens 2004). In some cases, movement through the matrix may be sufficient for immigration to offset extinction in local (sub)populations (Witt & Huntly 2001; Hudgens & Haddad 2003). Thus, knowledge of movements is necessary to design effective conservation strategies. Landscape connectivity is a combination of structural characteristics (habitat, patch and matrix configuration) and the behavior of individuals in response to landscape structure (Taylor et al.1993; Fahrig and Merriam 1994; Goodwin and Fahrig 2002). Understanding how habitat structure in the matrix influences permeability to animal movement is key to managing complex landscapes for conservation (Turchin 1998; Ricketts 2001; Vandermeer and Carvajal 2001). This study demonstrated the importance of vegetation structure in determining matrix conductance for a group of fruit feeding nymphalid butterflies. Further, it demonstrated a new method that can be used to measure matrix conductance in a cost effective manner while preserving valuable details about patterns of animal movement within matrix vegetation.

Table 1: Initial capture data demonstrating that fruit feeding nymphalids are not distributed randomly across shrub and forest vegetation with butterflies preferring shrub vegetation.

Distance from edge	Number in shrub	Number in forest	X^2	p
0-25 meters	114	63	14.69	0.01
50-100 meters	119	55	23.54	<0.001
150-250 meters	57	25	12.49	0.03

Table 2: Initial capture data demonstrating that fruit feeding nymphalids are not distributed randomly across shrub and forest vegetation with butterflies preferring shrub vegetation.

Distance from edge	Number in shrub	Number in youngfield	X^2	p
0-25 meters	431	155	129.99	<<0.001
50-100 meters	559	555	0.01	0.99
150-250 meters	521	34	427.33	<<0.001

Table 3: Butterfly recaptures across the shrub youngfield trap array. Butterflies show preference for shrub vegetation between 50 and 200 meters from the border

Distance from edge	Number in shrub	Number in youngfield	X^2	p
25 meters	26	20	0.78	0.38
50 meters	41	17	9.93	0.002
100 meters	45	22	7.89	0.005
150 meters	28	4	18.00	<<0.001
200 meters	26	5	14.23	<0.001
250 meters	27	17	2.27	0.13

Table 4: Butterfly recaptures across the shrub forest trap array. Butterflies show preference for shrub vegetation between 25 and 150 meters from the border

Distance from edge	Number in shrub	Number in forest	X^2	p
25 meters	34	9	14.53	<0.001
50 meters	32	5	19.70	<<0.001
100 meters	37	16	8.32	0.004
150 meters	33	18	4.41	0.03
200 meters	21	18	0.23	0.63
250 meters	19	18	0.03	0.86

Table 5: Butterfly recaptures within forest matrix and youngfield matrix. Recapture numbers have been adjusted by dividing the total number of butterflies captured in the forest:shrub array by the total number in the youngfield:shrub array and multiplying all observations in the youngfield:shrub array by the resulting number. This corrects for different sample sizes across the two trap arrays.

