The conflicting role of matrix habitats as conduits and barriers for dispersal

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Abstract. Determining connectivity within complex landscapes is difficult if habitats that facilitate dispersal differ from habitats where animals normally are found or enter. We addressed the question of how landscape features affect dispersal by quantifying two critical aspects of animal movement behavior that determine dispersal rates across complex landscapes: conductivity of major habitat types and behavior at boundaries between habitat types. Our tests consisted of behavioral experiments and observational surveys of a wetland butterfly, *Satyrodes appalachia*. Displacement rates varied among habitats, with the longest moves and straightest paths leading to greater displacement rate in open habitat and shortest moves and most sinuous paths causing the slowest displacement rate in riparian forest habitat. We found a strong negative relationship between the probability of entering a habitat and the speed of moving through it. Recognizing this central conflict between entering and moving through habitat is important for assessing the connectivity of complex landscapes.

Key words: animal movement behavior; boundary behavior; butterflies; connectivity; landscape mosaic; movement ecology; random walk; Satyrodes appalachia.

Introduction

Conventional paradigms for spatially structured populations, including metapopulations, stepping stones, or corridors, typically dichotomize the landscape into parts that are suitable and unsuitable. In doing so, they ignore or oversimplify the matrix of non-preferred or unsuitable habitat. Matrix habitats influence populations by affecting the dispersal of individuals between suitable habitats, either by affecting entry at the edge or by altering movement rates (Ricketts 2001, Levey et al. 2005, Jonsen et al. 2007). In real landscapes, there are grades of matrix habitat that may vary in their role as barriers to or as conduits for dispersal (Ricketts 2001). Thus, suitable and varying grades of unsuitable matrix habitat may vary in the functional connectivity they create on a landscape. We have taken a behavioral approach to research and quantify the connectivity provided by a range of matrix habitat types for an uncommon butterfly, synthesizing multiple behaviors across a variety of habitat types and their boundaries.

The effects of matrix habitats on dispersal can be decomposed into two behaviors, that of leaving one habitat to enter another and the dispersal rate in each habitat type. Since Lima and Zollner's (1996) important paper calling for behavioral approaches to understand

landscape ecology, a number of studies have analyzed each of these aspects of dispersal behavior (e.g., Rizkalla and Swihart 2007, Walston and Mullin 2008). When organisms are leaving one habitat to enter another, it is clear that habitat boundaries with less suitable habitats can serve as barriers to dispersal, and that the strength of those barriers varies across habitat types (Haddad 1999, Ries and Debinski 2001). If a reluctance to cross boundaries is coupled with reduced movement in less preferred habitats, larger areas of less preferred habitat would serve to restrict landscape-level dispersal rates. However, if animals move faster and straighter in less preferred habitats (Schultz 1998, Haddad 1999, Schultz and Crone 2001, Dickson et al. 2005, Kuefler and Haddad 2006), restrictions on movement imposed by boundaries may be mitigated by faster movements in matrix habitats when boundaries are crossed. In such a case, lower-quality habitats where animals are infrequently observed may still provide dispersal conduits. We ask: What is the relationship between these two characteristics of animal behavior, the probability of crossing habitat boundaries and habitat-specific movement rate?

Our study tests key behavioral components of dispersal by empirically linking movement characteristics to external features of a complex landscape in a framework that fits well within prevailing movement ecology paradigms (Nathan et al. 2009). We use a novel, well-replicated design, combining experimental and observational studies of an uncommon butterfly in and at the boundary of all major habitats in the landscape

where it occurs. We provide strong empirical support for assessing theoretical predictions about how animals move through complex landscapes by demonstrating an important conflict between behaviors at habitat boundaries and movement rates in different habitat types.

