# Local versus landscape determinants of butterfly movement behaviors

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Large-scale patterns of animal distributions and abundances may be determined by mechanisms that act at local or landscape scales. We studied the movement behaviors of four species of bottomland butterflies in a natural setting to examine the determinants of movement behavior across different scales. We tested the relative importance of three landscape attributes: drainage slope, boundary type, and stream proximity, and local habitat attributes related to food plants and plants that influence habitat structure. Across species, we tested the relative importance of organism size and habitat specificity to explain response variation. In general, butterfly responses to landscape features were more universal than responses to local features. Specifically, results from this study showed that drainage slope did not influence movement behaviors but boundary type, stream proximity, and host plant abundance all influenced movement patterns. Responses to local features varied by species and often complemented landscape effects on movement. Responses to all features were not related to butterfly size, but did vary in accordance with butterfly host plant specificity. These behaviors help to explain landscape-level variation in population distribution among species.

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Animal movement impacts the spatial arrangement of populations, with implications for population persistence (Levins 1969, Hanski et al. 1995, Gutierrez et al. 1999), species interactions (Huffaker 1958, Fagan et al. 1999, Case et al. 2005), and rates of evolution (Baker 1978, Leimer et al. 2003). Though the importance of dispersal is well established, the need remains to understand what factors influence dispersal across complex landscapes. One possible approach to understanding the mechanisms behind large-scale dispersal is through observations of local behaviors (Conradt and Roper 2006). Lima and Zollner (1996) suggest that patterns of behavior that remain common across local and landscape scales may explain dispersal, and ultimately the dynamics and spatial distribution of populations (Levey et al. 2005). Local-scale determinants of movement are attributes that define the composition or structure of an individual habitat. Landscape-scale determinants are gross physical attributes that define the arrangement of and relationships between individual habitats. Here, we apply the term "landscape" to address patterns of variability in habitat and geography rather than a spatial scale. Using these definitions, we investigated 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 over relatively small scales. In these cases, changes in both 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 natural landscapes; boundaries between

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habitats exist as ecotonal gradients rather than clear and functional barriers. In real landscapes and using continuous delineations of habitat it becomes feasible to separate proximate determinants of movement at different scales. Animals within these landscapes often are regarded to make decisions based on local habitat characteristics (Jonsen et al. 2001, Matter et al. 2004) and landscape position (Ellner and Fussman 2003, Fagan et al. 2003).

One landscape factor that has been shown to influence dispersal of upland butterflies is topography; aggregation on hilltops, for example, is common (Alcock 1985, Henning 1990, Pinheiro 1990, Rutowski 1991, Pe'er et al. 2006). The high incidence of upland butterflies orienting uphill urges the question of whether bottomland butterflies orient downhill (Neve et al. 1996). No studies address the directionality of movement in wetland species with respect to landscape slope.

A second landscape factor that may influence butterfly dispersal 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 the landscapes in which the streams are situated (Jonsen and Taylor 2000). In our study system, riparian habitats may function as dispersal corridors through the landscape. Therefore, we examined whether proximity to streams affects the movement behaviors of butterflies.

Habitat boundaries provide 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 and Bondrup-Nielsen 1999), and arthropods (Berggren et al. 2002). For arthropods, physical aspects of boundaries, such as increased foliar density or height, may impede transitions between habitats (Fry and Robson 1994). Inhibitory behaviors (e.g. "edge avoidance") may also constrain emigration in edge-sensitive animals (Shultz 1998, Haddad 1999, Merckx et al. 2003). In this study, we examined how different boundary types affect movement by testing whether butterflies released in different forest habitats directed movements toward adjacent riparian habitats.

We also examined relationships between butterfly behaviors and several local, site-specific characteristics of habitat. A few studies that focused on the relationships between movement and local characteristics have shown that physical characteristics of non-habitat, such as canopy cover and plant composition, can affect the dispersal propensities of butterflies between habitats (Roland et al. 2000, Ricketts 2001, Leimer et al. 2003). Further, the spatial arrangement of specific host and nectar plants can constrain movements (Brommer and Fred 1999). Very little research on movement, however, addresses habitats as they commonly exist in nature: gradients of structural 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. We address this question by comparing butterfly movements through vegetative gradients between habitats.

We 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, we expected that steeper drainages would illicit faster and more directed movement toward streams. With respect to boundary type, we expected that butterflies would travel faster and orient more movements toward riparian habitat when the boundary with the surrounding forest was more distinct. Furthermore, we expected that butterflies would tend to orient along stream corridors and that this response would become stronger closer to streams. Finally, with respect to local habitat characteristics, we expected that butterflies would orient toward areas of equal or higher host plant abundance.

To assess the generality of our results, we also tested whether local and landscape factors evoked similar behavioral responses across a range of different species in a single butterfly subfamily. Specifically, we addressed the question of whether physical size or habitat specificity affected butterfly responses. Having shorter wing margins and smaller wing areas, smaller butterflies are generally less vagile and therefore may perceive and react to environments on smaller spatial scales than larger species (Van Dyke and Matthysen 1999). Butterfly specialists can be sensitive to the spatial arrangement of local resources (Brommer and Fred 1999). Hence, we expected that two smaller, generalist species would show weaker responses to both local and landscape determinates than two larger, specialist species.