Distance from edge	Number in forest	Number in youngfield	X^2	p
25 meters	9	12	0.43	0.51
50 meters	5	16	5.76	0.02
100 meters	16	20	0.44	0.51
150 meters	17	11	1.29	0.26
200 meters	16	15	0.03	0.86
250 meters	17	6	5.36	0.02
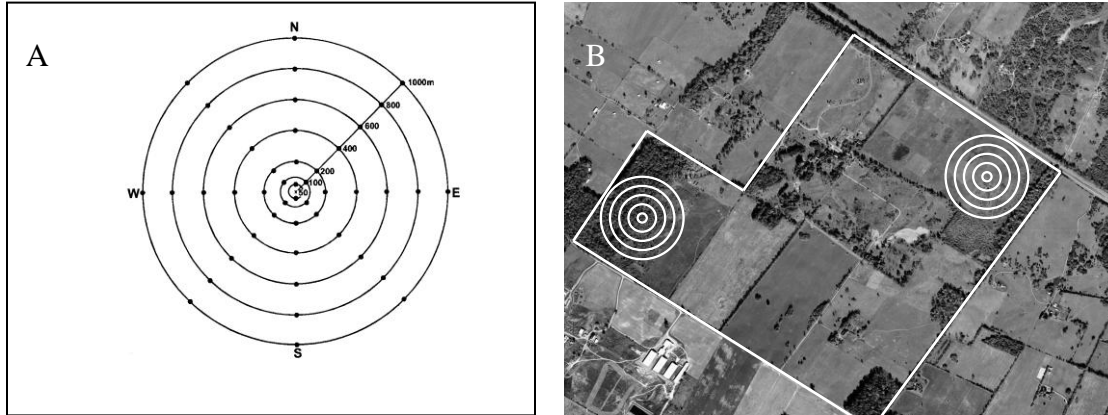
Figure 1: A. The basic trap array configuration (Turchin and Thoeny 1993). The radius in this experiment was 250m instead of the 1000m in the original design. B. An estimated picture of the location of these trap arrays at Blandy Experimental Farm. The left array is centered at the forest-shrub vegetation border while the array in the upper right hand corner is centered at the shrub-youngfield vegetation border.
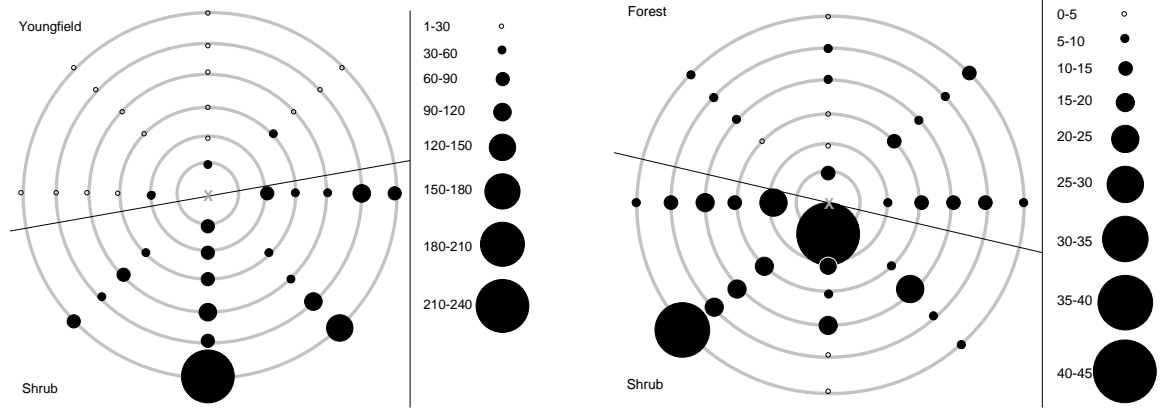
Figure 2: Representation of the initial capture rates in the two trap arrays, diagonal lines represent the border between vegetation types and the size of circles represent the number of fruit feeding nymphalids captured at each trap.
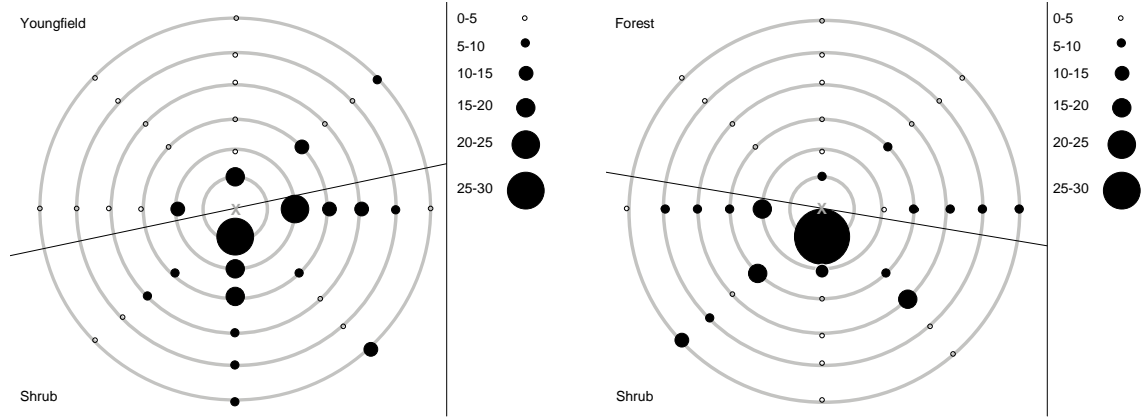
Figure 3: Representation of the recapture rates in the two trap arrays, diagonal lines represent the border between vegetation types, grey Xs represent the release points of captured butterflies and the size of circles represent the number of fruit feeding nymphalids captured at each trap.
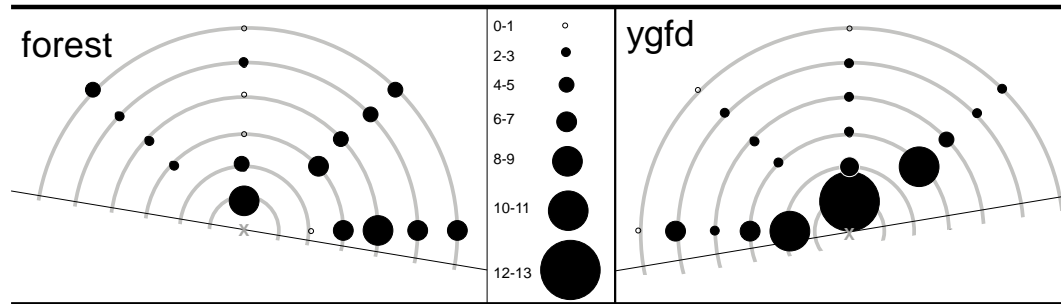
Figure 4: Representation of the recapture rates in the two different matrix vegetation types, recaptures were rescaled to a total of 80 for each array to account for the differences in capture rates between the forest:shrub array and the youngfield:shrub array. Butterflies moved more readily through forest vegetation $t_{s(\infty)}$=4.85, p<<0.001

CHAPTER 4: Identifying the drivers of butterfly vegetation choice

INTRODUCTION

In order to exist in fragmented landscapes, organisms must navigate a mosaic of habitat patches embedded in non habitat (matrix) vegetation. Determining how organisms behave in such landscapes is necessary to evaluate how fragmentation will influence species distributions, abundance and persistence (Hanski et al. 1994; Summerville and Crist 2001; Fahrig 2003; Schtickzelle and Baguette 2003). An organism's ability to move through a landscape is determined by the conductance of different types of vegetation and the relative abundance and location of vegetation types within a landscape (Merriam 1984; Baudry and Merriam 1988; Merriam 1991; Taylor et al. 1993; Fahrig and Merriam 1994; Goodwin and Fahrig 2002). Some types of matrix vegetation can act as corridors for movement between habitat patches, while others may act as barriers (Ricketts 2001; Bélisle 2005). Organisms may avoid particular vegetation types or the conditions prevalent in certain vegetation types (Ross et al. 2004). In spite of the clear importance of understanding matrix conductance, we still have little knowledge of the cues that make certain types of matrix vegetation more conducive to movement. I examined a variety of potential cues and measured how they affected the movement behavior of a guild of fruit feeding nymphalid butterflies. Butterflies are an excellent target group for studies of movement decisions. Their decision making is simpler than that of many other organisms, such as birds and mammals, which are often used in landscape behavioral ecology. Further, the cues butterflies use to make movement decisions are easily manipulated. While butterfly behaviors are relatively more consistent and less complicated than other organisms, experimental work shows that butterflies can distinguish between different types of matrix vegetation (Roland et al. 2000; Ricketts 2001; Leimar et al. 2003; Ross et al. 2005).

