EDGE-MEDIATED DISPERSAL BEHAVIOR IN A PRAIRIE BUTTERFLY

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Abstract. Animal responses to habitat boundaries will influence the effects of habitat fragmentation on population dynamics. Although this is an intuitive and often observed animal behavior, the influences of habitat boundaries have rarely been quantified in the field or considered in theoretical models of large scale processes. We quantified movement behavior of the Fender’s blue butterfly (Icaricia icarioides fenderi) as a function of distance from host-plant patches. We measured the butterfly’s tendency to move toward habitat patches (bias) and their tendency to continue to move in the direction they were already going (correlation). We found that butterflies significantly modify their behavior within 10–22 m from the habitat boundary.

We used these data to predict large scale patterns of residence time as a function of patch size, using three dispersal models: homogeneous response to habitat, heterogeneous response to habitat, and heterogeneous response to habitat with edge-mediated behavior. We simulated movement for males and females in eight patch sizes (0.1–8 ha) and asked how residence time varies among the models. We found that adding edge-mediated behavior significantly increases the residence of Fender’s blue butterflies in their natal patch. Only the model with edge-mediated behavior for females was consistent with independent mark–release–recapture (MRR) estimates of residence time; other models dramatically underestimated residence times, relative to MRR data.

Key words: biased correlated random walk; dispersal; edge behavior; Fender’s blue butterfly; habitat fragmentation.

INTRODUCTION

Ecologists face a fundamental challenge in understanding how populations respond to habitat fragmentation. Meffe (1997:148) defines fragmentation as “the breakup of extensive habitats into small, isolated patches.” From an applied perspective, understanding habitat fragmentation is central to interpreting the effects of habitat loss on endangered species (Noss and Cooperrider 1994, Wiens 1997, Gascon and Lovejoy 1998). From a basic perspective, responses to fragmentation are influenced by the ability of animals to disperse among patches, the population dynamics in habitat patches of different sizes, and the factors that control whether animals remain in or disperse from suitable habitat (Forman and Godron 1986, Turchin 1998, Fagan et al. 1999). Recent theoretical studies highlight fragmentation effects and potential consequences for population processes (e.g., Holmes et al. 1994, Pulliam and Dunning 1995, Turner et al. 1995, Hanski and Gilpin 1997, Tilman and Kareiva 1997, Fagan et al. 1999).

The most common obstacle to linking models to predictions of large-scale processes is lack of understanding of the basic ecology of dispersed behavior—how and when animals move through heterogeneous landscapes (Wennergren et al. 1995, Lima and Zollner 1996, Ruckelshaus et al. 1997).

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This obstacle persists, at least in part, because of a wide gap between many of the analytical models used to study spatial ecology and on-the-ground studies of dispersal behavior (Turchin 1998). Analytical spatial models are often so abstract that it is difficult for field ecologists to estimate model parameters, to test models or simply to know how or when to use them (but see Kareiva and Shigesada 1983, Turchin 1991). For example, the connection between parameters in partial differential equation models (e.g., Othmer et al. 1988) and empirical data is not often clear. Similarly, too often empirical estimates of dispersal are not done in ways that can be translated into parameters for models. For example, measures of tortuosity and fractal dimension are useful in describing the movement behavior of animals in heterogeneous landscapes (Stapp and Horne 1997, Etzenhouser et al. 1998) but such descriptions of movement patterns are difficult to translate into movement parameters that could predict population distributions and dynamics in novel landscapes. A number of experimental studies have investigated the effects of fragmentation phenomenologically by experimentally fragmenting a system and reporting the responses (e.g., Bierregaard et al. 1997, Andreassen et al. 1998). However, in many systems (e.g., endangered species), the experimental approach is not possible. Finally, studies documenting immigration and colonization have been done in the context of metapopulation dynamics (see review by Ims and Yoccoz 1997), but
these studies rarely investigate movement using methods from which mechanistic “rules” can be described to predict an organism’s responses to new habitat loss or creation. Pattern-oriented approaches such as incidence function models often assume simple rules about dispersal processes, assumptions which are rarely explicitly tested and may lead to misleading interpretations of population dynamics (Crone et al. 2001).

