

## ABSTRACT

Kuefler, Daniel Cory. Local versus landscape determinants of butterfly movement behaviors.

(Under the direction of Nick M. Haddad)

A thorough understanding of the mechanisms driving larger scale consequences of movement first requires an understanding of whether movement behaviors are related to local or landscape scale determinants. I studied the movement behaviors of four species of bottomland-dwelling butterflies in a natural setting to examine the determinants of movement behavior across different scales. Across spatial scales, I tested the relative importance and predictive value of three landscape attributes: topography, boundary contrast, and stream proximity, and two local habitat attributes: host plant cover and comprehensive vegetative structure. Across species, I tested the relative importance of organism size and habitat specificity to explain response variation. In general, butterfly responses to landscape features were stronger and more universal while responses to local features were weaker and more variable by species. Specifically, results from this study showed that topography does not influence movement behaviors but boundary contrast, stream proximity, and host plant abundance all contributed to movement patterns. Orientation to these features was not related to organism size, but did vary in accordance with habitat specificity. These results suggest that studies on dispersal in fragmented landscapes should consider the effects of that fragmentation on multiple scales. This consideration is particularly important in the management of rare species, when specific behaviors may ultimately affect the success of conservation efforts.

**LOCAL VERSUS LANDSCAPE DETERMINANTS OF BUTTERFLY  
MOVEMENT BEHAVIORS**

By  
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## **BIOGRAPHY**

In my youth, I spent most of nearly every summer camping throughout Northwestern Canada with my family. I passed many languid afternoons peering over the end of a rowboat into shallow beaver pools, contemplating the mysteries beyond my reflection. From that very early age, I have tried to design my life toward simple goals: exploring the mysteries of the world and spending a lot of time in the woods.

Through my undergraduate education, I became fascinated by the integration of social and ecological issues in the field of conservation biology. After obtaining a B.Sc. in Conservation Biology from the University of Alberta, I spent several years scrambling for work as a research technician to both satisfy my intrinsic curiosity and to obtain a stock of experience with different systems and species. After such grandiose experiences as assessing grizzly bear habitat in the Canadian Rockies and rescuing myriad endangered beasts in the highlands of Guatemala, a job humbly catching butterflies in the woods of South Carolina auspiciously provoked me to enter a graduate program in ecology.

I am grateful to have spent the last three years working on a project that, while providing an apt education, will ultimately aid in the management of an endangered butterfly. Armed with new skills and new friendships, I look forward to continuing the pursuit of my simple goals.

## ACKNOWLEDGEMENTS

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**LOCAL VERSUS LANDSCAPE DETERMINANTES  
OF BUTTERFLY MOVEMENT BEHAVIORS**



## ABSTRACT

A thorough understanding of the mechanisms driving larger scale consequences of movement first requires an understanding of whether movement behaviors are related to local or landscape scale determinants. I studied the movement behaviors of four species of bottomland-dwelling butterflies in a natural setting to examine the determinants of movement behavior across different scales. Across spatial scales, I tested the relative importance and predictive value of three landscape attributes: topography, boundary contrast, and stream proximity, and two local habitat attributes: host plant cover and comprehensive vegetative structure. Across species, I tested the relative importance of organism size and habitat specificity to explain response variation. In general, butterfly responses to landscape features were stronger and more universal while responses to local features were weaker and more variable by species. Specifically, results from this study showed that topography did not influence movement behaviors but boundary contrast, stream proximity, and host plant abundance all contributed to movement patterns. Orientation to these features was not related to organism size, but did vary in accordance with habitat specificity. These results suggest that studies on dispersal in fragmented landscapes should consider the effects of habitat variability on multiple scales. This consideration is particularly important in the management of rare species, when specific behaviors may ultimately affect the success of conservation efforts.

## INTRODUCTION

Animal movement impacts the spatial arrangement of populations across landscapes via a variety of mechanisms. Through genetic exchange or recolonization, for example, the dispersal of relatively few individuals can be vital for a species' persistence (Huffaker 1958, Levins 1969, Hanski et al. 1995, Gutierrez 1999). The findings arising from these studies illustrate the need to understand what drives the dispersal of individual animals across landscapes. One possible approach to understanding the mechanisms behind large-scale dispersal is through observations of local behaviors. Lima and Zollner (1996) suggest that an understanding of animal movements and larger scale processes may be bridged by seeking patterns of behavior that remain common across different spatial scales. One way to make this link is to examine individual responses to determinants that act on behaviors at different scales. Local scale determinants of movement, such as plant composition or structure, are attributes that define the composition of an individual habitat. Landscape scale determinants are gross physical attributes that define the arrangement of and relationships between individual habitats. On a landscape scale, an individual habitat type can be considered a single element that affects general movement patterns. Examined in part, however, the physical constituents of a habitat may have an effect on movement that is independent of the relative position or arrangement of that habitat on a landscape. In this study, I address how scale influences movement by examining the behaviors of individual butterflies. From this examination, I am able to evaluate whether movement patterns are predominantly influenced by local or landscape determinants.

Classical models often assume landscapes to be binary with regards to habitat and non-habitat (Forman and Godron, 1981). In landscapes fragmented by human activity, adjacent habitats often differ dramatically and immediately over relatively small scales. In these cases, the contrast between local vegetation and landscape habitat type are, effectively, one and the same. Consequently, it is difficult to determine the individual roles of local and landscape factors on movement decisions in such ‘binary’ landscapes. Stamps et al. (1987) emphasize the continuous nature of real landscapes; boundaries between habitats exist as ecotonal gradients rather than clear and functional barriers. Animals within these landscapes often are regarded to make decisions based on local characteristics (Jonsen 2001, Matter, 2004), but these characteristics are often related to landscape processes (ie. fire-driven succession) and landscape position (Fagan et al. 2003, Ellner and Fussman 2003). Both local and landscape features, depending on the scale over which an animal responds to its environment, may therefore determine movement decisions. In this study, I investigated several landscape elements, including topographic relief, the proximity of riparian corridors, and the level of contrast between riparian corridors and forest boundaries. I also investigated local elements, including the change in plant abundance and structure along habitat gradients.

One landscape factor that may influence butterfly dispersal is topography, and topographic effects on the movement of upland butterflies are relatively well studied; aggregation on hilltops, for example, is common (Alcock 1985, Pinheiro 1990). Outcroppings and geologic landmarks can influence mate location in low-density populations (Henning, 1990, Rutowski 1991). Gender-specific responses to topography can predictably alter dispersal patterns (Pe'er et al. 2004). The high incidence of upland

butterflies orienting uphill urges the question of whether bottomland butterflies orient downhill. Neve et al. (1996) illustrate how the butterfly *Procllossiana eunomia* exhibits movement affinities to wetland corridors; however few, if any, studies address the directionality of movement in wetland species with respect to the slope of the landscape surrounding streams.

A second landscape factor that may influence butterfly orientation is the distance from and orientation to a riparian corridor. The use of prominent landscape elements for navigation has been previously observed in other arthropods; congeneric damselflies, for example, differ in their propensities to travel along or away from streams depending on the structure of landscape in which the streams are situated (Jonsen and Taylor 2000). In my study system, riparian corridors may function as dispersal corridors through the landscape. With this idea in mind, I chose to examine whether proximity to streams surrounded by pine forest affect the movement patterns of butterflies.

The contrast between habitats provides a third landscape factor that may affect butterfly movement. Boundaries influence dispersal and subsequent demographic structures across a range of taxonomic groups, including birds (Matthysen 2002), mammals (Basquill 1999) and arthropods (Berggren et al. 2001). In arthropods, such habitat boundaries may affect movement by several mechanisms. Physical aspects of habitat architecture, such as increased foliar density or height, may impede the transition across a habitat edge (Fry and Robinson, 1994). Inhibitory behaviors (e.g. ‘edge avoidance’) may also constrain emigration in edge-sensitive animals (Haddad 1999, Shultz 2001). Merckx et al. (2003) show that such boundary behaviors can influence mobility patterns of butterflies across fragmented landscapes. As a potential landscape

determinant on movement, I examined edge sensitivity by testing whether butterflies that were released in different forest habitats directed movements toward adjacent riparian habitats.

I also examined relationships between butterfly behaviors and several local, site-specific characteristics of habitat. Many studies address habitat types as discrete entities; Roland (2000), for example, determined that the type of habitat surrounding alpine patches partially determines the probability that an individual butterfly will complete an inter-patch movement event. A few studies that focused on the relationships between movement and local elements have shown that physical characteristics of non-habitat, such as canopy cover and plant composition, evoke differences in the dispersal propensities of butterflies between habitats (Leimer et al. 2003, Ricketts 2001). Brommer and Fred (1999) illustrated that the spatial arrangement of specific host and nectar plants constrained within-habitat movements of Apollo butterflies. Very little research on movement, however, addresses habitats as they commonly exist in nature: gradients of physical characters that are complex, dynamic, and non-discrete. Particularly lacking is information regarding how the characteristics of habitat gradients affect whether and how an animal moves through the landscape. I address this question by comparing butterfly movements through vegetative gradients of ecotonal habitats.