## Methods

### Study species

We studied four butterfly species in the subfamily Satyrinae that primarily inhabit wooded bottomlands and wetland glades along streams: *Hermeuptychia sosybius* (Carolina satyrs), *Satyroides appalachia* (appalachian browns), *Enodia portlandia* (southern pearly-eyes), and *Megisto cymela* (little-wood satyrs). Although these butterflies co-occur, their specific habitat requirements differ. Larval host plants for *H. sosybius* and *M. cymela* include a variety of wetland grasses, whereas *S. appalachia* larvae feed on wetland sedges, notably *Carex stricta*, and *E. portlandia* larvae predominantly feed on cane, *Arundinaria* spp. (Glassberg 1999). These four

species also differ considerably in size; *H. sosybius* and *M. cymela* have approximately twenty percent shorter wingspans than *E. portlandia* and *S. appalachia* (Kuefler unpubl.). These butterflies make ideal test animals for behavioral studies, as they are abundant and easily monitored. Adult satyrine butterflies do not usually feed on flowering plants, so their vegetation requirements are simple (Scott 1986). As such, we could restrict analyses of movement responses to vegetation to abundances of larval food plants.

## Study site

We conducted our studies at Fort Bragg, North Carolina, USA between May and August in 2003 and 2004. This 65 000-ha military base is dominated by long-leaf pine savannah ecosystem. Dendritic streams traverse forested areas and are bordered by riparian forest in low areas. We chose release plots and observational grids along these riparian tracts where satyrine butterflies were abundant. While these sites were selected because of their specific landscape characteristics, they are representative of the natural variation that exists in this system.

## General field methods

In the first field season, we experimentally released butterflies to test for effects of two landscape factors: boundary type and drainage slope. In the second field season, guided by results in the first year, we observed naturally occurring butterflies to test one landscape factor, stream proximity, and several local factors relating to habitat characteristics. We discuss experimental releases and observational studies in turn.

## Drainage slope and boundary type: methods for experimental releases

From May through August of 2003, we released wild-caught butterflies to investigate the influence of topography and the type of boundary between three different forest habitats and adjacent riparian habitats on butterfly movement. We first established release plots at twelve locations on two different stream drainages that were ca 5 km apart. We created 16 × 16 m plots that immediately abutted riparian vegetation (Fig. 1A). Adjacent plots on a given drainage were separated by >100 m if they were on opposites sides of a stream or >400 m if they were on the same side. We demarcated these plots with PVC poles and measured topographic relief for each of the plots by taking an average of three clinometer readings. With slopes ranging between 2 and 18 degrees, the plots characterized a wide range of the topographic variation
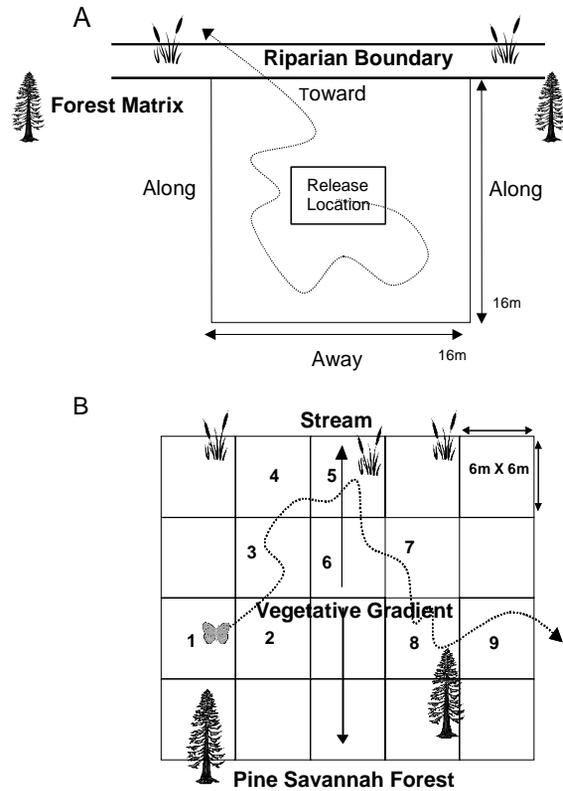


Fig. 1. Design of A) Experimental release plots in which the riparian boundary was clearly distinguished by an abrupt transition to lush vegetation, and B) Butterfly observation grids that were demarcated with PVC poles, and spanned an area that included stream, ecotone, and forest habitat. The dotted line in each panel represents a butterfly's movement path.

found at our site. In addition to topographic variation, the plots encompassed different boundary types, chosen to reflect different levels of contrast between riparian and forest habitats. Four plots were located immediately adjacent to streams in upland forest that had been burned within two months of the study (high contrast), four plots were located in unburned upland forest along streams (intermediate contrast), and four plots were located in unburned bottomland forest along streams (low contrast). Compared to the forest, riparian boundaries were characterized by a transition to dense briar and shrubs with a prominent herbaceous understory. The strong differences in these habitat types created strong differences in habitat boundaries between plots. For example, burned forest plots contrasted starkly with the riparian habitat, whereas bottomland forest plots did not.

Butterflies were caught in areas away from release plots, transported to an experimental plot, and released in the center of a plot within one hour of capture (similar release protocols are described by Conradt et al. 2000). Upon release, individual butterflies were visually followed until they exited plots. Standing outside the plots

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at different locations, observers monitored butterfly movement and recorded two components of behavior, "direction" and "duration". "Direction" was recorded as the side of the plot ultimately exited by the butterfly relative to orientation of the stream corridor (toward, along, or away from the stream; Fig. 1A). "Duration" was recorded as the cumulative time a butterfly spent flying between the time of release and the time the plot was first exited. We released at least four individuals of each species in each experimental plot.