An additional complication is that dispersal studies often assume that organisms’ responses to habitat are uniform—as if the habitat were homogeneous—because the studies only occur within high quality habitat (e.g., Stenseth and Lidicker 1992; but see Zalucki and Kitching 1982, Miyatake et al. 1995, Kindvall 1999). Fragmented habitat is, by definition, heterogeneous. Assuming a homogeneous landscape may produce misleading predictions if organisms change movement rates between habitats. For example, if organisms increase their movement rates to move quickly through hostile habitats (as was observed by Miyatake et al. 1995, and Schultz 1998a), models assuming homogeneous movement will underestimate organisms’ rate of dispersal through a landscape. Several insect studies have measured features of dispersal behavior that are useful in modeling dispersal processes (movement rates, turning angles, and subsequent “diffusion rates”) and have shown that these features vary between habitats (Kareiva and Odell 1987, Morris and Kareiva 1991, Turchin 1991, Schultz 1998a, Haddad 1999, Kindvall 1999) and are affected by population density (Kindvall et al. 1998). When investigators have measured sensitivity to habitat quality, they have found that these differences influenced the expected spatial distributions of insects (see review by Turchin 1991).

Finally, to understand how organisms move across fragmented landscapes, we need to understand the “permeability” of habitat-nonhabitat interfaces—the degree to which organisms leave high quality habitat (Wiens et al. 1985, Stamps et al. 1987, Fagan et al. 1999, Kindvall 1999). To some organisms, certain habitat edges form an absolute barrier (e.g., the ocean to a nonflying terrestrial mammal). To other organisms, a habitat edge may merely slow dispersal a bit. Edge permeability influences responses to landscape structures, such as how well a corridor serves as a conduit connecting habitat patches (Lidicker and Koenig 1996, Schultz 1998a, Haddad 1999). This view of an edge is distinct from the literature on “edge effects.” Edge effects usually refer to changes in an organism’s density at the edge, such as changes in density due to biotic or abiotic effects (Yahner 1988, Meffe and Carroll 1997). These views examine the edge as a distinct habitat type. Instead, we view edge as a habitat boundary that influences organisms’ behaviors. Fagan et al. (1999) refer to this as an “edge-mediated” process. In this context, animals may respond to clearly defined edges, such as a clearcut boundary, or less discrete boundaries, such as a meadow edge.

Here, we present an investigation of edge-mediated dispersal behavior in a prairie butterfly, the Fender’s blue. The Fender’s blue system is a useful model system in which to investigate this behavior. From past research we know that movement behavior and diffusion rates differ inside preferred lupine habitat vs. outside lupine habitat and that butterflies are not randomly distributed over the landscape (Schultz 1998a). In addition, based on coarse-scale experiments, we know that the butterflies released near patch edges are more likely to stay in habitat than to leave habitat (Schultz 1998a). Also, in anecdotal observations of butterflies within habitat near patch boundaries, it appeared that after butterflies left the patch, they markedly changed their behavior by stopping less often and flying in a more directed fashion. However, these field observations do not provide quantitative insight into how butterflies respond to patch boundaries, or a mechanism for predicting the consequences of habitat loss or creation. The Fender’s blue is an appropriate study system because techniques to quantify dispersal behavior are well established and because patch boundaries are easy to distinguish in the field.

Given past research on the Fender’s blue and the potential to investigate response to patch boundaries in this system, we ask two central questions. First, how do organisms respond to habitat edges? Second, what are the implications of this behavior for residence time (the number of days butterflies spend in their natal patch before leaving)? For butterflies like the Fender’s blue, residence time is a key feature of the effects of habitat fragmentation because if residence time varies with patch size, individuals will leave smaller patches and contribute fewer young to future generations in that patch, decreasing population viability (Crone and Schultz 2001). To answer the first question, we develop a straightforward methodology to consider the butterfly’s response to habitat edge. This model is based on empirical parameter estimation of butterfly dispersal in the field. Second, we incorporate the results of this analysis into simple models of dispersal to ask how edge-mediated behavior could influence residence time.