I studied the behaviors of both released and naturally occurring butterflies to test several predictions about how landscape and local factors influence movement. With respect to drainage slope, I expected that steeper drainages would illicit faster and more directed movement toward streams. With respect to boundary contrast, I expected that butterflies would travel faster and orient movements toward riparian habitat more

frequently when the boundary between that habitat and the surrounding forest was more distinct. Furthermore, I expected that butterflies would tend to orient along stream corridors and that this response would become stronger closer to the stream. Lastly, with respect to local habitat characteristics, I expected that movements through areas with similar vegetation would be more direct and that movements would orient toward areas of higher host plant abundance.

To assess the generality of my results, I also tested whether local and landscape factors evoked similar behavioral responses across a range of different species in the same butterfly family. Recent literature emphasizes the need for comparisons that span both taxa and scales of influence (Hudgens and Haddad 2003, Jonsen and Taylor 2003, respectively). Species-specific behavioral differences have variable effects on the distribution of populations at multiple taxonomic levels (Beetles: Collinge and Palmer 2002, Squirrels: Goheen et al. 2003). By focusing my studies on four species of Satyrine butterflies, I addressed the question of whether physical size or habitat specificity affected butterfly responses. These four species represent the full size range in this butterfly subfamily and they differ in their dependence on wetland habitat. I examined patterns of behavior for each of these different species separately with the expectation that the two smaller, generalist species would show weaker responses to both local and landscape determinates than the two larger, specialist species.

## METHODS

### *Study Species*

I compared the behaviors of bottomland forest butterflies to investigate the influence of local and landscape determinants on their movement. Butterflies make ideal test animals, as they are highly visible, abundant, and easily monitored. In addition, they are relatively vagile and show behavioral sensitivity to both local habitat structure (Schtickzelle and Baguette 2003, Haddad 1999) and landscape elements such as topography (Wettstein and Schmid 1999; Weiss and Weiss 1998). I focused on four phylogenetically similar butterfly species of the subfamily Satyrinae. These forest butterflies exhibit a different natural history than that of many open-meadow butterflies. First, these satyrine butterflies do not feed on flowering plants as adults, simplifying their vegetation requirements. Second, these butterflies primarily inhabit wooded bottomland habitats and wetland glades along streams.

For this study, I worked with Carolina satyrs (*Hermeuptychia sosybius*), Appalachian browns (*Satyroides appalachia*), southern pearly-eyes (*Enodia portlandia*), and little-wood satyrs (*Megisto cymela*). Although these butterflies cohabitate, their specific habitat requirements differ. Larval host plants for Carolina satyrs and little wood satyrs include a variety of wetland grasses, whereas Appalachian brown larvae feed on wetland sedges, notably *Carex stricta*, and southern pearly-eye larvae predominantly feed on cane, genus *Arundinaria* (Glassberg 1999). These four species also differ considerably in size; Carolina satyrs and little wood satyrs have approximately twenty percent shorter wingspans than the pearly-eyes and Appalachian browns (Kuefler, unpublished data).

### ***Study Site***

I conducted my studies at Fort Bragg, North Carolina, between May and August in 2003 and 2004. This 65,000-ha military base is dominated by long-leaf pine savannah ecosystem that is maintained by prescribed burns on a three-year rotation. Dendritic streams traverse forested areas and are bordered by riparian forest in low areas. I chose release plots and observational grids along these riparian tracts where satyrine butterflies were abundant. It is important to note that while these sites were, in some cases, selected because they emphasize focal characteristics, such as boundary contrasts, they are representative of the natural variation that exists in this system. As public use of these areas is nearly non-existent, plots and grids were undisturbed through the duration of the study.

### ***General Field Methods:***

In the first season of my study, I experimentally released butterflies in 16x16m plots to test for effects of two landscape factors: habitat contrast and drainage slope. In the second year, I observed naturally occurring butterflies in grids roughly four times larger to test one landscape factor – stream proximity - and several local factors relating to habitat characteristics. My experiences from the first season guided my methodology for the second season in two ways. First, the 2003 season illuminated logistical and theoretical constraints involved with catch-and-release studies. By observing only undisturbed butterflies in 2004, I was able to collect much more data on butterflies that were exhibiting natural behaviors. Second, by recognizing the need to test movement over spatial scales that are objective with respect to the determinants being examined, I set up 7 grids in 2004 based on the habitat features I was testing.



### ***Drainage Slope and Boundary Contrast: Methods for Experimental Releases***

During May through August of 2003, I experimentally released wild-caught butterflies to investigate the influence of topography and the boundary contrast between riparian and forest habitats on butterfly movement. I first established release plots at twelve locations on two different stream drainages that were approximately three miles apart. I created 16x16m plots that immediately abutted riparian vegetation (Figure 1). Adjacent plots on a given drainage were separated by >100m if they were on opposite sides of a stream or >400m if they were on the same side. I demarcated these plots with PVC poles and I measured topographic relief in degrees, for each of the plots, by taking an average of three clinometer readings. With slopes ranging between two and eighteen degrees, the plots characterized a wide range of the streamside topographic variation found on Fort Bragg. In addition to topographic variation, the plots differed in contrast between riparian and forest vegetation. High contrast plots were located immediately adjacent to streams in upland forest that had been burned within two months of the study. Intermediate contrast plots were located in unburned upland forest, and low contrast plots were located in bottomland forest along streams. Compared to the pine forest, riparian boundaries were characterized by an abrupt transition to dense briar and shrubs with a prominent herbaceous understory.

Butterflies were caught in areas where they occurred in abundance away from release plots, measured for wingspan using calipers, uniquely marked (Ehrlich & Davidson 1960), transported to an experimental plot, and released in the center of a plot within one hour of being caught (similar releases are described by Conradt et al. 2000). Butterflies that appeared injured from handling were recorded, but these data were not

used in analyses. Upon release, individual butterflies were visually followed until the time they exited the plot. The cooperation of multiple observers was needed to keep track of released butterflies because they were all inconspicuously colored and generally flew below the height of understory vegetation. Standing outside the plots at different locations, observers monitored butterfly movement and recorded two components of behavior. First, the side of the plot ultimately exited by the butterfly indicated a movement direction that was recorded as being toward, along, or away from the stream corridor (Figure 1). Second, the cumulative time a butterfly spent strictly flying, in seconds, was calculated from stopwatch measurements of flights and periods of rest between the time of release and the time the plot was first exited. I released at least four individuals of each species in each experimental plot. Approximately 50 butterflies of each species were released throughout the season.

### ***Analyses of Drainage Slope and Boundary Contrast***

I used several different analyses to investigate behavioral patterns of released butterflies. First, I compared regression models using an Information-Theoretic approach (Burnham and Anderson, 2002) to determine the relative importance of topography and boundary contrast for each species. I fit five different regression models to compare the behaviors of each species with the following variables: a null model, topography only, the level of boundary contrast only, both of these factors, and, as the full model, both of these factors plus their interactions (Table 1). All models except for the null model included site as block, as these studies were replicated on different streams. Flight direction and flight duration were modeled using LOGISTIC and MIXED procedures, respectively (SAS v. 8.2). Akaike Information Criterion (AIC) values were compared to

determine the best fitting model for each species. As it is relatively complicated to interpret the influence of parameters from logistic regression models with more than two responses, I illustrated the influence of these parameters with subsequent chi-square tests or simple regressions against specific components of movement. To illustrate directional responses to drainage slope, I tested whether the proportion of butterflies moving toward or along a stream varied significantly with the slope. To more closely examine directional responses to boundary contrast, I calculated six chi-square statistics for each species. The first three of these calculations tested whether direction was random within each of the three contrast levels using expected probabilities for movements toward, along, and away from the stream of 0.25, 0.5, and 0.25, respectively. The remaining set of three calculations tested whether movement patterns differed among contrast levels. The expected movement probability for these tests was calculated by averaging the probabilities of movement for a given direction observed across each of the three boundary levels. All of these chi-square statistics were compared to a critical value of 5.99 with 2 degrees of freedom. Finally, I conducted a simple regression of the average flight duration for each species against the average topographic relief for each release site.

### ***Stream Proximity and Local Habitat Characteristics:***

#### ***Methods for Observational Studies***

During May through August of 2004, I observed naturally occurring butterflies to investigate their behaviors as they moved, *in situ*, through ecotonal habitat. I first established seven plots in four different drainages where species cohabitated in abundances great enough to make passive observations practical. Locations on a given

drainage were separated by a distance of >200m. At each site, I demarcated grids by erecting 10ft PVC poles at a 6x6m resolution (Figure 2). The overall perimeter of these grids varied slightly by location for the following reason. I established the first row of a grid by placing poles either at the stream's edge or far enough into the riparian corridor so that the addition of another row would not capture an obvious change in the local riparian vegetation. I then placed rows of poles at six-meter intervals away from the stream corridor and into the forest until the forest vegetation became homogenous. Thus, the grids established at each site encompassed a gradient of vegetative structure and composition that spanned an area from the forest, through the ecotonal boundary, and into the riparian corridor. Dimensions of these grids ranged between 30x30m and 36x42m, and individual cells were uniquely numbered. Flexible grid size allowed me to demarcate grids at different sites more objectively with respect to the local habitat gradient but, as grids differed by 12 meters at most, this flexibility did not represent a difference between landscape and local spatial scales.