## Analyses of drainage slope and boundary type

We compared statistical models using an information-theoretic approach to determine the relative importance of drainage slope and boundary type for each species. We fit five models to compare the behaviors of each species with the following variables: a null model, slope only, the type of boundary only, both of these factors, and, as the full model, both of these factors plus their interaction. All models except for the null model included site as a block. For each species, the best model was selected as the one with lowest Akaike information criteria (AIC) value (Burnham and Anderson 2002). Flight direction and duration were modeled using LOGISTIC and MIXED procedures, respectively (SAS v. 8.2). We note that logistic regression can be used in analyses of more than two levels of response (Angresti 2002) and was applied here to test for differences among treatments. In addition, for each species, we conducted chi-square analyses of movement directions pooled across all treatments to test for departures from random movement directions, regardless of treatment.

## Stream proximity and local habitat characteristics: methods for observational studies

During May through August of 2004, we observed behaviors of naturally occurring butterflies at seven locations on three different drainages. Locations on a given drainage were separated by a distance of >200 m. At each site, we demarcated grids by erecting 3.3 m PVC poles at a 6 ×6 m resolution (Fig. 1B). We established the first row of a grid either at the stream's edge or far enough into the riparian corridor so that the addition of another row would not capture any change in riparian vegetation. We then placed rows of poles at 6 m intervals away from the stream corridor and into the forest until the forest vegetation became homogeneous. Grid dimensions ranged between 30 ×30 and 36 ×42 m.

With the aid of several technicians, we 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 recorded the grid-cell location of that butterfly and started 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. Movement paths for each butterfly included a series of grid-cell locations, directions from those locations relative to the stream corridor (i.e. toward, along, or away), and the amount of time it spent at each location (Fig. 1B). Two observers simultaneously began surveys at separate poles along a grid's edge. After completing a 15 min survey at one pole, each observer proceeded to the next pole in line. Moving parallel with each other, researchers walked through the grid once.

Several potential sampling biases were mitigated by additional protocols. Butterflies that began moving as we walked between poles were not recorded. Our observations were thereby restricted to natural behaviors. The two observers cooperated to avoid repetitive observations of an individual butterfly. Observations ended at a particular pole once observers could no longer distinguish whether nearby individuals were previously recorded. We did not survey sites on consecutive days, so that the natural migration and mortality of animals would reduce the likelihood of re-sampling the same individual. Finally, to mitigate the potential bias of "herding" butterflies in a particular direction, transects through grids were initiated at alternating edges.

## Quantifying local habitat characteristics

We sampled each grid to determine local features that might affect movement behavior. To obtain an estimate of vegetation structure, we visually surveyed every cell within a grid for the following attributes: percent cover of broadleaf plants, percent cover of cane, and percent cover of all other graminoid plants. As host plants for our study species generally include wetland grasses and sedges, measurements of cane and graminoid cover provided a rough estimate of potential host plant abundance.

## Analyses of stream proximity and local habitat characteristics

Unlike in our experimental releases, we were interested in the responses of butterflies in habitats that varied continuously across our plots, determined at the level of an individual cell. Thus, no single measure of an entire butterfly path could characterize the responses to variation encountered by individuals, and we used movement data from each cell as our response variable. We do not believe there are problems with independence

in our data: 1) because of the small size of our plots, 85% of all observations were 2–4 cells (since two cells were needed to quantify a movement response, this means 1–3 observations/butterfly), 2) the observations were spread nearly uniformly across 7 different sites, and 3) behaviors quantified at the level of entire paths in the release study were consistent with the results in this one. 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 stream orientation. Butterflies that exited a cell diagonally (10.2% of all movements) were randomly assigned to one of the two directions that make up the exit corner (Fig. 1B). "Fidelity" is a binary response describing whether a movement from a cell continued in the same direction as the movement through the previous cell (i.e. whether a movement was autocorrelated). This simple metric corresponds to a correlated random walk analysis, in that it provides an expression of movement that is independent of movement direction (Karieva and Shigesada 1983). "duration" measures the length of time spent in a cell, and was log transformed prior to analysis. Regression models for "direction" and "fidelity" were analyzed using Proc LOGISTIC. "Duration", a continuous response, was modeled using Proc MIXED. All analyses were conducted using SAS v. 8.2.

Six independent variables were used to parameterize the regression models. These variables include the grid identifier ("site", as a block), three local variables, and one landscape variable. The local variables, "broadleaf", "cane", and "gram", define differences in broadleaf plant cover ( >1 m), cane cover ( >1 m) and graminoid cover, respectively, between the two cells the butterfly traveled. These local parameters are included in the models categorically, as decreasing, increasing, or unchanging cover between movements. The single landscape-level parameter, "proximity", defines the grid row

relative to distance from the stream in which a movement was initiated. We verified the independence of all model variables in a correlation analysis.

Suites of sixteen regression models were fit to each response, including models with local variables only, stream proximity only, and combinations of both (Table 2). The global model included all of the local parameters, the landscape parameter, and all local-landscape interactions. As with the released butterflies, models with the lowest AIC values were used to compare movement responses between treatments. We also conducted additional chi-square analyses of movement directions, pooled across all treatments, to test departure from random movement directions regardless of other variables.