**METHODS**

**Fender’s blue butterfly biology and habitat**

The Fender’s blue butterfly (Icaricia icarioides fenderi) resides in remnant native prairies of western Oregon. It is an indicator species for Willamette Valley upland prairies and was recently listed as endangered under the U.S. Endangered Species Act (Anonymous 2000). At the same time, its primary larval host plant, Kincaid’s lupine (Lupinus sulphureus spp. kincaidii), was listed as threatened (Anonymous 2000). Currently only about three thousand of these butterflies remain, confined to a dozen isolated patches across the Willamette Valley (Hammond 1998, Schultz and Fitzpat-
Fig. 1. Map of Bailey Hill area at The Nature Conservancy’s Willow Creek Natural Area. Outlines indicate patches of Kincaid’s lupine. Small squares indicate release points for Fender’s blue butterfly dispersal observations.

Rick 1999). Upland prairies are the most endangered habitat in western Oregon. They occupy less than one percent of their presettlement range, and urbanization and invasion by nonnative species further threaten the prairies (Alverson 1993).

The Fender’s blue’s habitat is defined by presence of its lupine hostplant and the presence of native wildflowers as nectar sources (Schultz and Dlugosch 1999). This makes it easy to divide the landscape into habitat and nonhabitat. We studied Fender’s blue behavior at The Nature Conservancy’s Willow Creek Natural Area (44° N, 123° W), an area which supports the largest remaining population of the Fender’s blue. Three areas at Willow Creek maintain Kincaid’s lupine and Fender’s blue butterflies: the Main Butterfly area, a 2.3-ha area with 500–700 butterflies and abundant lupine throughout the area; the Bailey Hill area, a 1.9-ha area with 60–120 butterflies and vigorous lupine in several discrete patches; and the Burn Trail area, a 0.3-ha area with 6–15 butterflies and stunted lupine in a few small patches (Schultz and Fitzpatrick 1999). We conducted behavioral observations at Bailey Hill because the boundaries of Kincaid’s lupine habitat were clearly defined and easily observable. In contrast, lupines in the Main Butterfly Area often grow throughout large blackberry patches, which makes behavioral observations difficult.

Behavioral observations

In spring 1996, observations were conducted to assess the relationship between movement behavior and habitat. We mapped lupine patches in the Bailey Hill area to a 2 × 2 m resolution (Fig. 1). To distribute butterfly flight paths over a range of distances from lupine patches, behavioral observations were begun within lupine and at distances of 2, 4, and 8 m from the lupine patches. Four sets of “release points” were selected outside of lupine to minimize potential effects of wind or compass bias in the movement paths (Fig. 1). We caught butterflies, cooled them in a paper cup and released them individually for observation. These techniques have previously been shown to have negligible effects on the butterfly’s behavior (Schultz 1998a). We conducted observations between 1100 and 1500 on 17 sunny or partly sunny days in May and June.

Observation techniques were the same as described in Schultz 1998a. To map flight paths, we followed each butterfly and dropped a flag every time the butterfly landed or every 20 s during flight (Fig. 2a, sample flight path). When each flag was dropped, the butterfly’s behavior (fly, perch, bask, nectar, oviposit, or chase) and the time of the event were recorded on a hand-held computer. We observed 5–20 moves per path. After each flight path was flagged, flag locations were mapped to the nearest centimeter using the triangulation method described by Turchin et al. (1991). These data were transformed into centimeter coordinates for further analysis. To reduce any potential effects on handling in the data, we removed the first two moves of each path from all analyses.