METHODS

Study site and species

We conducted our research at Fort Bragg, North Carolina, USA, between May and August in 2006 and 2007. This 65 000-ha military base is dominated by longleaf pine forest. Interspersed within relatively contiguous pine stands are open fields, which are used for military training activities, and bottomland habitats, which include riparian forests, riparian shrub thickets, and wetlands. We identified five common habitat types for our experiments: upland forest, riparian forest, open field, wetland meadow (high-quality habitat for our species), and urban development. Within our study landscape, upland-forest and open-field habitats each cover ~40–45% of the land surface; wetlands and riparian tracts each account for <5% of the land surface. Our work focused on *Satyrodes appalachia* Chermock (Appalachian browns), which are commonly found across Fort Bragg despite being relatively rare across their southeastern U.S. range. Like several other rare butterflies on Fort Bragg, *S. appalachia* exhibit a strict habitat preference for wet forest (Shapiro and Carde 1970). Also, these butterflies make ideal test animals as they are locally abundant, are easily monitored, and are behaviorally affected by habitat type and fragmentation (Kuefler and Haddad 2006).

Butterfly choices at multiple boundary types

We examined habitat choices made by *S. appalachia* butterflies that we released at distinct boundaries between pairs of habitats. We performed releases because encounters with most boundaries would occur too rarely for us to study. We established release sites at all realistic habitat boundaries across Fort Bragg for a total of six boundary types at 16 different locations. There were release sites at three different locations for each of five different boundary types: wetland to riparian forest, wetland to upland forest, riparian forest to upland forest, upland forest to open field, and upland forest to urban development. Additionally, we established one site at a rare boundary type, riparian forest to open field boundary.

At each site, we released *S. appalachia* that were collected and transported from an area where they occurred in abundance (as in Conradt et al. [2000] and Kuefler and Haddad [2006]). Upon their release we visually tracked each butterfly until it was lost in one of the two habitats. We recorded the habitat it first flew into, the habitat it spent the most time in before it was lost by the observer, and the habitat in which it was lost. We defined the "preferred habitat" to be the one that the

butterfly chose by two or more of the above three criteria. For each pair-wise choice we then calculated the frequency of selecting either habitat based on these preferences. Finally, for each habitat, we calculated an overall probability of entry as the average selection frequency across all the pair-wise choices where that habitat was an option. Each butterfly used was uniquely marked on the wing with an ultra-fine-tip marker to ensure that we did not use the same individual twice.

Butterflies were observed until they were lost in a habitat or until no movement had occurred for 30 minutes. We collected data from 59 individual butterflies released at boundaries, with at least 8 individuals for every boundary type with the exception of only 3 individuals at the riparian forest–open field interface. For more common boundary types, such as an upland forest–open field interface, we were able to collect choice data from an additional 9 butterflies that were released for movement-path experiments (described in the section below). For each boundary type, we tested the hypothesis that there was no preference for either habitat using a binomial test. Additionally, for each habitat type we analyzed butterfly choices using the Freeman-Halton extension of Fisher's exact probability test (effectively a G test for low sample sizes) to test whether the probability of choosing a certain habitat depended on the adjacent habitat.

Quantifying habitat-specific movement characteristics

To quantify habitat-specific movement, we conducted releases within continuous areas of single habitat types. We established release sites at three different locations for each of four habitat types: wetland, riparian forest, upland pine forest, and open field. We then released naive butterflies at each site and collected data on spatial aspects of movement. Butterflies were uniquely marked, individually released, and, whenever possible, re-caught after the trial and returned to their original place of capture.

We collected spatial data on butterfly movement using two different techniques, depending on the type of habitat. In upland pine forests and open fields we were able to walk or run behind butterflies while maintaining a suitable distance so as to not influence their movements in any obvious way. One observer called out at 5-s intervals, and at each call the second observer dropped a numbered marker at the butterfly's location. This process was repeated until the butterfly perched for 30 min or was lost from sight. We then measured the bearing and distance between sequential markers (which we defined as a "move") and used them to calculate a sequence of move lengths and turn angles (i.e., the angle between successive bearings) for each movement path. If a butterfly did not move during an interval, we designated that interval as a "rest period." For these movement-path analyses we used data from releases at boundaries if butterflies clearly flew in a specific habitat

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for two or more moves. If butterflies moved through both habitats, then flight paths of the same butterfly in each respective habitat were treated as independent paths.