With the aid of several technicians, I observed butterflies at these locations throughout the summer. Cell-by-cell movements of individual butterflies within grids were monitored according to the following protocol. Immediately upon detecting a flying butterfly, an observer would record the grid-cell location of that butterfly and begin a timer. When the butterfly moved into a new cell, both the new location and the time of transition between cells were recorded. In this fashion, individual butterflies were followed from the time they were first seen to the time they either flew out of the grid or were lost from sight. Thus, a recorded sequence of movements for each butterfly included a series of grid-cell locations, directions from those locations, and the amount of time it

spent at each location, regardless of whether that time was spent flying or resting (see Figure 2). Working cooperatively, two observers began surveys at separate poles along a grid's edge. After completing a 15 minute survey, each observer proceeded to the next pole in line. Moving parallel with each other, researchers thus walked through the grid once between poles, while stopping to record data for 15 minutes at each pole. The total time spent surveying a grid, therefore, ranged between 60 and 90 minutes, depending on the size of the grid. All observers exercised caution in avoiding excessive trampling of the vegetation while walking between poles.

Several potential sampling biases were mitigated by additional protocols. First, butterflies that were “flushed” as we walked between poles were not recorded. Our observations were thereby restricted to natural behaviors. Second, the two observers cooperated to avoid repetitive observations of an individual butterfly. Observers also ended observations at a particular pole once they could no longer reasonably distinguish whether nearby individuals were previously recorded. Third, surveys of any grid were separated by a period of several days so that the natural migration and mortality of animals would provide a more randomized pool of sampled individuals. Fourth, to mitigate the potential bias of “herding” butterflies in a particular direction, transects through grids were initiated at alternating edges.

### ***Quantifying Local Habitat Characteristics***

I sampled each grid to determine local features that might affect movement behavior. To obtain an estimate of both the plant community structure I visually surveyed every cell within a grid for the following attributes: percent cover of broadleaf plants, percent cover of cane, percent cover of all other graminoid plants, and the proportion of

bare ground. The first two of these attributes were further broken down into height classes of greater or less than one meter tall. As host plants for my study species generally include wetland grasses and sedges, these measurements of cane and graminoid cover provided a rough estimate of potential host plant abundance. I also measured how deep (in cm) I could push a 2” diameter soil probe into the soil at the center of every cell before hearing or feeling the grainy resistance of an underlying mineral horizon. Hydroperiodicity is an important determinant of wetland plant communities on Ft. Bragg (*Tom Wentworth, personal communication*). As such, my “depth-to-resistance” measure of organic accumulation was intended to be a rough surrogate to capture possible changes in plant species composition.

Pooling data from each grid, I conducted an ordination of all grid cells (n=372) using a non-metric multidimensional scaling (NMS) procedure in PCORD. I used a Sorensen distance measure and randomized seeds to iterate 15 model runs using real data. Once ordinated, I then clustered the cells into three categories. Each cluster was labeled as most closely exhibiting riparian, ecotone, or forest habitat characteristics. This metric provides an objective measure of each cell’s vegetative structure that is independent of its position within a grid. Along with direct values of certain characteristics, these cellular ordination labels (henceforth referred to as ORD values) were used in the parameterization of comparative statistical models.

### ***Analyses of Stream Proximity and Local Habitat Characteristics***

Movement paths of butterflies observed flying through the grids were analyzed at a cell-by-cell resolution (n=1645). These data were refined into three distinct response variables: DIRECTION, FIDELITY, and DURATION. DIRECTION describes where a

butterfly flew upon exiting a cell, with respect to the stream orientation. This response includes three levels corresponding to movements toward, along, and away from the stream. Butterflies that exited a cell diagonally (10.2% of all movements) were randomly assigned a direction toward or along, or away or along, depending on the diagonal direction. FIDELITY is a binary response describing whether a movement from a cell continued in the same direction as the movement through the previous cell. This simple metric is similar to a correlated random walk analysis, in that it provides an expression of movement that is independent from the direction of movement (Karieva and Shigesada, 1983). DURATION measures the length of time, in seconds, spent in a cell. These three responses were analyzed separately using SAS version 8.2. Regression models for the first two responses were analyzed using Proc LOGISTIC. FLYTIME, a continuous response, was modeled using Proc MIXED.

Six independent variables were used to parameterize the regression models. These variables include the grid identifier (SITE, as a block), three local determinants, and one landscape determinant. The first of the local variables, ORD, is defined as the difference in ordination values (see classification methods) between the cells for given movement. The other local variables, CANE and GRAM, define differences in cane (>1m) cover and graminoid cover, respectively, between the two cells the butterfly traveled. These local variables were chosen for their biological significance and lack of correlation. The single landscape-level parameter included in models, PROXIMITY, defines the grid row relative to distance from the stream in which a movement was initiated. This simple metric considers the influence that overall proximity to the stream corridor has on

movement. I verified the independence of these model variables in a correlation analyses (SAS v.8.2).

A suite of seventeen regression models were fit to each response, including variations with local variables only, landscape variables only, and combinations of both (Table 2). The global model includes, all of the local parameters, the landscape parameter, and all local-landscape interactions. All models included site as a block. These models were compared using Akaike Information Criterion (AIC) values to determine the relative influence these respective parameters have on model fit. For each species, a ‘best-fit’ model was selected as the one with the fewest parameters while maintaining a difference of less than two from the minimum AIC value (Burnham and Anderson 2002). I also compared AIC values from these ‘best-fit’ models with AIC values produced by a null model that fits a y-intercept to mean data without the aid of external parameters. This comparison allowed me to test whether parameters that showed some relative importance had any influence on responses. Finally, I selected several parameters for closer comparison from those that were included in the best-fit models for multiple species. I illustrated the influence of these parameters with subsequent chi-square tests or simple regressions against the specific component of movement for which they were important model constituents.

## **RESULTS**

### ***Relative Influence of Local and Landscape Determinants***

Results of my combined studies revealed that both landscape and local features influence butterfly movement. In particular, the experimental release study showed that, across species, boundary contrast is a more important determinant of both flight direction



and duration than drainage slope (Table 1). The study of naturally occurring butterflies showed that both stream proximity and habitat characteristics affect movement. In particular, movement direction was unanimously determined by stream proximity and habitat characteristics combined (Table 2), movement fidelity was variably determined by stream proximity and/or habitat characteristics (Table 3), and flight duration was predominantly determined by habitat characteristics alone (Table 4).

### ***Effect of Drainage Slope on Flight Direction and Duration***

In 2003, I recorded the movements of approximately 150 experimentally released butterflies. For all species, slope-only models for direction and duration models were not selected among the better-fitting models. The full model, including drainage slope, was selected as the best-fit duration model for Appalachian browns. In this unique case, regression analyses indicate that slope was not a significant variable in the model, however it did provide a significant interaction with boundary contrast ( $p=0.0115$ ). Regression analyses subsequently confirmed that drainage slope alone does not induce movement toward streams (Carolina satyrs  $R^2 = 0.070$ , Appalachian browns  $R^2 = 0.369$ , pearly-eyes  $R^2 = 0.011$ ; Figure 3) and that flight duration was also unrelated to drainage slope (Carolina satyrs  $R^2 = 0.032$ , Appalachian browns  $R^2 = 0.106$ , pearly-eyes  $R^2 = 0.026$ ).

### ***Effect of Boundary Contrast on Flight Direction and Duration***

Model comparisons for flight direction indicated that boundary contrast is a significant predictor of direction for most species (Table 1). Species-specific biases are more clearly illustrated by the following chi-square results. Over all contrast levels, both Carolina satyrs (41%) and Appalachian browns (45%) moved toward the stream more

often than would be predicted by random direction (25%), however significant variability in direction for both of these species was seen at high contrast levels only ( $X^2_{2df}=13.23$ ,  $p=0.001$  and  $X^2_{2df}=7.38$ ,  $p=0.025$ , Figure 4). Also, both Carolina satyrs and Appalachian browns moved along streams most frequently when boundary contrast was low. Pearly-eye movements, conversely, did not vary significantly between or within any level of contrast (Figure 4). Model comparisons show that boundary contrast outperformed slope in predicting flight duration for all species. Butterflies exited the plot most rapidly at intermediate levels of boundary contrast (Figure 5).