## Results

### Effect of drainage slope on flight direction and duration

In 2003, we recorded the movements of 204 experimentally released butterflies. These included 65 movement paths for *S. appalachia*, 67 for *H. sosybius*, and 72 for *E. portlandia*. Slope-only models were never selected among the best-fitting models for any aspect of movement (Table 1). Also, the best-fit models for movement directions of *S. appalachia* and *E. portlandia* did not include slope. The full model, including slope, best described movement direction of *H. sosybius*. In this unique case, slope alone did not explain a significant deviation in movement from random. Rather, slope significantly interacted with a high boundary contrast, whereby *H. sosybius* were more likely to move toward streams. Flight duration of *H. sosybius* and *E. portlandia* was not affected by slope. For *S. appalachia*, the

Table 1. Model comparison for released butterflies. AIC values, by species, were generated by fitting a suite of models to each response. Best fitting models are those that produce the lowest AIC values. For each species and response, the best models are in bold face.

| Released: direction | | AIC values by species | | |
| --- | --- | --- | --- | --- |
| Model | Parameters tested | *H. sosybius* | *S. appalachia* | *E. portlandia* |
| 1 | Null (intercepts only) | 110.2 | **104.2** | 116.1 |
| 2 | Full with interactions | **109.9** | 112.9 | 117.7 |
| 3 | Full without interactions | 114.4 | 111.2 | 116.8 |
| 4 | Boundary type only | 112.7 | 109.2 | **114.7** |
| 5 | Slope only | 112.4 | 107.5 | 119.0 |
| Released: duration | | AIC values by species | | |
| Model | Parameters tested | *H. sosybius* | *S. appalachia* | *E. portlandia* |
| 1 | Null (intercepts only) | **91.3** | 109.4 | 60.8 |
| 2 | Full with interactions | 97.1 | **101.0** | 57.9 |
| 3 | Full without interactions | 95.7 | 107.4 | 54.4 |
| 4 | Boundary type only | 94.0 | 108.3 | **52.3** |
| 5 | Slope only | 94.1 | 110.3 | 63.7 |

interaction was significant, as flight duration increased with slope at high contrast sites.

## Effect of boundary type on flight direction and duration

Boundary type consistently explained movement direction of both *H. sosybius* and *E. portlandia* in best-fit models (Table 1). *Hermeuptychia sosybius* biased movements toward the stream in all habitats ($\chi^2_{2df} = 12.9$, n = 67, p = 0.002) and this bias was pronounced in burned forests (Fig. 2A). *Enodia portlandia* did not show a directional bias in general. Rather, *E. portlandia* tended to move toward streams only in unburned upland forests (Fig. 2B). Boundary type did not affect movement directions of *S. appalachia* (Fig. 2C). However, *S. appalachia* biased movements toward streams in all habitats ($\chi^2_{2d} = 16.2$, n = 65, p < 0.001). Flight duration for *H. sosybius* was unaffected by boundary type.

Boundary type affected flight duration for both *S. appalachia* and *E. portlandia*, as both of these species exited the plot most rapidly in unburned upland forest (Fig. 3). In all habitats, *E. portlandia* tended to exit the plot more quickly than the other two species. This response is likely due to physical rather than behavioral differences, as *E. portlandia* are larger and stronger fliers than the other species (Kuefler unpubl.).

## Effect of stream proximity on direction, fidelity, and duration

In 2004, the movement paths of 451 individuals were recorded through observation of naturally occurring butterflies. These included 143 movement steps of *S. appalachia*, 434 of *H. sosybius*, 114 of *M. cymela*, and 188 of *E. portlandia*. In general, butterflies were present in greater abundances within ecotonal habitat at an intermediate distance from the stream; ca 70% of all movement paths observed were initiated at a distance of 12–30 m from the stream. In particular, <6% of all movements by *H. sosybius*, *M. cymela,* and *S. appalachia* occurred either within 6 m of the stream or >36 m from the stream. In contrast, movements by *E. portlandia* similarly diminished at the streams edge but remained evenly distributed into the forest; 28% of all *E. portlandia* movements occurred >36 m from the stream.