A variety of biotic and abiotic factors likely play important roles in determining matrix conductance. For example, physical aspects of the matrix such as foliar height, canopy cover, plant composition and vegetation density are likely all important in determining species movement probability (Fry and Robson 1994; Desrochers et al. 2003; Keufler and Haddad 2006). Further, some organisms, including butterflies, are more likely to respond to contrast rich vegetation borders, those between vegetation types that have very different structure (Berggren et al. 2002; Ries and Debinski 2001; Ricketts 2001). Matrix vegetation with significant vertical structure may form a barrier to movement (Roland et al 2000; Vandermeer and Carvajal 2000;

Jonsen et al. 2001; Ricketts 2001; Schooley and Weins 2004, Stasek et al. 2008). Light levels also likely influence movement decisions (Ricketts 2001; Ross et al 2005). Butterflies are heliotherms, controlling their body temperature by exposure to the sun (Dennis 1993; Dover et al. 1997; Dennis 2004), and therefore occupy sites with suitable radiation intensity (Watt 1968; Kingsolver 1983; Heinrich 1986; Ohsaki 1986; Ravenscroff 1994; Rutowski et al. 1994). Several studies have demonstrated that butterfly flight is strongly influenced by light levels, with increased light increasing flight in *Parnassius smintheus* (Ross et al. 2004), and several other species avoiding low light environments (Ide 2002). While many butterfly species prefer high light environments, species associated with forested habitats may exhibit the opposite pattern, preferring low light conditions and displaying reluctance to cross areas of high light (Leimar et al. 2003). When making movement decisions butterflies are also likely tracking resources such as larval host plants (Sharp et al. 1974; Watanabe 1978; Schultz 1998; Smiley et al. 1998; Keufler and Haddad 2006) and food availability (Brakefield 1982; Murphy et al. 1984; Novotny et al. 1991; Ravenscroft 1994; Loertscher at al. 1995). The spatial arrangement of host plants and food resources can therefore also be expected to influence butterfly movement (Brommer and Fred 1999). For example, Ide (2002) was able to show that butterflies utilizing tree sap rather than nectar as a food resource were found in close association with sap sources. Some scientists are now calling for a resource rather than vegetation based approach to modeling butterfly distribution (Vanreusel and Van Dyck 2007).

In a field setting it may be impossible to identify a single cue driving movement behavior. In reality, it may only be possible to determine that organisms are associated with a particular vegetation type and to then infer which qualities of that vegetation type make it attractive to the organism (Matter et al. 2004). For butterflies, a combination of vegetation structure and floral variables are likely to be important for defining movement (Dover 1996; Ide 2002). In some cases it may be necessary to combine host plant distribution, nectar resources, light availability and vegetation layers in order to accurately predict butterfly distribution (Vanreusel and Van Dyck 2007). To determine which microclimatic and vegetation variables butterflies use as cues to make movement decisions, I conducted a variety of choice experiments in a screen house. Previous experiments designed to test color discrimination in nectar feeding butterflies have used choice experiments in a Y shaped apparatus (Takeuchi et al. 2006). I modified this apparatus to determine the response to larger scale variables (Figure 1). By

uncoupling cues such as light levels, structural complexity and host plant availability that are usually linked across vegetation types in nature, I was able to assess the relative importance of these cues individually. Fruit feeding nymphalids are generally associated with mature vegetation that is structurally complex (Ch 1; Ch2; Glassberg 1993). As such, I predicted that fruit feeding nymphalids would respond favorably to structurally complex vegetation, and that they would choose lower light levels like those associated with shrub and forest vegetation. I also predicted that that they would react to the presence of host plants.

METHODS

STUDY SITE AND SPECIES

I conducted this research at Blandy Experimental Farm and E. Orland White Arboretum, a 280-hectare site, located in Clarke County, Virginia. Eleven species of fruit feeding nymphalid butterflies are found at Blandy Experimental Farm. The two most common species are the Hackberry Emperor (*Asterocampa celtis*) and the Question Mark (*Polygonia interrogationis*). Hackberry Emperors and Question Marks are both fruit feeding nymphalids, adults feed primarily on tree sap, fruit, carrion and dung. The wingspan of Hackberry Emperor is between 3.5 and 6.3 cm with males generally smaller than females. The slightly larger Question Mark has a wingspan between 5.75 and 7.6 cm, again males tend to be smaller than females (Clark and Clark 1951; Langlois and Langolis 1964). Various species of hackberry, *Celtis,* are used as larval host plants for both species. Question Mark also uses the, American elm, red elm and members of the Urticaceae, including false nettle, *Boehmeria*; hop, *Humulus* and nettle, *Urticau* (Glassberg 1993).

Shrub vegetation is the primary habitat for both species. This designation is based on the fact that butterflies were most abundant in this vegetation type during inventory trapping (Chapter 1). The common hackberry, *C. occidentalis*, is most abundant in this vegetation type.

BUTTERFLY COLLECTING AND HANDLING

Butterflies were captured using 24 Van Someren Rydon traps (DeVries 1987) baited with a mixture of eight parts banana pulp and one part rum. Traps were located throughout Blandy Experimental farm, eight in each of four vegetation types; lawn, youngfield, shrub and forest. I chose a stratified trapping effort across vegetation types to minimize the chances of capturing

populations associated with a particular vegetation type to avoid bias in later behavioral experiments.

I checked traps every morning between 0730 and 1100. All butterflies were removed from the traps and they were then reset with fresh bait. Butterflies were brought into the lab where I recorded their sex and species. They were placed singly in 4oz. Dixie cups which were then covered with lemon covers (small mesh covers with elastic bands) purchased from a restaurant supply store. I then placed the cups inside a Styrofoam cooler with an ice pack inside, designed to chill the butterflies to 5-10 degrees below ambient daytime temperature, thus minimizing agitated dispersal (Southwood 1996).