### ***Effect of Stream Proximity on Direction, Fidelity, and Duration***

In 2004, approximately 500 individual movement paths were recorded through passive observation. In general, butterflies were present in greater abundances within ecotonal habitat at an intermediate distance from the stream; approximately seventy percent of all movement paths observed were initiated at a distance of 12-30 meters from the stream. Carolina satyr, little wood satyr, and Appalachian browns diminished toward either stream or forest (Figure 6). Pearly-eyes similarly diminished at the streams edge but remained abundant into the forest (Figure 6).

The best direction model for each species included both habitat variables and stream proximity, however directions with respect to stream orientation were not consistent across species. Carolina satyrs and little wood satyrs exhibited random movements with respect to stream orientation, Appalachian browns showed an along-stream bias, and pearly-eyes showed a toward-stream bias (Figure 7).

The proportion of correlated movements within movement paths generally increased as the distance from streams at which paths were initiated increased (Carolina

satyrs  $R^2 = 0.952$ , little wood satyrs  $R^2 = 0.189$ , Appalachian browns  $R^2 = 0.457$ , pearly-eyes  $R^2 = 0.477$ ; Figure 8). In other words, movements at the stream's edge were generally more sinuous than movements in the forest. Proximity was not correlated with flight duration for any species.

### ***Effect of and Local Habitat Characteristics on Direction, Fidelity, and Duration***

The best direction models for all species included some habitat variables, suggesting that local vegetation affects movement decisions (Table 2). Model comparisons for movement fidelity showed that specific habitat characteristics vary in their relative importance and predictive value between species. Responses to the overall vegetative gradient offer an example of this variability: little-wood satyrs and pearly-eyes both exhibited a small increase (~5%) in correlated movements when they traveled along vegetation gradients while Carolina satyrs and Appalachian browns, conversely, exhibited a similar decrease (~5%) in correlated movements if they traveled along gradients. In addition, Appalachian browns and pearly-eyes exhibited an increase in correlated movements if they were moving into areas with greater cover of potential host plants (Appalachian browns  $R^2 = 0.312$ ; Figure 9, pearly-eyes  $R^2 = 0.668$ ; Figure 10). Model comparisons show that the local vegetation gradient was included among good fitting models for all species. (Table 4). Carolina satyrs, little wood satyrs, and Appalachian browns moved slightly faster if they were flying away from stream-structured vegetation while pearly-eyes moved slightly faster if they were flying away from forest-structured vegetation (Figure 11).

## DISCUSSION

This study showed that both landscape and local features influence butterfly movement and that related species vary in how they are influenced by these features (Table 5). At a landscape level, all species responded to the proximity of a stream corridor and showed a higher affinity to fly toward streams when boundaries had higher contrast. Carolina Satyrs and Appalachian browns, furthermore, flew parallel to boundaries most frequently when the boundary contrast was low. No species responded to drainage slope. Although subtle topographic mechanisms have been shown to explain differences in upland butterfly behaviors and assemblages (Peterson 1997, Weiss and Weiss 1998), it appears that topography does not directly influence the behavior of these bottomland butterflies. Indirectly, topography may influence movement by affecting the structure of habitat boundaries. At a local level, all species were influenced by vegetation structure but the response varied by species, with habitat specialists showing the strongest responses to host plant cover. Below I will discuss several specific results in the context of a general understanding of both local and landscape influences on movement, two limitations to this study and some potential applications of this work.

Responses to landscape features were not determined by the size of the organism. Having shorter wing margins and smaller wing areas, smaller butterflies are generally less vagile and therefore may perceive and react to shared environments on smaller spatial scales than larger species (Van Dyke & Matthysen, 1999). Based on size alone, Carolina satyrs and little-wood satyrs should consequently illustrate weaker responses to landscape features than the two larger species, as they were measured across equivalent

spatial scales. Contrary to this prediction, model comparisons showed that the smaller species were equally sensitive to landscape features as the larger species, indicating that differences in responses are likely not due to size.

Responses to landscape features can be explained by edge-related resource distribution, a phenomena that commonly affects behaviors at habitat transitions (Fagan et al. 1999). Except for pearly-eyes, all butterflies were more frequently observed traveling through the riparian ecotone, at an intermediate distance from the stream, than in either the stream or forest habitats. The dynamics of my study system include forests that are regularly burned and streams that are regularly flooded. Ecotonal habitat, being wet enough to resist burning and elevated enough to evade flooding, may offer a refuge for facultative wetland host plants on which these butterflies depend. As all butterflies generally illustrated greater probabilities of correlated travel if a transition was made to an area with more graminoid cover, random movements initiated towards or along a lush ecotone would be more likely to continue in the same direction. Conversely, movements directed away from the ecotone would degrade to a more random path, thereby increasing the probability that a butterfly would return to the ecotone habitat.

The habitat-specific movement rates of released butterflies corroborate this explanation of the spatial concentration of naturally occurring butterflies by confirming butterfly affinity for ecotone habitat. All butterflies exited release plots slower in ecotone habitat which, supporting a denser suite of tall shrubs than the forest, offers shade and potential shelter from predators. Butterflies also exited plots in burned forest habitat slower than unburned forest habitat, but the slower exits seen in burned habitats may have been attributable to disorientation; butterflies released in burned habitat would stop

frequently and often fly in roundabout paths. Exits out of plots in ecotone and upland habitat were generally more direct, and may therefore reflect more comparable differences in flight speed. As butterflies may increase movement rates to escape through hostile habitat (Shultz 1998), this bias to move slowly through ecotone habitat suggests that butterflies prefer it. In addition to directing movement, therefore, it is plausible that butterflies benefit from increased survival when dispersing through ecotone habitats.

In addition to explaining common patterns, resource distribution may also explain why species differed in their responses to landscape features. Carolina satyrs and Appalachian browns tended to move parallel to streams only at the low boundary contrast. Behavioral mechanisms in boundary-sensitive arthropods have more frequently been demonstrated to affect dispersal patterns by reflecting movements parallel to hard edges (Ries and Debinski 2001, Berggren et al 2002), however these studies monitored animals that were released in suitable habitat. The low-contrast bias I observed in released butterflies is consistent with the ecotone bias I observed in naturally occurring butterflies, considering that low-contrast release habitat was basically a riparian ecotone. While explaining butterfly affinity for riparian habitat, the concentration of host plants along streams also provides an impetus for an along-stream dispersal strategy for some species, which is supported, for example, by the behavioral biases of Appalachian browns.

The unique deviation of both naturally occurring and released pearly-eyes to both strongly bias movements perpendicular to the stream (Figures 4.3 & 7.4) and to initiate more movements at greater distances from the stream (Figure 6.4) reasonably links their behavior with a resource-distribution hypotheses. At rest, pearly-eyes are frequently

observed camouflaged against leaf litter or on the trunks of pine trees. As strong, large-bodied fliers, they frequently rise to treetop level and traverse distances >30m in fast bursts (personal observation). Pearly-eye host plants grow along streams, at outcroppings of underwater springs throughout the pine savannah, and in low areas between streams that are occasionally inundated with water. This scattered distribution of resources provides an impetus for a between-drainage dispersal strategy, for which pearly-eyes appear to be phenotypically and behaviorally adapted.

Responses to local features can largely be explained by habitat specificity. The two habitat specialists generally showed stronger responses to local features, akin to other satyrine specialists that have been shown to orient toward sites with abundant host-specific sedges and grasses (Bergman 1999, Brommer and Fred 1999, Shuey 1997). Modeling comparisons show that Appalachian browns retained graminoid change as an important variable in best fitting models for fidelity whereas pearly-eyes retained only the cane variable (Table 3). Although the cane-only model did not fit better than the null model for pearly eyes, the lack of model fit is likely a result of insufficient data for pearly-eyes across all rows. Indeed, the movement fidelity of Appalachian browns and pearly-eyes was positively correlated with graminoid and cane cover, respectively (Figures 9&10). Appalachian browns and pearly-eyes also showed the strongest responses in flight duration across the overall vegetative gradient (Figure 11). Although responses to local features were generally more variable and relatively weak compared with responses to landscape features, the behaviors exhibited by specialist species confirm that the spatial distribution of larval food resources within a given habitat may influence butterfly movement patterns.

If manipulated butterflies released in a unfamiliar environment are likely to either exhibit escape behavior or return directly to preferred habitat, the behaviors of butterflies I released may not have exhibited normal searching strategies (such as those discussed by Conradt 2001, 2003). Their behaviors, rather, may be indicative of how butterflies perceived the relative hostility of release habitat compared to the adjacent stream. As all butterflies were handled and released according to rigid protocol, however, relative comparisons of their responses to the boundary contrast remain valid. Moreover, the consistent behaviors seen in both low contrast release plots and observational grids validate the comparison of data collected using the two techniques. The release study may have benefited from an increased sample size, as the lack of predictive value indicated by model comparisons for the direction of released butterflies may be attributable to an inadequate number of butterflies released at each site (n=4).

A second limitation to my study is that I measured landscape determinants at a scale smaller than that characterizing landscape scale displacement between species. However, behavioral studies such as those by Haddad (1999), Merckx et al. (2003), and Schitzelle and Baguette (2003) clearly illustrate that movement propensities defined on smaller scales have a good deal of explanatory power as surrogates for physical displacement across a landscape. Results from these studies validly suggest that the distribution of all of my study species may be affected by multi-scale changes to their habitat.