Stream proximity affected movement direction of *E. portlandia*, which biased movement toward streams ($\chi^2_{2df} = 19.4$, n = 188, p < 0.001) and showed an increased bias toward streams at greater distances from streams (Fig. 4). *Satyroides appalachia* showed a trend to bias movement along streams at all distances from the stream ($\chi^2_{2df} = 5.15$, n = 143, p = 0.08). However, *S. appalachia* movements were not affected by stream proximity (Fig. 4). Also, stream proximity affected the movement fidelity of *H. sosybius* and *S. appalachia*. Movements of
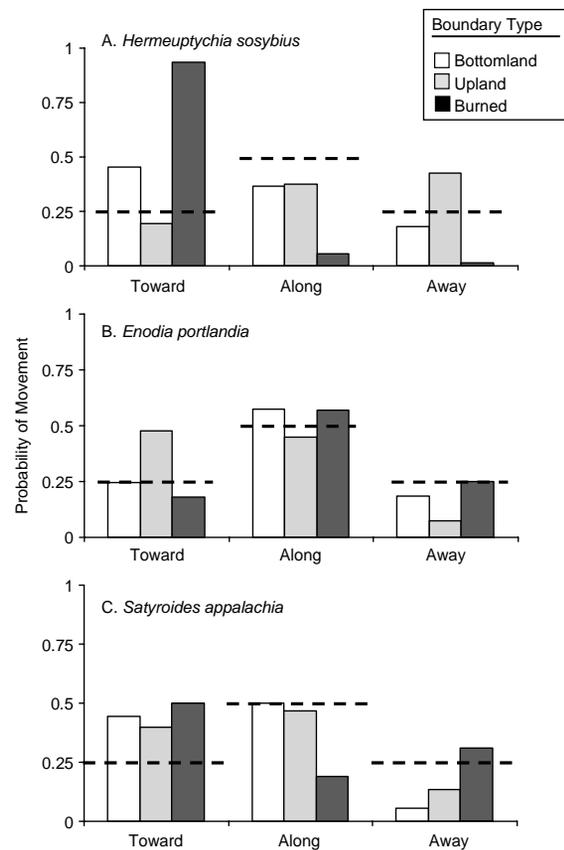
Fig. 2. Predicted probabilities of movement with respect to the riparian corridor. Movements of *H. sosybius* and *E. portlandia* vary significantly depending on whether they were released in low contrast, intermediate contrast, or high contrast forest habitats adjacent to the riparian corridor. Dashed lines show movement probabilities if butterflies selected movement directions at random.
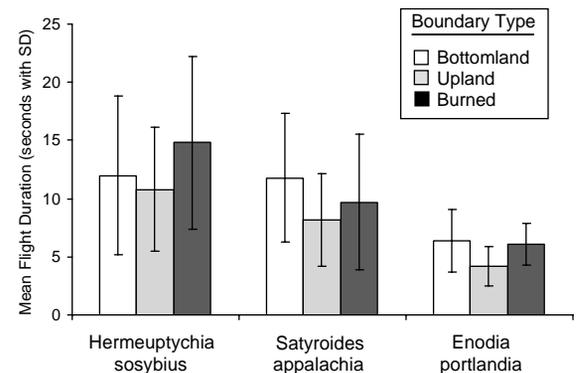
Fig. 3. Average times released butterflies spent flying before exiting a plot. Low contrast plots are situated in bottomland forest, intermediate plots in upland forest, and high contrast plots in freshly burned upland forest. Error bars show the standard deviation associated with average movement durations.
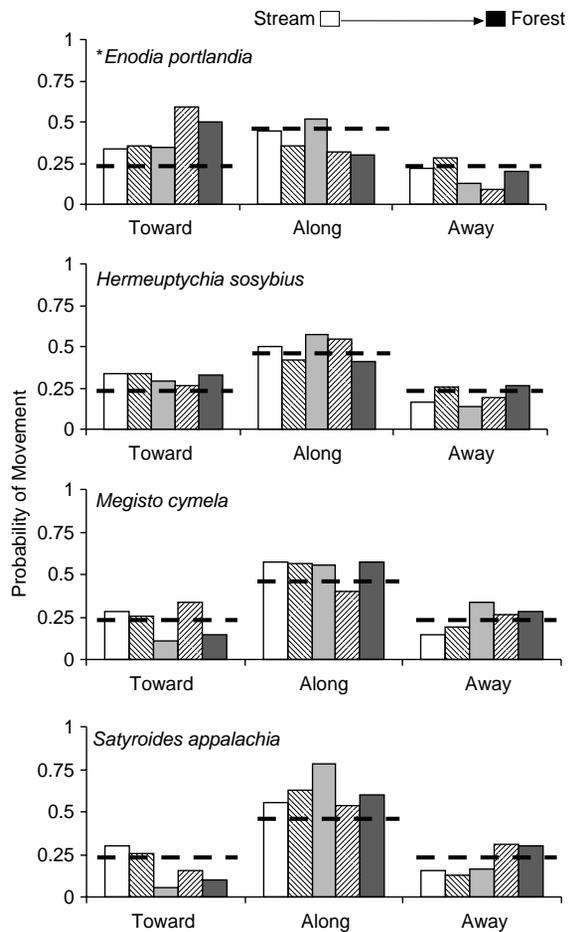
Fig. 4. Predicted probabilities of movement toward, along, and away from streams derived from logistic regression models. Each bar represents a 6 m increase in distance from the stream. Dotted lines show the distribution of movements one would expect if butterflies selected movement directions at random. An asterisk indicates that stream proximity was a significant parameter affecting movement direction for that species.

*H. sosybius* and *S. appalachia* at the stream's edge were generally more sinuous than movements in the forest (Fig. 5). Proximity was not correlated with flight duration for any species (Table 2).

### Effect of local habitat characteristics on direction, fidelity, and duration

Movement direction of all species was sensitive to changes in graminoid cover, however responses differed by species (Table 2, Fig. 6). *Hermeuptychia sosybius* and *E. portlandia* showed an increased bias toward streams as they moved into areas with higher graminoid cover. Conversely, *S. appalachia* and *M. cymela* showed an increased bias along streams as they moved into areas with higher graminoid cover. In addition, *S. appalachia*

and *M. cymela* tended to move away from streams as graminoid cover decreased. Movement fidelity of the habitat generalists was not affected by local characteristics. In contrast, the two specialists, *S. appalachia* and *E. portlandia*, exhibited an increase in correlated movements if they were moving into areas with greater cover of their potential host plants. Finally, the abundance of broadleaf plants affected the flight duration of *E. portlandia*, which tended to move more quickly as it flew toward areas with increasing broadleaf cover. The flight duration of all other species was unaffected by local habitat characteristics.

### Discussion

This study showed that both landscape and local features influence local butterfly movement and that related species vary in how they are influenced by these features (Table 3). These results suggest that studies on dispersal in fragmented landscapes should consider the effects of habitat variability at local and landscape scales. At a landscape level, all species responded to the presence of a stream corridor. Specifically, they all showed a greater affinity to fly toward streams when adjacent habitats had a greater degree of contrast. *Hermeuptychia sosybius* and *S. appalachia* flew parallel to streams most frequently in unburned bottomland forest that contrasted weakly with the riparian habitat. Furthermore, biases in baseline movement show that *S. appalachia* tend to move towards stream more often than would be predicted by random movement, regardless of topography or boundary type (Fig. 2). These two species flew quickly toward streams and, once reaching a stream, they flew slowly parallel to it. 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. At a local level, all species were influenced by graminoid abundance but the response varied by species, with habitat specialists showing the strongest responses to host plant cover. Responses to landscape features were not determined by butterfly size, as we had predicted. Based on size alone, we predicted that *H. sosybius* and *M. cymela* would show weaker responses to landscape features than the two larger species. Contrary to this prediction, model comparisons showed that the smaller species were equally sensitive to landscape features.