In bottomland forests and wetlands, where walking was difficult and the habitat was sensitive to trampling, we could not physically follow butterflies. In these habitats, we used pairs of digital compasses and triangulation techniques, rather than numbered markers, to determine move lengths and turn angles for each movement path (see also Zalucki et al. [1980]). We worked in pairs, with each observer standing at a fixed location. Each observer operated a KVH DataScope (digital compass; KVH Industries, Middletown, Rhode Island, USA) affixed to a swivel on a PVC pole. The poles were pushed into the ground to maintain their position relative to each other. Upon release the observers worked cooperatively to take synchronous bearings of the butterfly's position at 5-s intervals, until the butterfly either perched for 30 min or was lost from sight. We also used this observational approach to track the movements of undisturbed *S. appalachia* in their native wetland habitats and used these data on non-released butterflies to gauge the effect of release on *S. appalachia*'s behavior. To collect data for undisturbed butterflies, paired observers stood at fixed locations within areas where butterflies were abundant, began taking data as soon as an individual was sighted, and continued until the butterfly was lost from sight or perched ≥30 min.

We used Kolmogorov-Smirnoff (K-S) tests to determine whether the distributions of move lengths and turn angles differed between all pair-wise combinations of habitats. Tests were performed on the magnitude of a turn angle regardless of whether it was a left or right turn (i.e., turn angles were between 0 and 180 degrees). We assumed all turn angles were independent, even if measured from the same individual, as we found no between-move autocorrelation in step length or turn angle.

To compare movement rates among habitats, we computed a single index that integrates two components of movement: move lengths and turn angles. In particular, Kareiva and Shigesada (1983; see their Eq. 2) used a correlated random-walk model with turn angles symmetrically distributed around 0 to derive the following expression for $\bar{R}_n^2$, the mean squared displacement (the average of the square of the distance travelled), as a function of the number of moves n:

$$\bar{R}_n^2 = nm_2 + 2m_1^2 \frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right) \qquad (1)$$

where m_1 is the mean move length, m_2 is the mean squared move length, and c is the mean cosine of the turn angle. Because c is less than 1 (unless butterflies always move in perfectly straight lines), c^n approaches 0 and the second term in parentheses in Eq. 1 approaches the constant $1/(1-c)$ as n increases. Hence for n large,

the mean squared displacement increases by an amount

$$r = m_2 + 2m_1^2 \frac{c}{1-c} \qquad (2)$$

with each successive move. We used bootstrapping to place confidence intervals on our estimates of mean square displacement. Specifically, we repeatedly sampled entire movement paths at random, with replacement, until we had the same number of move lengths and turn angles as in the original data set. We then recomputed r for each sample, and identified the upper and lower 2.5th percentiles of the resulting distribution. We corrected for bias using the percentile method in Dixon (2001) to obtain confidence limits. We note that because r is the per move increment in mean squared displacement, it does not account for the fraction of time spent moving. *S. appalachia* spend a large fraction of time resting (our unpublished estimates are 67–96% of time during the day). Based on many observations, we have no reason to believe these differ across habitats, and we recognize that habitat-specific time spent resting could change relative movement rates among habitats.