The behavioral responses to both local and landscape features I observed can dictate the spatial structure of populations by affecting movement rules associated with dispersal. Behaviors that restrict emigration across habitat boundaries, thereby limiting



dispersal, might produce a more spatially fragmented arrangement of populations across a landscape whereas behaviors that promote emigration across habitat boundaries might produce a spatially homogeneous arrangement of populations across a landscape. This idea that behaviors can induce population structure is supported by a comparison between Appalachian brown and pearly-eye distribution. Appalachian browns, which show an aversion to move away from riparian ecotones, are restricted to specific streamside habitats at Ft. Bragg and occupy a relatively limited range in the southeastern states. Pearly eyes, which also occupy streamside habitats but are less behaviorally restricted by ecotone boundaries, are relatively common throughout habitats in the southeastern states.

Furthermore, in spatially fragmented populations, landscape factors that effect dispersal can have a large effect on population dynamics (Zollner and Lima 2005, Ovaskainen 2004, Schtickzelle and Baguette 2003, Schultz and Crone 2001). However the mechanisms underlying the landscape's effect on dispersal often involve specific local movement behaviors. For example, the potential for corridors to enhance dispersal can be determined by behavioral responses to habitat boundaries (Haddad 1999), and the potential for stepping-stones to enhance dispersal can be determined by habitat specific movement patterns (Shultz 1998). By examining the efficacy of riparian habitat to act as a dispersal corridor in the context of this study, I have highlighted how subtle behavioral responses to natural variation in local and landscape elements might impact butterfly distributions on a larger scale.

The linkage between individual behavior and population structure is becoming an increasingly influential topic in applied ecology, particularly with respect to the management of threatened species (Schultz 1998, Morales and Ellner 2002, Revilla et al.

2004). Applications of this study provide a direct example of how behavioral studies can inform management decisions for a population of concern. The endangered Saint Francis satyr (*Neonympha mitchellii francisci*) is a small satyrine specialist that exists in a metapopulation structure on Ft. Bragg (Hall et al. 2001) and generally shares both phenotypic similarities and bottomland associations with those investigated in this study (Scott 1986). Conservation efforts for this Saint Francis satyr, such as habitat modification or restoration, or the enhancement of dispersal corridors, could benefit from a better understanding of how the Saint Francis satyr reacts to landscape and local features. However, direct experiments with this rare species may ultimately be detrimental and are subsequently prohibited. The behaviors of my study species may therefore be useful in predicting how the management of local and landscape features will impact Saint Francis satyr butterflies. For example, this study illuminated behavioral mechanisms whereby ecotone habitat may facilitate stream-wise dispersal in Appalachian browns. Assuming that Saint Francis satyrs will exhibit similar behaviors, the management of more lush riparian boundaries by restricting stream flows or appropriately adjusting prescribed burns along streams may serve to promote Saint Francis satyr dispersal along riparian corridors. Furthermore, if the acquisition of specific data is deemed critical, the non-intrusive methods tested in my study of naturally occurring butterflies have demonstrated that spatially explicit behavioral data can be collected with minimal impact to sensitive habitat and little disturbance of the focal organism.

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Table 1. Model Comparison for released butterflies. This table shows the AIC values, by species, generated by fitting a suite of models to direction and duration responses. Best fitting models are those that produce the lowest AIC values. For each species and response, the best models are highlighted, along with any that differ by <2.

Released: DIRECTION		AIC Values by Species		
Model	Parameters Tested	CS	BROWN	PE
1	All ( <i>Full model</i> )	109.9	112.9	117.7
2	All - Interactions	114.4	111.2	116.8
3	Boundary Contrast only	112.7	109.2	114.7
4	Slope Only	112.4	107.5	119.0
5	Intercept ( <i>Null model</i> )	110.2	104.2	116.1

Released: DURATION		AIC Values by Species		
Model	Parameters Tested	CS	BROWN	PE
1	All ( <i>Full model</i> )	97.1	101.0	57.9
2	All - Interactions	95.7	107.4	54.4
3	Boundary Contrast only	94.0	108.3	52.3
4	Slope Only	94.1	110.3	63.7
5	Intercept ( <i>Null model</i> )	91.3	109.4	60.8



Table 2. Model Comparison for naturally occurring butterflies. This table shows the AIC values, by species, generated by fitting a suite of models to direction responses. Best fitting models are those that produce the lowest AIC values. For each species and response, the best models are highlighted, along with any that differ by <2.

Model	Nat. Observed: DIRECTION Parameters Tested	AIC Values by Species			
		CS	LWS	BROWN	PE
1	All, with interactions ( <i>full model</i> )	731.5	177.0	225.9	323.3
2	Full - Habitat Interactions	731.2	173.9	225.6	325.3
3	Full - Proximity Interactions	732.9	175.5	238.1	329.5
4	Full - All interactions	733.3	171.9	236.9	326.8
5	Proximity, Gram, Cane	751.8	192.1	224.6	336.1
6	Proximity, Ord, Cane	753.2	177.3	234.5	323.0
7	Proximity, Ord, Gram	728.4	172.8	235.6	333.9
8	Proximity	792.4	203.6	251.1	358.6
9	Ord, Gram, Cane	731.5	177.4	236.1	331.2
10	Site ( <i>Model Block</i> )	790.7	204.2	249.4	360.4
11	Cane, Proximity	786.5	197.1	233.9	341.4
12	Cane	782.8	196.7	242.4	346.2
13	Gram, Proximity	761.0	190.1	234.2	343.2
14	Gram, Proximity	760.3	190.9	234.7	342.2
15	Ord, Proximity	749.9	175.4	241.8	333.4
16	Ord	749.3	176.5	238.1	333.7
17	Intercept ( <i>Null Model</i> )	784.1	195.1	239.3	350.3

Table 3. Model comparison for naturally occurring butterflies. This table shows the AIC values, by species, generated by fitting a suite of models to fidelity responses. Best fitting models are those that produce the lowest AIC values. For each species and response, the best models are highlighted, along with any that differ by  $<2$ .

Nat. Observed: FIDELITY		AIC Values by Species			
Model	Parameters Tested	CS	LWS	BROWN	PE
1	All, with interactions ( <i>full model</i> )	420.0	112.3	149.0	206.5
2	Full - Habitat Interactions	417.3	110.8	157.5	208.9
3	Full - Proximity Interactions	420.9	118.2	148.0	202.1
4	Full - All interactions	419.5	118.3	156.3	203.7
5	Proximity, Gram, Cane	420.7	119.5	157.5	205.9
6	Proximity, Ord, Cane	417.6	107.6	157.7	202.3
7	Proximity, Ord, Gram	414.2	107.2	148.1	208.8
8	Proximity	421.4	119.1	160.7	213.9
9	Ord, Gram, Cane	421.5	116.2	162.7	200.9
10	Site ( <i>Model Block</i> )	423.0	117.2	172.1	212.3
11	Cane, Proximity	418.1	116.6	158.7	203.0
12	Cane	417.3	113.6	171.7	199.6
13	Gram, Proximity	417.0	116.2	158.4	204.4
14	Gram, Proximity	417.2	112.5	168.2	201.3
15	Ord, Proximity	411.6	105.5	158.3	204.5
16	Ord	416.5	113.4	167.3	201.0
17	Intercept ( <i>Null Model</i> )	429.4	106.9	162.5	197.3

Table 4. Model Comparison for naturally occurring butterflies. This table shows the AIC values, by species, generated by fitting a suite of models to duration responses. Best fitting models are those that produce the lowest AIC values. For each species and response, the best models are highlighted, along with any that differ by <2.

Nat. Observed: DURATION		AIC Values by Species			
Model	Parameters Tested	CS	LWS	BROWN	PE
1	All, with interactions ( <i>full model</i> )	906.2	253.4	318.6	417.2
2	Full - Habitat Interactions	902.8	249.4	320.0	420.1
3	Full - Proximity Interactions	904.1	248.1	313.7	415.3
4	Full - All interactions	900.1	244.2	315.4	415.6
5	Proximity, Gram, Cane	902.9	245.5	325.0	416.4
6	Proximity, Ord, Cane	902.5	247.4	317.3	413.6
7	Proximity, Ord, Gram	901.1	249.5	318.5	419.2
8	Proximity	904.3	244.8	327.0	420.4
9	Ord, Gram, Cane	902.2	246.2	312.1	416.7
10	Site ( <i>Model Block</i> )	902.7	243.3	325.3	420.5
11	Cane, Proximity	900.3	241.6	324.6	414.1
12	Cane	896.6	238.3	321.3	413.7
13	Gram, Proximity	899.4	243.6	322.6	413.4
14	Gram, Proximity	896.4	239.8	320.2	412.8
15	Ord, Proximity	897.5	243.7	316.7	415.3
16	Ord	895.9	239.9	314.0	413.8
17	Intercept ( <i>Null Model</i> )	906.9	241.8	322.1	418.1

Table 5. Summary of species information and responses to tested variables.