CHOICE EXPERIMENTS

To identify the signals butterflies are using to make movement decisions, I tested cues individually. I erected a 20 by 30 foot steel framed screenhouse in an open field, selecting a PVC screen that provided minimal (15%) shade. The screenhouse was split into three sections; two 12 x 20 foot sections representing the cue being tested, and a third neutral 6 x 20 foot section that had been cleared of vegetation (Figure 1). The trials were conducted between July 29th and August 24th 2008. For each trial, chilled butterflies were released singly in the center of the screenhouse. Butterflies were released between 1130 and 1330 to minimize the influence of the direction of the sun.

On either side of the neutral release strip, butterflies were presented with a 12 x 20 foot area designed to test the importance of a particular cue (Table 1). The positions of the presented treatments in the screenhouse were switched once during each experiment. The three likely candidate cues identified from the literature and previous experiments were vegetation structure, host plant availability and light levels. In addition to testing each of these cues singly, I combined structure and host plant availability to simulate habitat vegetation. Cues were designed using the methods below:

> **Structure-** Structurally diverse vegetation was simulated by placing potted plants on top of an existing grassy field. Potted plants were a mixture of native and ornamental trees and shrubs between 18 inches and 8 feet in height. Plants were placed close together with between 1 and 3 plants per square yard. To determine the importance of structural

complexity, this cue was tested against lawn vegetation that had been recently mowed and was no more than 6 inches high.

Host plant availability- Structurally complex vegetation was created as described above. Within this vegetation, I placed 35 four foot tall potted Common Hackberries *Celtis occidentalis* saplings. To determine the importance of host plant availability, this cue was tested against structurally identical vegetation with 35 four foot tall potted Alder *Alnus serrulata* saplings. These non-host plants share a common growth form and have similar leaf morphology to the Common Hackberry.

Light levels- Structurally complex vegetation was again created as described above. One half of the screenhouse was then covered with 60% shade cloth designed for a commercial shade house. This shaded area was compared with structurally similar vegetation at ambient light levels.

Simulated habitat- To determine if the combined signals of structure and host plant availability would create a stronger preference than either alone, I created structurally complex vegetation embedded with host plants as described in the host plant availability section above. I then compared it to lawn vegetation that was freshly mowed and no more than 6 inches high.

Butterflies released in each trial were scored as having chosen one option over the other when they left the neutral strip and landed within one of the 12 x 20 foot options. If butterflies landed on the walls of the screenhouse, they were scored as having chosen that option if they remained on the wall associated with that option for 10 minutes or more. Butterflies that remained in the neutral strip for more than 15 minutes were removed from the screenhouse and released. All choice experiments were analyzed using Chi Square tests (Sokal and Rohlf 2000). Expected values assumed that individuals without a preference were equally likely to choose either of the choices available within the screenhouse.

RESULTS

Experiments demonstrated that butterflies reacted to simulated shrub. When given the choice between simulated shrub (vegetation that approximated the structure of shrub habitat and contained host plants) and lawn vegetation, butterflies preferred simulated shrub more often, with 95 individuals choosing simulated shrub and 35 choosing the lawn ($\chi^2_{[9]}$=29.98, p << 0.001; Figure 2). Further experiments indicated that vegetation structure is likely the major cue butterflies use when making decisions about vegetation choice. When I presented butterflies with the choice between vegetation that structurally approximated shrub vegetation in the absence of host plants and lawn vegetation, fruit feeding nymphalids still chose the structurally complex vegetation more often, with 87 individuals choosing the structurally complex vegetation and 21 choosing the lawn ($\chi^2_{[7]}$ = 41.95 p<<0.001; Figure 3). To determine if butterflies would differentiate between structurally similar vegetation based solely on the presence of host plants, I compared simulated vegetation with and without potted host plants. I found that butterflies did not differentiate between these two choices, with 52 individuals choosing the shrub with the host plant; only marginally more than the 40 that chose the shrub without host plants ($\chi^2_{[9]}$=4.66, p=0.86 ; Figure 4). Since females are likely more motivated by the presence of host plants, I examined them separately. While the pattern was stronger when females were considered alone, it was still non significant, with 11 individuals choosing the shrub and 21 choosing the shrub with embedded host plants ($\chi^2_{[9]}$=5.28, p=0.81; Figure 5). Finally, I observed no indication that butterflies were choosing vegetation based on light levels. When presented with the choice between simulated shrub vegetation under ambient light and simulated shrub vegetation with 60% shade, butterfly behavior did not deviate from random. A total of 31 individuals chose the shaded vegetation while 27 individuals chose the vegetation under ambient light ($\chi^2_{[5]}$=0.74, p=0.98; Figure 6).

DISCUSSION

It is likely that no one cue controls butterfly movement behavior. Abiotic factors like light availability, physical aspects of vegetation, such as foliar height, vegetation density and plant composition, and resources like host plants and food availability all likely combine to make certain vegetation types more conducive to movement (Stamps et al. 1987; Fry and Robson 1994; Collinge and Palmer 2002; Desrochers et al 2003; Haynes and Cronin 2003; Keufler and

Haddad 2006). The choice experiments used in this study allowed me to identify the cues fruit feeding nymphalids use to make movement decisions at vegetation borders. I expected that butterflies would respond to vegetation structure, light availability and host plant abundance. While I found that butterflies responded to simulated habitat that combined vegetation structure and host plant availability, I also found that they responded to vegetation structure alone. I found no evidence that butterflies used light availability as a cue, though the thermal aspect of light availability may have been compromised by the chilling of butterflies during the handling process. Finally, it was difficult to test host plant availability as a cue because the presence of the host plant could not be divorced from the structural complexity that host plants create. To minimize these effects, we presented host plants embedded in structurally complex vegetation and compared it to structurally complex vegetation without host plants. There was some weak evidence that fruit feeding nymphalids, especially females, may have used host plant availability as a movement cue. Host plants were most effective at changing movement behavior when they were presented to butterflies in combination with structurally complex vegetation as an alternative to lawn vegetation.