RESULTS

Choices of Satyrodes appalachia *released at habitat boundaries*

Experimentally released *S. appalachia* had the highest probability of moving into riparian forest habitat (Pr {entry} = 0.84) and wetland habitat (0.59), and they exhibited a strong aversion to open-field and urban-developed habitat types (0.03) (Table 1). In all cases where open-field habitat was a potential choice, released butterflies rejected it in favor of the other habitats. Likewise, in all but one case in which urban development was a choice, butterflies favored the other habitat. Overall, upland forest was neither strongly favored nor rejected (Pr {entry} = 0.53). Comparisons across pair-wise combinations show that the adjacent habitat can make a difference in selection frequency of a habitat. By every measure (initial choice, most occupied, final choice) preference for either riparian ($p = 0.026, 0.006, 0.002$ for each respective measure, df = 2) or upland forest ($p < 0.001$ for all measures, df = 3) differed among pair-wise choices. There was a strong preference for riparian habitat unless it was adjacent to a wetland. Upland forest was strongly favored when paired against open or developed habitat but strongly avoided when paired against riparian forest and mildly avoided when paired against wetlands. By no measure did preferences differ among choices involving either wetlands or open habitats, as we observed a consistent preference for wetlands and a consistent avoidance of open habitats. Our analyses with binomial tests mirrored these results. Butterflies showed no preference between wetland and riparian forest habitats, and between wetland and upland-forest habitats (Table 1). Wetter habitats tended to be selected over drier ones, although only significantly so for the riparian forest-to-upland forest comparison.

TABLE 1.   Results from a series of binomial tests for choices at habitat boundaries.

| Boundary type | | Butterfly choices | | | | | | | | | Selection frequency§ | |
| | | Initial choice | | | Habitat most occupied | | | Final choice | | | | |
Habitat, a vs. b†	No. released‡	a	b	p	a	b	p	a	b	p	a	b
R vs. O	5	5	0	0.0313	5	0	0.0313	5	0	0.0313	1	0
R vs. U	16	12	4	0.0280	14	2	0.0018	15	1	0.0002	0.87	0.13
U vs. D	12	12	0	0.0000	11	1	0.0029	10	2	0.0161	0.92	0.08
U vs. O	11	10	1	0.0050	11	0	0.0005	11	0	0.0005	1	0
W vs. R	11	7	4	0.1610	7	4	0.1610	7	4	0.1610	0.64	0.36
W vs. U	13	4	9	0.0873	7	6	0.2095	9	4	0.0873	0.54	0.46

Note: For the column heads, "*p*" denotes the probability of observing each result, assuming that each habitat (*a* or *b*) in a paired choice has an equal chance of being selected.

† Habitat key: R, riparian forest; O, open field; U, upland forest; D, urban development; W, wetland.

‡ Sample size reflects the number of individual *Satyrodes appalachia* butterflies released at each boundary type.

§ A frequency of selection is provided, where a positive habitat choice is defined by a butterfly satisfying two of the three criteria described in the text (see *Methods: Butterfly choices...*).

However, upland forest habitat was chosen significantly more frequently than developed or open-field habitat.

Habitat-specific movement characteristics

We analyzed data from the individual movement paths of 116 *S. appalachia*, including habitat-specific movement data from 62 of the butterflies released for habitat-choice experiments, 25 additional butterflies that were released in continuous stretches of habitat, and 29 naturally occurring butterflies observed moving through large areas of native habitat. Movement paths ranged from 1 to 32 moves, with median and mode each being 4 moves. Move lengths varied between habitats, with Kolmogorov-Smirnoff (K-S) tests showing significant differences ($P < 0.001$) between mean step lengths for all pair-wise combination of habitat types with the exception that step lengths did not differ between riparian forest and wetland habitats ($D_n = 0.150$, $P > 0.2$; Fig. 1). Specifically, the step lengths decreased in order from open (median, 25–75% quartiles = 14.2, 7.5–19.5 m) to upland forest (9.0, 5.1–12.9 m) to riparian forest (3.1, 1.5–5.5 m) to wetland (2.9, 1.3–6.2 m) habitats. We collected too few data from butterflies in developed habitats to include in analyses.