<b>Species</b>	<b>Carolina Satyr</b>	<b>Little wood Satyr</b>	<b>Appalachian Brown</b>	<b>Pearly-Eye</b>	<b>Shared Responses</b>
<b>Larval Host Plants</b>	Wetland Grasses and Sedges	Wetland Grasses and Sedges	Wetland Sedges (genus <i>Carex</i> )	Cane (genus <i>Arundinaria</i> )	---
<b>Relative Size</b>	Small	Small	Large	Large	---
<b>Distribution</b>	Common in S.E. & Ft. Bragg Bottomlands	Common in S.E. & Ft. Bragg Bottomlands	Rare in SE; Common in Carex-rich Ft. Bragg Wetlands	Common in S.E. & Ft. Bragg Bottomlands and Canebreaks	---
<b>Drainage Slope</b>	None	N/A	None	None	No response to slope.
<b>Boundary Contrast</b>	Moves toward stream at high contrast	N/A	Moves toward stream at high contrast	No Bias	Flew fastest at int. Contrast (in unburned upland forest).
<b>Stream Proximity</b>	No Bias (random direction)	Moves along streams	Moves along streams	Moves toward streams	Abundance is greatest at 12-30m. Movements more random at stream edge.
<b>Habitat Gradient</b>	Less correlated along gradient	More correlated along gradient.	Less correlated along gradient.	More correlated along gradient	No Shared Responses
<b>Host Plant Abundance</b>	See Shared Responses	See Shared Responses	See Shared responses	More correlated if toward cane	More correlated if toward greater gram

Figure 1. Design of Experimental Release Plots. The riparian boundary was clearly distinguished by an abrupt transition to lush vegetation. The dotted line represents the path of butterfly released in the center of the plot. Directions were recorded as toward, along, or away from the stream, as indicated here.

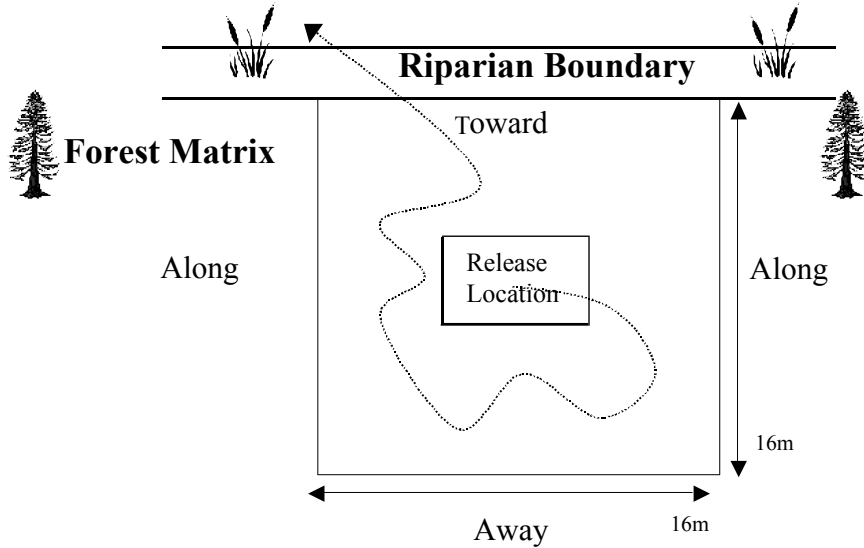


Figure 2. Design of Butterfly Observation Grids. Grids were demarcated with PVC poles, and spanned an area that included stream, ecotone, and forest habitat. The dotted line represents a movement path through uniquely identified cells.

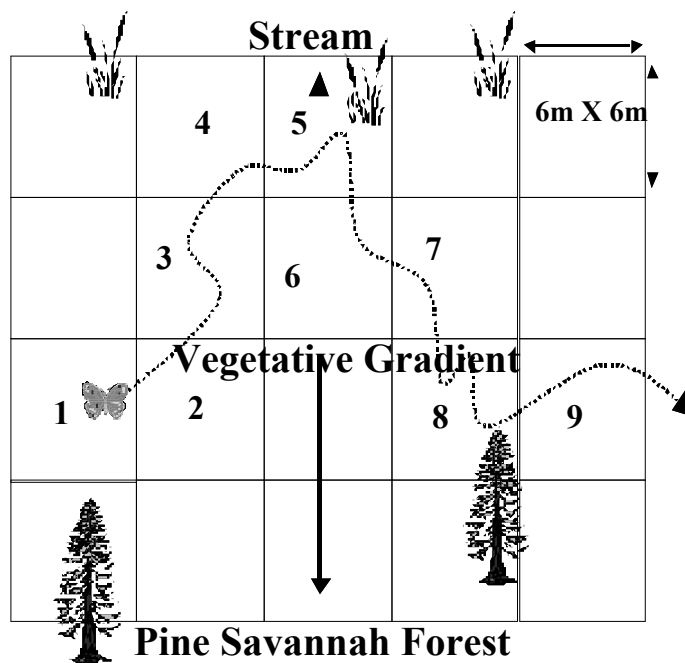


Figure 3. Topographic Relief. The proportion of each species' movement toward the riparian boundary when released along drainages that ranged from 'Flat' (avg. slope of 1%) to 'Steep' (avg. slope of 15%).

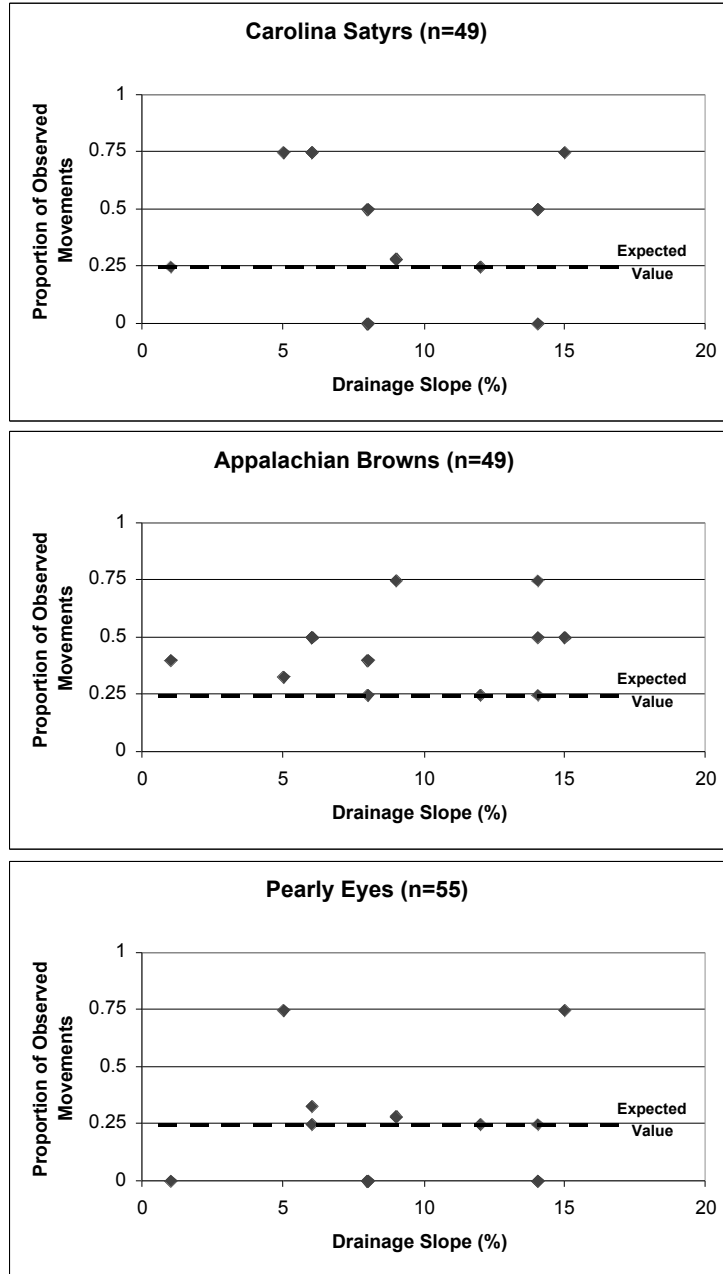


Figure 4. Boundary Contrast. The proportion of each species' movement directions with respect to the riparian boundary when released in forests with different levels of contrast. The '\*' and '+' symbols indicate p-values of <0.05 and <0.1, respectively, for chi-square analyses with 2 d.f. On legend labels, these p-values reflect differences for a given boundary treatment as compared to random (expected) movement. On x-axis labels, these p-values reflect comparisons between boundary treatments.