The results of my study were not consistent with previous work that identified the importance of host plant availability (Sharp et al. 1974; Watanabe 1978; Schultz 1998; Smiley et al. 1998; Keufler and Haddad 2006) and light levels (Brdar 2000; Ide 2002; Leimar et al. 2003; Ross et al. 2004) in driving butterfly micro-distribution and movement. While several studies have identified the ability of butterflies to perceive discontinuities in vegetation and alter their movements in response (Schultz 1998; Schultz and Crone 2001; Schtickzelle and Baguette 2003), few studies have directly manipulated vegetation structure and measured the effects on butterfly movement. Two notable exceptions are the work of Fry and Robson (1994) and Dover and Fry (2001), who demonstrated that butterflies responded to artificial hedgerows. This work indicated that visual structure was enough to affect butterfly movement in the absence of other cues associated with vegetation. While few studies have tested the importance of habitat structure alone, my results are consistent with those that correlated butterfly movement with differences in vegetation structure. Several studies have identified the ability of butterflies to perceive discontinuities in vegetation and alter their movements in response (Schultz 1998; Schultz and Crone 2001; Schtickzelle and Baguette 2003, Ch1). It has also been shown that a butterfly's willingness to cross the edge between habitat and matrix vegetation is often affected

by vegetation structural contrast (Duelli et al. 1990; Ries and Debinski 2001). Landscape context was important in determining the rate of patch emigration in the butterfly *Melitaea cinxa* (Kuussaari et al. 1996) and in several species of satyrine butterflies (Keufler and Haddad 2006). Further, the structural complexity of vegetation has been suggested to be an important factor determining the conductance of different matrix vegetation types for a variety of butterfly species (Ricketts 2001; Ross 2004; Stasek et al. 2008). The identification of structure as the putative cue used to make movement decisions is not unique to butterflies. Vegetation structure was also identified as important for movement in ground dwelling beetles (Collinge and Palmer 2002), flea beetles (Jonsen et al. 2001), plant hoppers (Haynes and Cronin 2003), cactus bugs (Schooley and Wiens 2004), bush crickets (Diekötter et al. 2007), birds (Castellon and Seiving 2006; Reino et al. 2009), natterjack toads (Stevens et al. 2006) and flying squirrels (Desrocher et al. 2003).

Vegetation structure plays a key role in influencing the likelihood that fruit feeding nymphalids will move through a vegetation type. This type of knowledge is critical for species conservation. Many studies have already suggested that the structure of matrix vegetation is a critical factor in determining matrix conductance. Understanding the cues butterflies use to make movement decisions is also critical in determining the utility of conservation measures like corridors and stepping stones designed to mitigate the effects of isolation on populations in fragmented landscapes (Saunders and Hobbs 1989; Harris and Scheck 1991; Fahrig and Merriam 1994). It has been shown that habitat corridors are effective for increasing interpatch movement for a variety of organisms, including plants (Pollard 1973), small mammals (Bennett 1990; Wegher and Merriam 1990), birds (Saunders 1990; Machtans et al. 1996), reptiles (Roasenberg et al. 1998), and insects (Burel 1989; Sutcliffe and Thomas 1996; Tischendorf et al. 1998; Haddad 1999; Haddad and Baum 1999; Haddad 2000; Tewksbury et al. 2002). What is not known is which cues organisms use to make the decision to move through these corridors. This lack of knowledge about which factors influence corridor use at least partially explains why some corridors succeed in increasing movement while others fail. Often corridors of pristine habitat connecting existing patches are unavailable, leaving conservation practitioners with only modified vegetation to work with (Beier and Noss 1998). Therefore, understanding the cues organisms use to make movement decisions has great potential for identifying the vegetation

types that are most conducive to movement, allowing for the creation of the most effective corridors.

In this study, I found that manipulation of individual cues provided valuable information about fruit feeding nymphalid behavior. Traditional methods of measuring animal movement often document the affinity of organisms for certain vegetation types and infer the biotic and abiotic factors that drive vegetation preference. While these correlative studies are valuable, they do not tell us which specific cues organisms use to make movement decisions. By manipulating host plant availability, light levels and vegetation structure in controlled screenhouse experiments, I was able to tease apart the effect of cues that often vary together across vegetation types. While labor intensive, these methods are easily modified to test the importance of a nearly endless array of potential cues. Further cues can be combined to test for additive effects or manipulated in ways that do not currently exist in nature, potentially accounting for effects of habitat or climate change. In sum, gaining a mechanistic understanding of corridor function (Dover and Fry 2001) opens up the potential for managers to manipulate existing vegetation in a targeted way to increase the movement of an organism of interest. Collecting behavioral information on how an organism perceives a particular landscape when making movement decisions ensures that any changes to vegetation result in increased connectivity. This study demonstrated the importance of vegetation structure in influencing movement decisions for nyphalid butterflies, which likely drives the behavior of these species at the habitat-matrix interface as well as matrix conductance.