S. appalachia turn angles varied among habitats (Fig. 1). Turn angle distributions were most similar in upland-forest habitats (52.5° ± 5.0° [mean ± SE]) and open habitats (63.6° ± 7.3°), where movements tended toward greater linearity (i.e., turn angles were clustered near 0°). Movement distributions were also similar in riparian forest (79.1° ± 15.7°) and wetland habitats (78.8° ± 5.1°), where movements tended toward greater sinuosity. K-S tests showed that turn-angle distributions differed significantly between wetlands and both open and upland forest habitats (wetland, open $D_n = 0.276$, $P < 0.001$; wetland, upland $D_n = 0.280$, $P < 0.001$). No other comparisons were significantly different. However, the lack of a significant difference in turn-angle distributions between riparian forest and either open or upland forest habitats is likely due to a lack of power associated with few ($n = 19$) turn angles available from riparian forest habitats.

The squared displacement rate of *S. appalachia* was highest in open habitats (estimate, 95% CI: 467 m²/5-s interval; 95% CI, 273.2–777.3 m²/5-s interval), slightly lower in upland forests (339 m²/5 s; 95% CI, 260.8–414.4 m²/5 s), nearly one third as large in wetlands (105 m²/5 s; 95% CI, 51.4–213.8 m²/5 s), and one fourth as large again in riparian forests (24 m²/5 s; 95% CI, 14.7–46.6 m²/5 s). Across habitats, movement rate was negatively correlated with the probability of entry (Fig. 2; $r = -0.91$; df = 3, $P < 0.09$).

DISCUSSION

Across disparate habitats we have found a strong, negative relationship between two characteristics of animal behavior that affect dispersal: the probability of entering a habitat and the rate of movement within that habitat. Our comparison of different matrix habitats illustrates the potential importance of non-breeding habitat in promoting landscape connectivity. In our study landscape, wetland and riparian-forest habitats support populations of our focal species, and are most frequently selected by butterflies, yet they promote the lowest rates of movement. Open fields, by contrast, promote rapid movement, yet butterflies very rarely cross into this habitat.