Consistent with studies of other animals (Fagan et al. 1999), this study shows how butterfly responses to landscape features can be explained by edge-related resource distributions. Except for *E. portlandia*, all butterflies were more frequently observed traveling
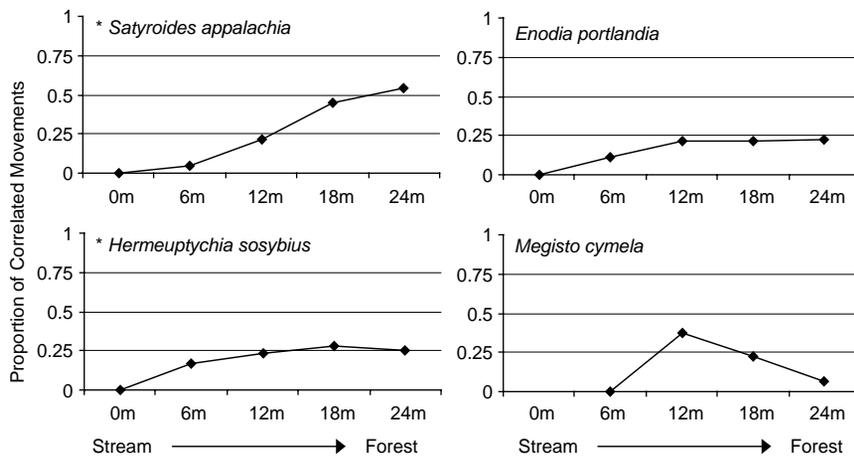
Fig. 5. Proportion of all movement events that resulted in a straight-line movement through a cell. These proportions are based on categorical distances from the stream, in 6 m intervals. An asterisk indicates that stream proximity was a significant parameter affecting this measure of movement auto-correlation, as described in the text as "movement fidelity".

through the riparian ecotone than in either the streamside or forest habitats. Our study system includes forests that are regularly burned and streams that are regularly flooded. Ecotonal habitat, being wet enough to resist burning and elevated enough to avoid flooding, may offer a perennial refuge for the wetland host plants on which these butterflies depend. The absolute abundance of graminoids increases closer to the stream yet the change in graminoid cover between movements (our model parameter) was not correlated with stream proximity. While movements of *S. appalachia*, *E. portlandia*, and *H. sosybius* were all more sinuous closer to the stream, movements of *S. appalachia* were more correlated when they moved into areas of higher graminoid abundance. Therefore, *S. appalachia* movements initiated toward or along a *Carex*-rich ecotone were more likely to continue in the same direction. Movements from the ecotone directed either toward the stream or toward the *Carex*-depapaurate forest degraded into less auto-correlated movements, increasing the probability that *S. appalachia* would return to the ecotone, where movements were directed parallel to the stream.

The habitat-specific movement rates of released butterflies support the affinity of naturally occurring butterflies for ecotone habitat. All butterflies exited release plots less quickly in unburned bottomland forests that is structurally similar to ecotone habitat. These habitats, supporting a denser suite of tall shrubs than the upland forest, offer shade and potential shelter from predators. Shaded habitat edges, for example, promote higher egg survival in other Satyrine species (Bergman 1999). Butterflies also exited plots in burned, upland forest habitat slower than in unburned forest habitat, but this may have been attributable to disorientation; butterflies released in burned habitat would stop frequently and often fly in roundabout paths. Flight from plots in unburned 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 (Schultz 1998), this bias to move slowly through bottomland habitat suggests that butterflies prefer it. Our regression models for naturally occurring butterflies were unable to distinguish significant biases in movement rates, probably because the habitat was similar to preferred habitat for these butterflies.

In addition to explaining common patterns, resource distribution may also explain why species differed in their responses to landscape features. *Hermeuptychia sosybius* and *S. appalachia* tended to move parallel to streams only in bottomland forest habitat. Behavioral responses of arthropods to boundaries have typically been demonstrated to affect dispersal patterns by reflecting movements through suitable habitat parallel to edges (Ries and Debinski 2001, Berggren et al. 2002). When we released butterflies in bottomland forest habitat, their movements along the stream's edge were consistent with those of naturally occurring butterflies in similar habitat. Dispersal along preferred habitat near streams may ensure butterflies remain near high concentrations of host plants, as supported by the behavioral biases of *S. appalachia*.

The unique behavior of naturally occurring *E. portlandia* to move perpendicular to the stream (Fig. 2) and to initiate more movements at greater distances from the stream may also be explained by resource distributions. At rest, *E. portlandia* are frequently observed camouflaged against leaf litter or on the trunks of pine trees. As strong, large-bodied fliers, they frequently rise to the canopy and traverse distances >30 m in fast bursts (unpubl.). In contrast to *S. appalachia*, *E. portlandia* 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. Speculatively, this scattered distribution of resources may favor a between-drainage dispersal strategy, for which *E. portlandia* appear to be morphologically and behaviorally adapted.