Table 1: List of choices available in screenhouse experiments

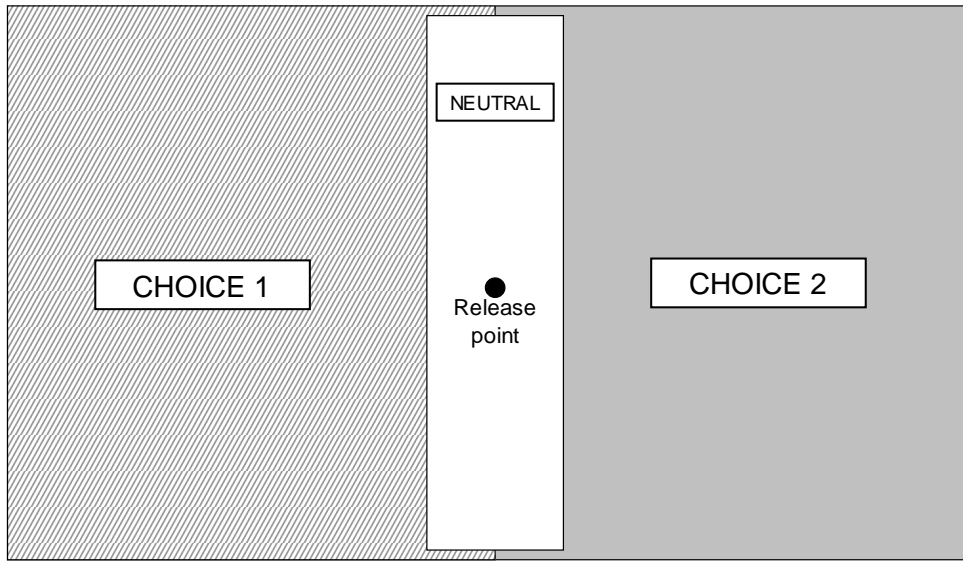| CUE TESTED	CHOICE 1	CHOICE 2
Simulated Habitat	Simulated shrub vegetation with host plants	Lawn
Structural Complexity	Non host shrub vegetation	Lawn
Host Plant Recognition	Simulated shrub vegetation with host plants	Simulated shrub without host plants
Light availability	Ambient light	Light levels simulating shrub/ forest light levels

Figure 1: 20 x 30 foot screen house experiment designed to test the importance of different cues on movement behavior. Each choice area is 12 x 20 feet while the neutral area in the center is 6 x 20 feet. Individual butterflies are released in the center of the neutral area.

Reaction to simulated habitat

Figure 2: When given the choice between simulated shrub vegetation constructed of potted plants mixed with larval host plants and lawn vegetation, fruit feeding nymphalids chose simulated habitat ($\chi^2_{[9]} = 29.98$, p << 0.001).

Reaction to structural complexity
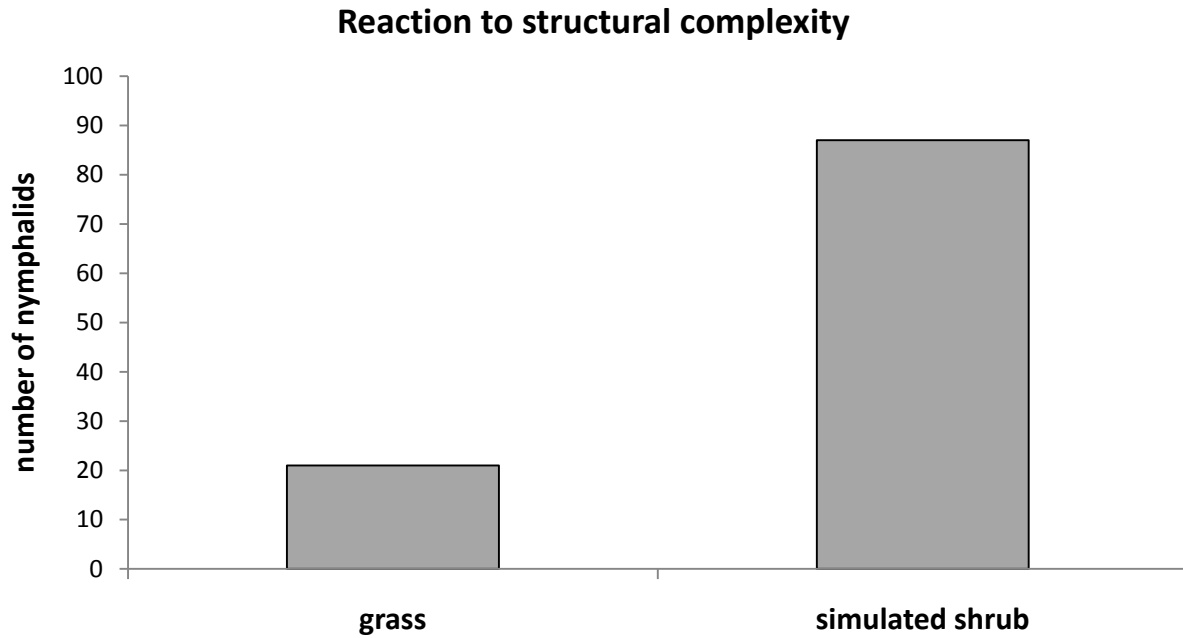
Figure 3: When given the choice between simulated shrub vegetation constructed of potted plants and lawn vegetation, fruit feeding nymphalids chose simulated shrub ($\chi^2_{[7]} = 41.95$ p<<0.001).
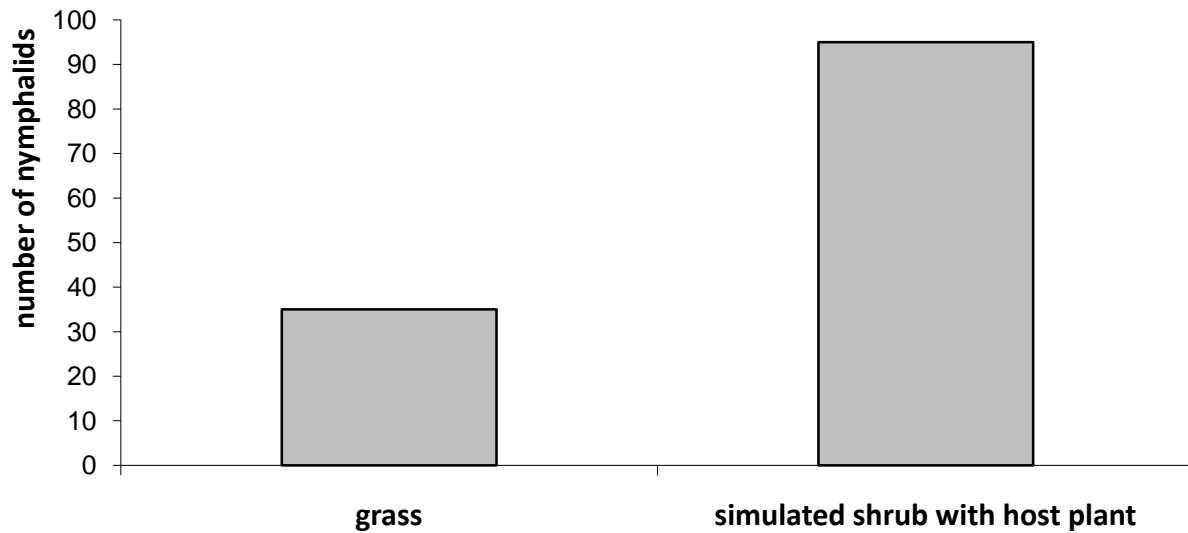
Reaction to host plant