Perhaps surprisingly, upland forest may be one of the most important habitat types for facilitating dispersal of our focal species among populations across this landscape. Upland forest habitats do not support breeding populations of wetland butterflies, yet they promote relatively high rates of movement and present a relatively "permeable" boundary. Unlike suitable wetland and riparian-forest habitats that account for a very small proportion (<10%, combined) of the landscape, upland forests account for nearly 50% of the landscape. Because upland forest habitat has relatively high permeability and rates of displacement (that is, it is the point well above the regression line in Fig. 2), and also occupies a large fraction of the landscape, connectivity
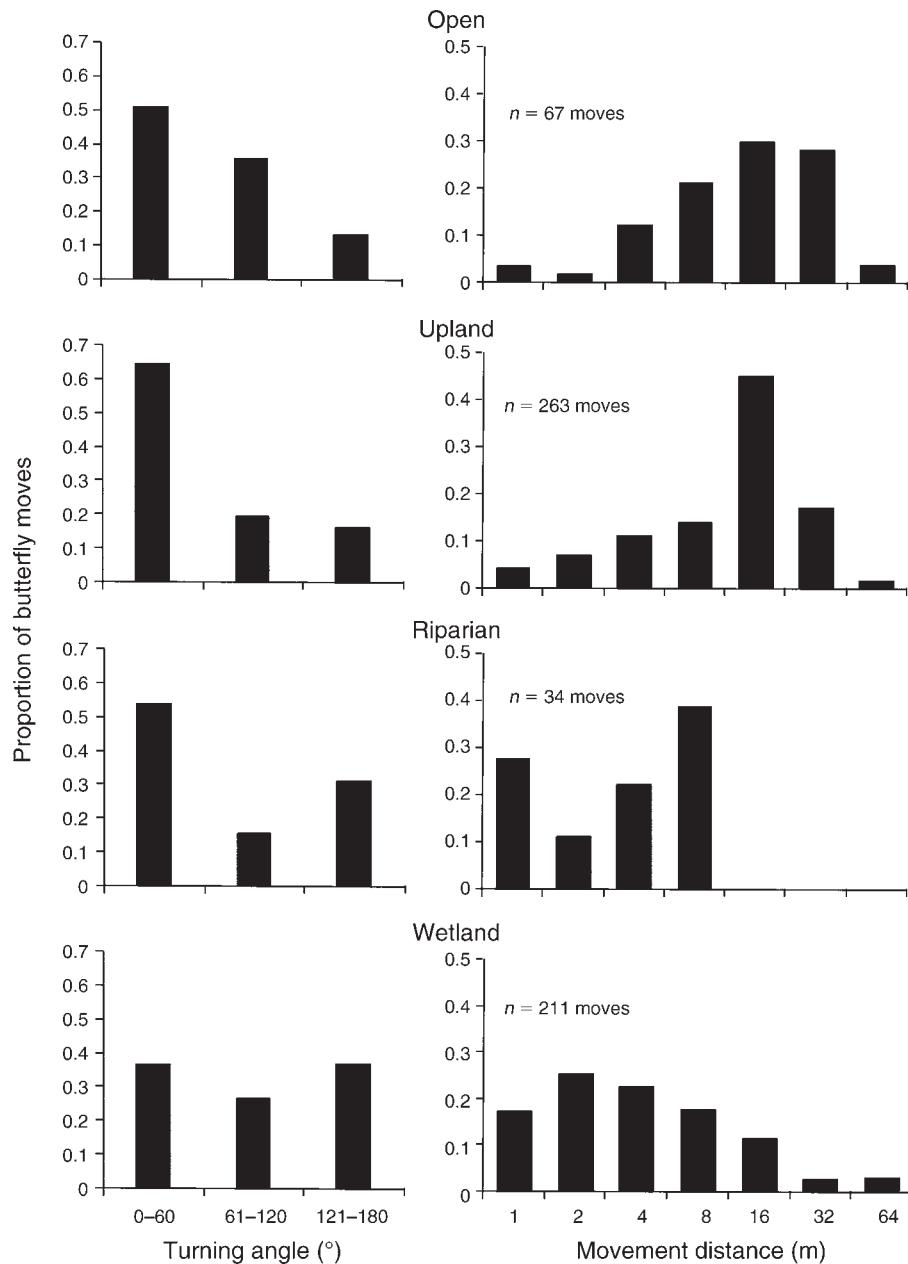
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FIG. 1. Histogram of turning angles and movement distances of each movement step for experimentally released *Satyrodes appalachia* (Appalachian brown) butterflies in four dominant natural habitat types. The lower two panels illustrating wetland habitats include data from released and naturally occurring butterflies combined.

created by this habitat type may be highest. When habitat preference, habitat-specific movement, and the natural fragmentation of suitable wetlands are taken into account, the value of breeding habitats in promoting landscape connectivity may be relatively low.

The apparent paradox between a low probability of entering a habitat and rapid movement within it is consistent with basic assumptions about adaptive responses to habitat quality. The propensity to enter a habitat is likely to be an adaptive trait, such that