Table 2a-b-c. Model comparisons for observational study. AIC values, by species, were generated by fitting a suite of models to each response. Best fitting models are those that produce the lowest AIC values. For each species and response, the best models are in bold face.

| (a) Observational: direction | | AIC values by species | | | |
|---|---|---|---|---|---|
| Model | Parameters tested | H. sosybius | M. cymela | S. appalachia | E. portlandia |
| 1 | Null (intercepts only) | 587.7 | 145.0 | 195.0 | 270.9 |
| 2 | Full, with interactions | 583.9 | 139.3 | 191.5 | 262.0 |
| 3 | Full, no habitat interactions | 574.9 | 132.9 | 188.1 | 254.2 |
| 4 | Full, no proximity interactions | 589.2 | 134.0 | 193.8 | 258.5 |
| 5 | Full, no interactions | 585.6 | **131.3** | 185.5 | **253.9** |
| 6 | Proximity, gram, cane | 579.6 | 146.4 | 189.0 | 275.5 |
| 7 | Proximity, broad, cane | 604.6 | 145.7 | 192.2 | 266.7 |
| 8 | Proximity, broad, gram | **574.6** | 139.1 | 194.2 | 260.5 |
| 9 | Proximity | 594.5 | 147.4 | 195.4 | 276.4 |
| 10 | Broad, gram, cane | 587.4 | 132.1 | 192.3 | 267.7 |
| 11 | Cane, proximity | 599.4 | 146.4 | 197.8 | 273.8 |
| 12 | Cane | 595.8 | 146.1 | 197.7 | 273.4 |
| 13 | Gram, proximity | 575.6 | 139.9 | 183.2 | 273.4 |
| 14 | Gram | 585.4 | 134.6 | **178.3** | 270.2 |
| 15 | Broad, proximity | 596.3 | 144.2 | 197.1 | 263.5 |
| 16 | Broad | 591.0 | 138.4 | 197.2 | 263.5 |

| (b) Observational: duration | | AIC values by species | | | |
|---|---|---|---|---|---|
| Model | Parameters tested | H. sosybius | M. cymela | S. appalachia | E. portlandia |
| 1 | Null (intercepts only) | 682.8 | 159.7 | 255.6 | 292.6 |
| 2 | Full, with interactions | 687.5 | **109.2** | 231.4 | 246.1 |
| 3 | Full, no habitat interactions | 691.8 | 145.8 | 257.8 | 293.2 |
| 4 | Full, no proximity interactions | 679.8 | 116.8 | 232.0 | **244.1** |
| 5 | Full, no interactions | 687.3 | 147.7 | 255.2 | 287.2 |
| 6 | Proximity, gram, cane | 682.9 | 137.8 | 249.1 | 278.8 |
| 7 | Proximity, broad, cane | 683.9 | 143.7 | 249.2 | 269.8 |
| 8 | Proximity, broad, gram | 697.3 | 137.1 | 249.6 | 273.7 |
| 9 | Proximity | 683.1 | 156.0 | 256.5 | 289.8 |
| 10 | Broad, gram, cane | **675.7** | 115.7 | **230.2** | 244.3 |
| 11 | Cane, proximity | 678.9 | 155.4 | 256.1 | 287.1 |
| 12 | Cane | 675.8 | 152.2 | 251.7 | 286.3 |
| 13 | Gram, proximity | 690.5 | 150.5 | 257.4 | 294.4 |
| 14 | Gram | 682.4 | 151.1 | 254.3 | 289.1 |
| 15 | Broad, proximity | 689.4 | 155.5 | 257.8 | 291.1 |
| 16 | Broad | 682.0 | 152.6 | 254.4 | 289.0 |

| (c) Observational: fidelity | | AIC values by species | | | |
|---|---|---|---|---|---|
| Model | Parameters tested | H. sosybius | M. cymela | S. appalachia | E. portlandia |
| 1 | Null (intercepts only) | 317.5 | **74.3** | 121.2 | 150.9 |
| 2 | Full, with interactions | 326.0 | 81.5 | 97.7 | 174.7 |
| 3 | Full, no habitat interactions | 323.7 | 88.4 | 128.3 | 166.5 |
| 4 | Full, no proximity interactions | 316.6 | 80.2 | 111.2 | 173.7 |
| 5 | Full, no interactions | 316.3 | 84.2 | 121.8 | 158.8 |
| 6 | Proximity, gram, cane | 323.8 | 91.3 | 126.2 | 165.4 |
| 7 | Proximity, broad, cane | 319.3 | 84.6 | 132.4 | 167.8 |
| 8 | Proximity, broad, gram | 319.1 | 81.1 | **88.0** | 163.3 |
| 9 | Proximity | **309.6** | 81.3 | 116.9 | 153.4 |
| 10 | Broad, gram, cane | 314.7 | 78.3 | 137.3 | 172.0 |
| 11 | Cane, proximity | 313.2 | 85.7 | 121.7 | 156.0 |
| 12 | Cane | 308.5 | 81.6 | 129.7 | **150.4** |
| 13 | Gram, proximity | 315.4 | 81.2 | 118.6 | 158.6 |
| 14 | Gram | 310.6 | 78.7 | 127.0 | 155.5 |
| 15 | Broad, proximity | 314.9 | 87.1 | 122.6 | 159.1 |
| 16 | Broad | 311.1 | 83.0 | 132.7 | 155.4 |

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 (Shuey 1997, Bergman 1999, Brommer and Fred 1999). The best fidelity model for *S. appalachia*