Figure 4: When given the choice between simulated shrub vegetation constructed of potted plants mixed with larval host plants and simulated shrub vegetation without host plants, fruit feeding nymphalids did not differentiate ($\chi^2_{[9]}$ =4.66, p=0.86).

Female reaction to host plant

Figure 5: When given the choice between simulated shrub vegetation constructed of potted plants mixed with larval host plants and simulated shrub vegetation without host plants, female fruit feeding nymphalids did not differentiate ($\chi^2_{[9]} = 5.28$, p=0.81).

Reaction to light

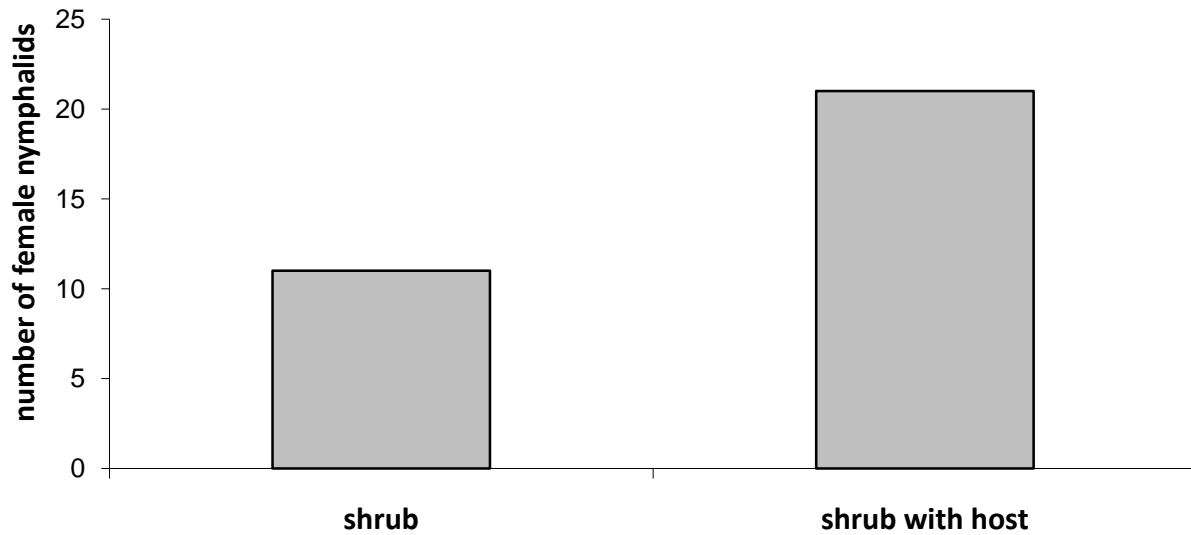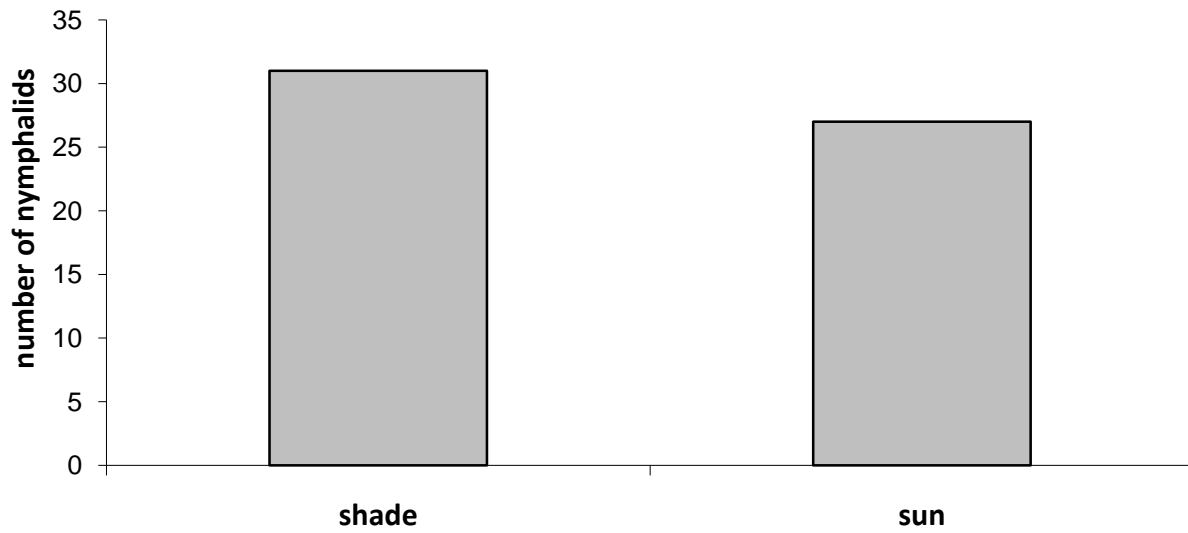
Figure 6: When given the choice between simulated shrub vegetation constructed of potted plants under 60% shade and shrub vegetation under ambient light, butterflies did not differentiate ($\chi^2_{[5]}$=0.74, p=0.98).