organisms avoid risky habitats (Merckx et al. 2003, Schtickzelle and Baguette 2003). Speed of travel through a habitat is also likely to be an adaptive trait, such that organisms move quickly through habitats that are either risky (Stamps 2001, Schtickzelle et al. 2007) or have few resources (Heinrich 1978). One consequence of this relationship is that, all else being equal, the overall connectivity value of a given habitat type depends on whether it offers a low enough mortality risk to enter, yet a high enough risk or few enough resources to
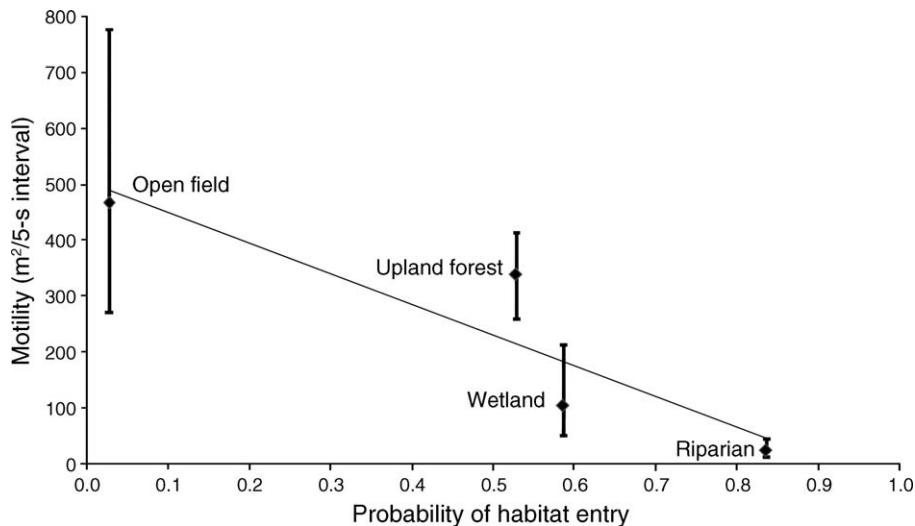
Fɪɢ. 2. Relationship between the probability of entering a given habitat and the motility within that habitat. Probability of entry is derived from values in Table 1 as the mean of all possible choices for a given habitat type. The probability of entry into open habitats pools choice data for open fields and urban developments. Data are means and 95% CI around each estimated value. All data were collected from experimentally released *Satyrodes appalachia*. Data used to estimate mean displacement were not collected for developed habitat.

expedite movement. Although differences among habitats in explicit riskiness or adverse abiotic factors may alter their dispersal value beyond what can be observed from movement behaviors alone, these qualities remain the least understood and most difficult to measure aspects of dispersal.

The role of a matrix habitat can also be conditional upon the composition of habitats in a landscape and the spatial scale of habitat heterogeneity (Johnson et al. 1992, Arellano et al. 2008, Ockinger and Smith 2008). Despite such complexities that are beyond the scope of this publication, some general habitat preferences emerge from our study as our experiments with habitat choice show that the probability of entering one habitat is dependent upon the adjacent habitat it was tested against. For example, the probability of *Satyrodes appalachia* entering upland forest habitat depended on whether it was bordered by riparian habitat (Pr {entry} = 0.13) or an open field (Pr {entry} = 1.0) (Table 1). These complexities also point to some of the limitations of our approach: our overall measure of permeability in Fig. 2 that included all pair-wise comparisons probably understated the preference for wetlands, as there were no boundaries of wetlands with open or developed habitat in our landscape to include in our experiment. Connectivity must be a function of relative habitat adjacencies on a landscape, and any given matrix habitat may differ in connectivity value depending on its position relative to others.

A richer understanding of the overall value of individual habitats in a landscape mosaic may be obtained by considering the multivariate nature of habitat value, in terms of how well the habitat promotes both breeding and dispersal within a landscape. In conservation and management, if dispersal and breeding functions of a habitat were combined in a single model for overall habitat value, then it would be possible to prioritize land acquisition with greater specificity. For example, although upland forests may promote maximum displacement across our study landscape, this matrix type enhances connectivity only to the extent that there are wetland (i.e., breeding) habitats embedded within the landscape among which butterflies can disperse. Ultimately, despite causing relatively low levels of displacement, wetland and riparian-forest habitats are the sources and destinations of dispersing individuals.

What should be clear from our work is that habitats where animals are not commonly seen may still promote dispersal (see Haddad and Tewksbury 2005). Furthermore, the demonstrated trade-off between movement rate and boundary behavior can play an important role in shaping large-scale population distribution (Ovaskainen et al. 2008). Measures of connectivity in complex landscapes for animals, including at-risk species for which connectivity is being actively managed, will be vastly improved by a more detailed understanding of the behavioral responses to landscape features that ultimately determine whether a habitat hinders or promotes dispersal through it.

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Jessica Abbott, Megan Chesser, Catherine Frock, and John McAllister.

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