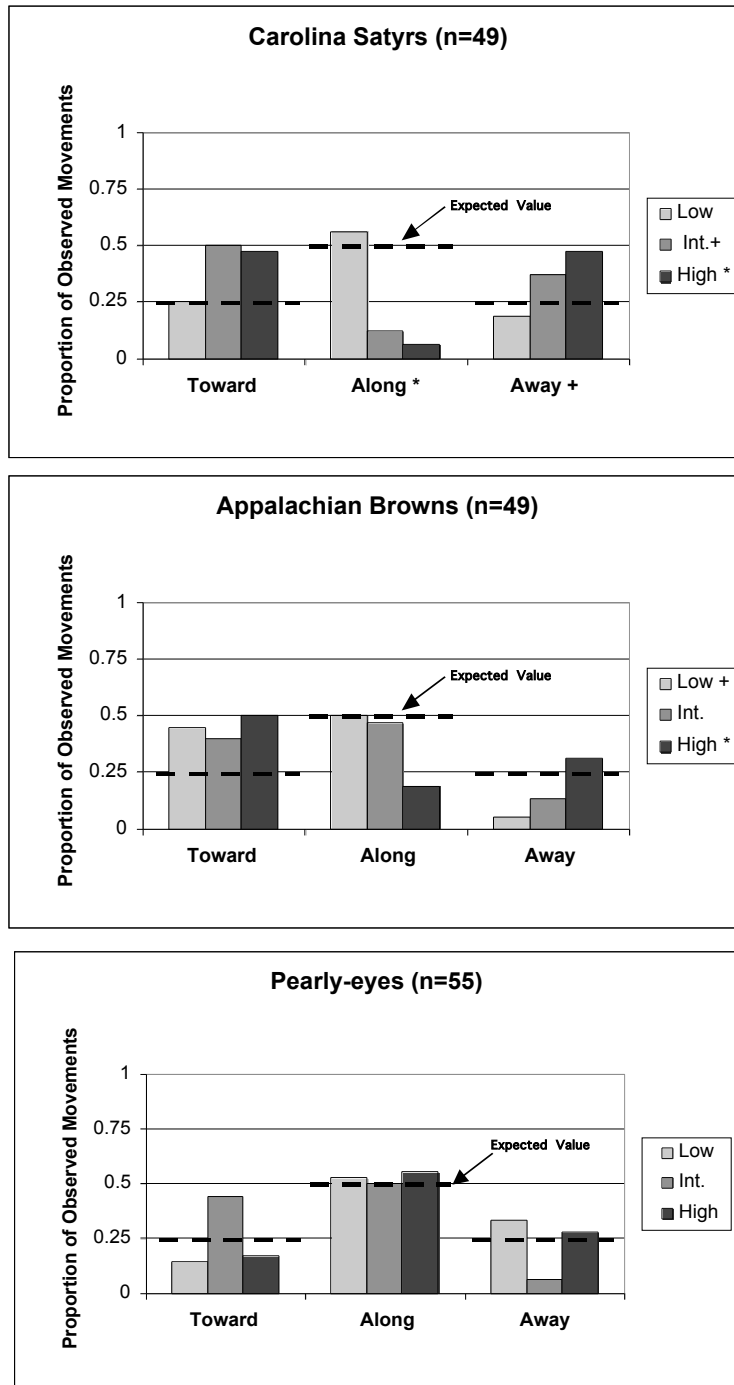


Figure 5. Boundary Contrast. The bars show the average time a released butterfly spent flying before it exited a plot. Low contrast plots are situated in bottomland forest, intermediate plots in upland forest, and high contrast plots in freshly burned upland forest. Error bars show the standard error associated with average times.

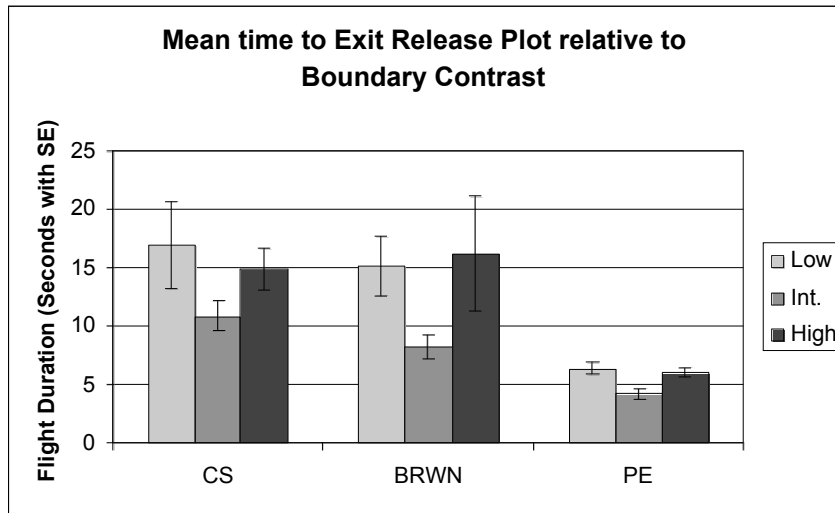
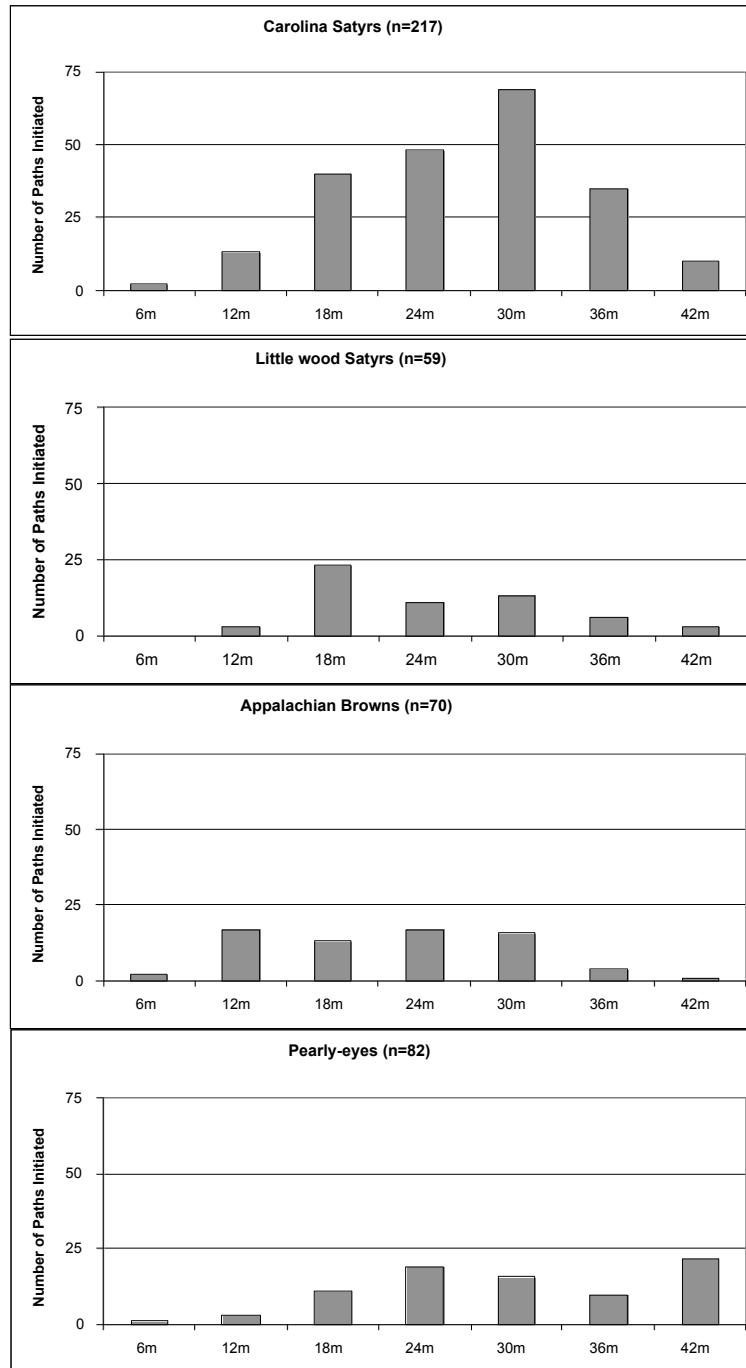




Figure 6. Abundance of movement relative to stream proximity. The graphs below illustrate the number of movement paths initiated in a given row (at 6m intervals away from the stream). Data were truncated to include the minimum number of rows shared by all sites.



Stream → Forest

Figure 7. Stream Proximity. The following graphs illustrate proportions of butterfly movements in a given direction, at six-meter increments away from the riparian core.