CHAPTER 5- CONCLUSIONS

The purpose of my dissertation was to measure fruit feeding nymphalids vegetation preference at a variety of spatial scales and to determine the cues butterflies are using to make movement decisions. In the course of my work, I quantified vegetation structure and conducted inventories of fruit feeding nymphalids to determine which types of vegetation butterflies preferred. I conducted behavioral field experiments to measure vegetation preference at the borders between matrix and habitat vegetation and used large scale trapping arrays to quantify matrix conductance. Finally, I conducted controlled experiments in a screenhouse to individually test the importance of factors such as light availability, structural complexity and host plant availability for butterfly vegetation preference.

Several studies have found relationships between local movement patterns and larger scale dispersal behaviors (Dennis 2004; Levey et al. 2005; Conradt and Roper 2006; Kuefler and Haddad 2006). What had not yet been determined was the relationship between these local movements and large scale vegetation preference. In chapter 2, I determined that vegetation types at Blandy Experimental Farm fell into three groups, structurally complex vegetation consisting of forest and shrub vegetation, vegetation of medium complexity consisting of youngfield vegetation and structurally simple lawn vegetation. Through systematic inventory trapping, I was able to determine that fruit feeding nymphalids butterflies were found most often in structurally complex vegetation like shrubs and forest. I identified this pattern and found that vegetation preference at the 5-10 meter scale was representative of vegetation preference at the landscape level. This suggests that small scale decisions being made at vegetation borders likely play a key role in determining the distribution of fruit feeding nymphalids in a landscape.

The results of chapter 3 built on those of chapter 2. In chapter 2, I identified that butterflies were most closely associated with structurally complex vegetation. Inventory trapping allowed me to identify shrub vegetation as primary habitat. In chapter 3, I compared the conductance of shrub habitat, structurally similar forest matrix and structurally dissimilar youngfield vegetation. The trap arrays demonstrated, as predicted, that butterflies moved farther in matrix vegetation that was structurally similar to habitat vegetation. Fruit feeding nymphalids were more numerous in the forest matrix than they were in the youngfield matrix. They were initially captured deeper in forest matrix and when they were released at the border between matrix and habitat vegetation, they moved farther into the forest matrix than into the youngfield

matrix. I also adapted a new method for measuring matrix conductance. Static trapping arrays combined some of the existing strengths of mark release recapture studies and individual based movement methods. These arrays proved effective for measuring butterfly distribution and movement and have potential for measuring matrix conductance for other species that will respond to baited traps.

Abiotic factors including light availability, physical aspects of vegetation, such as foliar height, vegetation density and plant composition, and resources such as host plant and food availability all likely combine to make certain vegetation types more conducive to movement (Stamps et al. 1987; Fry and Robson 1994; Collinge and Palmer 2002; Desrochers et al 2003; Haynes and Cronin 2003; Keufler and Haddad 2006). The choice experiments employed in chapter 4 allowed me to identify the cues fruit feeding nymphalids use to make movement decisions at vegetation borders. While I found that butterflies responded to simulated habitat that combined vegetation structure and host plant availability, I also found that they responded to vegetation structure alone. I found no evidence that butterflies used light availability as a cue. Finally, I found little support for butterflies using host plant availability alone as a movement cue. While there was some weak evidence that fruit feeding nymphalids, especially females, used host plant availability as a movement cue, this cue was most effective at changing movement behavior when it was presented to butterflies in combination with structurally complex vegetation.

The findings of my dissertation illustrate the benefits of examining vegetation preference at multiple scales. I found that fruit feeding nymphalids preferred structurally complex vegetation when making movement decisions at the border between habitat and matrix vegetation. This vegetation preference was echoed at the landscape scale with inventory trapping demonstrating that butterflies were found most often in structurally complex vegetation. Further, butterflies moved more easily through matrix vegetation types that were structurally similar to habitat vegetation. Finally, by examining the cues associated with vegetation singly, I was able to experimentally confirm that structural complexity is likely a major driver of fruit feeding nymphalids vegetation preference.

Combining field observations at multiple spatial scales with manipulative studies allowed me to gain a mechanistic understanding of butterfly vegetation choice. Understanding the cues butterflies use to make movement decisions is critical in determining the utility of conservation

measures like corridors and stepping stones (Saunders and Hobbs 1989; Harris and Scheck 1991; Fahrig and Merriam 1994). Often corridors of pristine habitat connecting existing patches are unavailable, leaving conservation practitioners with only modified vegetation to work with (Beier and Noss 1998). Exploring vegetation preference at multiple scales and understanding the cues organisms use to make movement decisions has great potential for identifying the vegetation types that are most conducive to movement, allowing for the creation of the most effective corridors. These types of studies provide the data managers need to manipulate existing vegetation in a targeted way to increase the movement of an organism of interest. These data could be used to design landscapes conducive to butterfly movement. Further, the tools that I have developed could be adapted to collecting information and designing landscaped for species of conservation concern.

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