included graminoid changes among other variables and the best fidelity model for *E. portlandia* included cane changes only (Table 2). Specifically, movement fidelity of *S. appalachia* and *E. portlandia* was positively correlated with increasing graminoid and cane abundance, respectively. Movement directions of all species were influenced by graminoid changes. *Satyroides appalachia* tended to
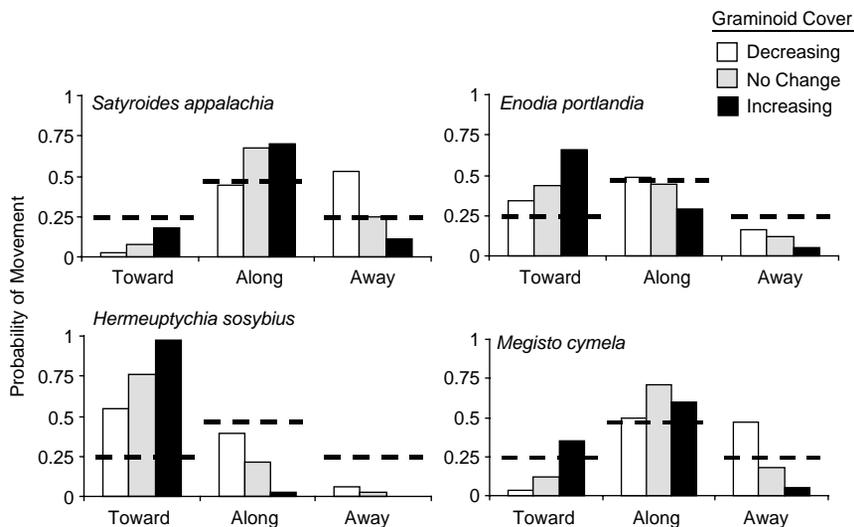
Fig. 6. Predicted probabilities of movement with respect to the riparian corridor, as movements result in a decrease, no change, or an increase in graminoid cover. Dotted lines show movement probabilities if butterflies selected movement directions at random.

move along streams into areas with increasing graminoid abundance, and *E. portlandia* tended to move toward streams into areas with increasing cane abundance. These directional biases are consistent with responses to stream proximity and boundary features, indicating that local habitat conditions complement landscape effects on movement. Responses to changes in broadleaf plant abundance were generally more variable and relatively weak. However, the behaviors exhibited by specialist species confirm that the local distribution of larval food resources may influence butterfly movement patterns.

One limitation to this study is that released butterflies may not exhibit normal searching strategies (such as those discussed by Conradt et al. 2001, 2003). In our study, we observed consistent behaviors in both released and naturally occurring butterflies, which we believe validates the comparison of data collected using the two techniques. Furthermore, behaviors using both techniques offer a relative comparison of how butterflies perceived the release habitat compared to the adjacent stream.

Behavioral responses to both local and landscape features often play a role in determining the spatial

Table 3. Summary of species information and responses to tested variables.

| Species | *Hermeuptychia sosybius* | *Megisto cymela* | *Satyroides appalachia* | *Enodia portlandia* | Shared responses |
|---|---|---|---|---|---|
| Larval host plants | Generalist: wetland grasses and sedges | Generalist: wetland grasses and sedges | Specialist: wetland sedges (genus *Carex*) | Specialist: cane (genus *Arundinaria*) | — |
| Relative size | Small | Small | Large | Large | — |
| Distribution | Common in bottomlands | Common in bottomlands | Rare in SE; common in *Carex*-rich Ft. Bragg wetlands | Common in bottomlands and canebrakes | — |
| Drainage slope | No response | Not tested | No response | No response | Unaffected by slope |
| Boundary contrast | Moves toward stream at high contrast and along at low contrast | Not tested | Moves along streams at low contrast | Moved toward streams at intermediate contrast | Flew fastest at intermediate contrast |
| Stream proximity | More sinuous movements at streams edge | No response | Moves along streams; and more sinuous movements at streams edge | Stronger bias toward streams at greater distance from stream | Abundance is greatest at 12–30 m |
| Host plant abundance | See shared responses | See shared responses | More correlated if toward greater abundances of hostplant (gram) | More correlated if toward greater abundances of hostplant (cane) | Move toward streams when abundance of graminoids increases |

structure of populations (Collinge and Palmer 2002, Goheen et al. 2003). Specifically, behavioral barriers can limit dispersal at habitat edges or along habitat corridors (Schultz 1998, Haddad 1999, Schtickzelle et al. 2003, Castellon and Sieving 2006). By restricting emigration across habitat boundaries, behaviors might produce a more spatially fragmented arrangement of populations across a landscape. Although we do not have direct evidence to test how local behaviors affect dispersal across landscapes, this idea that behaviors can affect population structure is supported by a comparison between *S. appalachia* and *E. portlandia* distributions. *Satyroides appalachia*, which show an aversion to move beyond riparian ecotones, are restricted to specific streamside habitats at Ft. Bragg and occupy a relatively limited range in the southeastern U.S. *Enodia portlandia*, which also occupy streamside habitats but are less behaviorally restricted by ecotone boundaries, are relatively common throughout bottomland habitats in the southeastern U.S. Considering *S. appalachia*'s affinity for streamside habitat, it seems likely that corridors of riparian habitat direct dispersal and subsequent distribution of this species, insofar as dispersal across landscapes is a function of multiple local movements that we observed.

Because this work was conducted on a range of species, the results may have direct management implications for populations of a related but endangered species. St. Francis' satyr *Neonympha mitchellii francisci* is a small satyrine specialist that exists in a metapopulation structure only on Ft. Bragg (Hall et al. 2001). It often co-occurs with, and is morphologically similar to, the species investigated in this study (Scott 1986, Parshall and Kral 1989, Hall 1993). Direct experiments with this rare species are prohibited, and observations are difficult. However, the behaviors of our study species may provide a useful surrogate for predicting how the management of local and landscape features will impact *N. m. francisci*. For example, this study illuminated behavioral mechanisms whereby ecotone habitat can facilitate dispersal in *S. appalachia*, the species that is most similar to *N. m. francisci* in that they both are restricted to *Carex*-rich wetlands along streams. If *N. m. francisci* exhibits behaviors similar to *S. appalachia*, the management of more *Carex*-rich riparian boundaries by restricting stream flows or appropriately adjusting prescribed burns along streams may serve to promote *N. m. francisci* dispersal along riparian corridors.

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