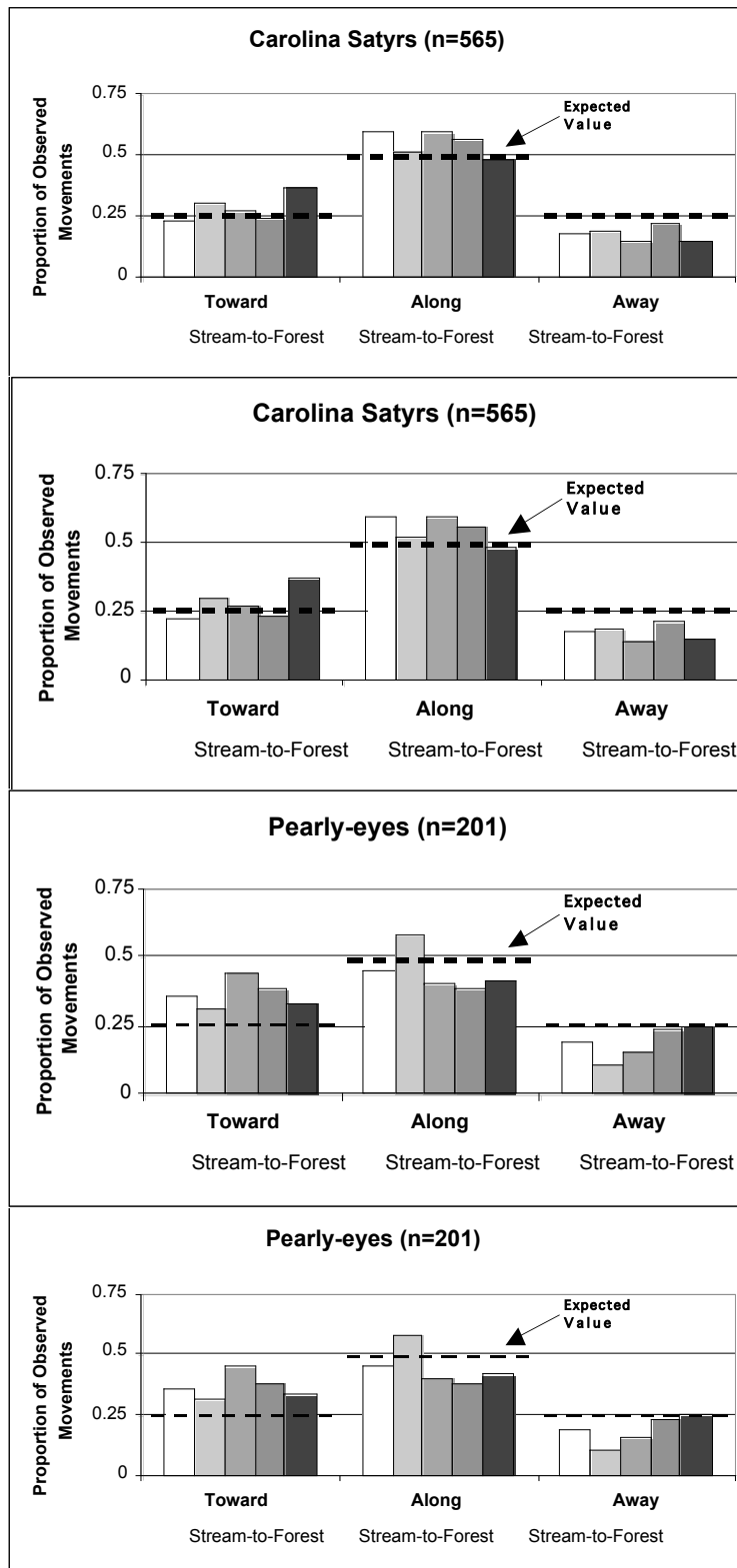


Figure 8. Stream Proximity. Points on a different lines show the proportion of auto-correlated movements exhibited by each species at intervals from the stream edge.

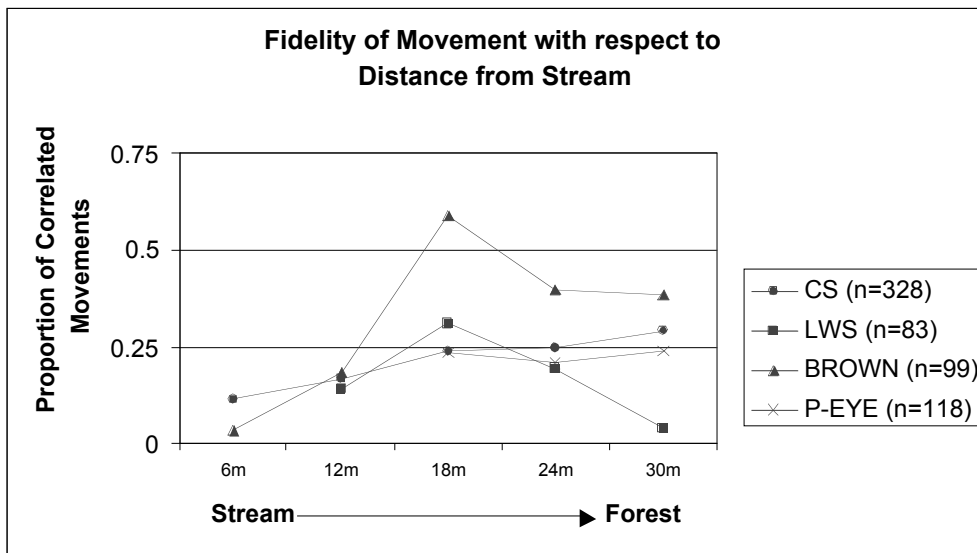


Figure 9. Host Plant Cover. Points on the line show the proportion of auto-correlated movements of appalachian browns associated with categorical increases in graminoid cover.

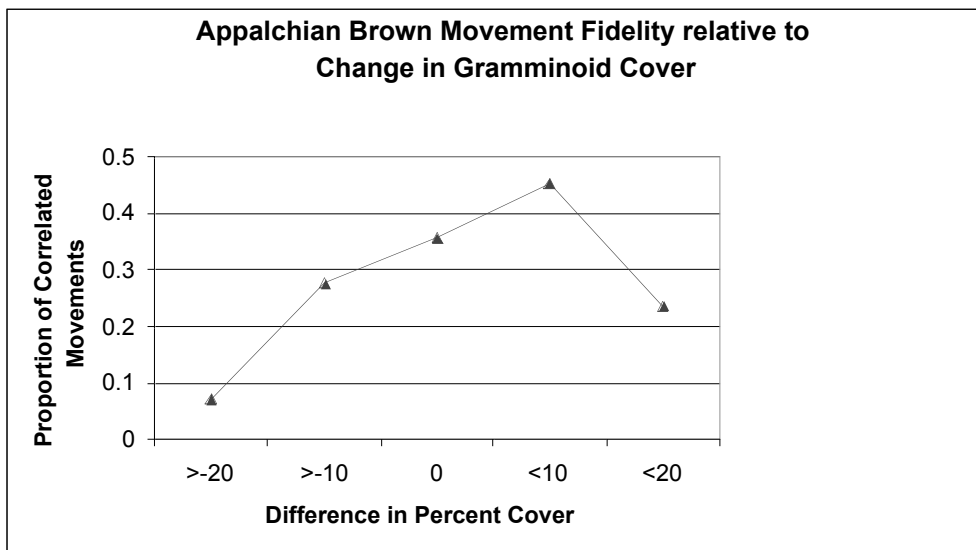


Figure 10. Host Plant Cover. Points on the line show the proportion of auto-correlated movements of pearly-eyes associated with categorical increases in cane cover.

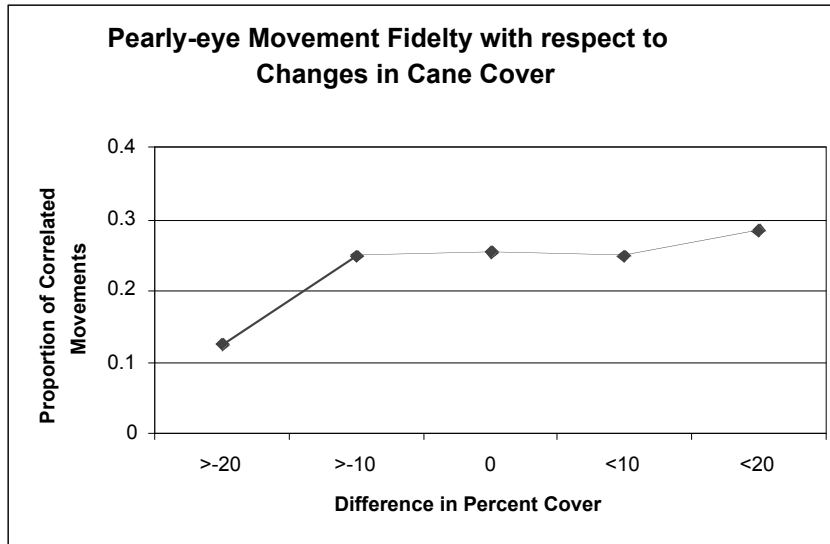


Figure 11. Vegetation Gradient. Bars show the average amount of time a species took to complete a given move, associated with categorical changes in the vegetative gradient. A movement to stream-like vegetation is defined as a movement into a cell with a lower ordination value, a movement to forest-like vegetation is defined as a movement into a cell with a higher ordination value. Movements exhibiting no change are movements into cells with the same ordination value.