Model of biased, correlated random walk

To interpret butterfly movement behavior, we adopt the framework of a biased, correlated, random walk, in which movement behavior varies with location, relative to habitat patches. General discussions of empirically based correlated random walk models are presented elsewhere (Kareiva and Shigesada 1983, Turchin 1998). In brief, continuous movement paths of individual insects are broken down into discrete steps, each of which is characterized by its distance (l) and direction (θ). Correlation and bias refer to the direction of movement (Fig. 3). Correlation refers to the tendency for individuals to move in the same direction as the previous movement, i.e., the absence of deviations from the direction of the previous movement. If movements were perfectly correlated, each move would be in the same direction as the previous move. If movement were perfectly random, the direction of each move would be independent of the previous move. Bias is the tendency of individuals to move in a particular direction (e.g., orientation of insects toward host...
plants; see Fahrig and Paloheimo 1987 and Morris and Kareiva 1991).

We divided the landscape into three categories: inside lupine, outside lupine, and lupine edge. “Lupine edge” was the distance over which butterflies respond to the lupine when outside the patch. The decision to look at behavior at the edge as a function of distance outside the patch rather than inside the patch was based on field observations that indicate that the butterflies visibly change their behavior after leaving a patch but have no observable differences at any point within the patch. The spatial extent of the edge was an empirically estimated parameter (see Methods: Data analysis and parameter estimation). We assumed that movement followed a correlated random walk inside and outside habitat, but that at edges butterflies might be biased toward turning toward lupine patches.

Specific details of model building and parameter estimation follow. In general, our mechanistic model/parameter estimation approach has three key advantages: (1) assumptions about likelihood distributions and residual variance are adjusted to match the structure of movement data (for which variables are not normally distributed, and parameters such as bias and correlation are inherently confounded; see Turchin 1998); (2) we can test the significance of processes using well-established likelihood methods for nested models (Hilborn and Mangel 1997); and (3) given a model, we can directly predict the implications of empirically estimated behavior on population redistribution over time. All maximum likelihood parameter estimation was done using the solver function in Microsoft Excel (Microsoft 2000), and built-in functions for normal, exponential, and beta distributions.

Data analysis and parameter estimation

Inside lupine, we estimated move lengths and deviations in turning angles using standard methods for correlated random walk analysis (Kareiva and Shigesada 1983). Outside lupine, we also fit a correlated

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**Fig. 2.** (a) Sample flight path of a female Fender’s blue butterfly. (b) The distribution of move lengths and deviation in turning angles in each habitat type for all female butterflies in the study. Exponential distributions were fit to move length data, and symmetric beta distributions were fit to deviation in turning angle data.
random walk model, except that for each parameter, an additional parameter was also estimated: the distance outside the patch at which edge behavior stops and outside behavior begins. At habitat edges, we tested whether movement was biased toward lupine patches, as well as correlated. A different edge width was fit for each aspect of the three movement behaviors (move length, bias and deviation in turning angle). In initial parameter fitting using maximum likelihood techniques, we estimated parameters by fitting the same edge width for all three movement behaviors. However, instead of finding one global maximum, we found several statistically indistinguishable local maxima. When, instead, we fit an independent edge width for each movement parameter, we succeeded in finding one global maximum likelihood edge width for each movement parameter. Thus fitting a different edge width for each aspect of the three movement behaviors provided a better qualitative match to the data than models that constrained the edge width to be the same for all aspects of movement behavior.

We assumed that move lengths were exponentially distributed with different means in each of the different areas (inside lupine, lupine edge and outside lupine, Fig. 2b). This meant that, within each area, the probability density function of move lengths (x) was as follows:

Pr(x|inside lupine) = \( l_{\text{inside}} \exp(-l_{\text{inside}}x) \)
Pr(x|<d_{\text{move}} meters outside lupine) = \( l_{\text{edge}} \exp(-l_{\text{edge}}x) \)
Pr(x>|d_{\text{move}} meters outside lupine) = \( l_{\text{outside}} \exp(-l_{\text{outside}}x) \)

where \( l_i \) (three fitted parameters) were the mean move lengths in area \( i \) (inside lupine, lupine edge, and outside lupine), \( x \) was the distance moved in a particular step, and \( d_{\text{move}} \), a fitted parameter, was the spatial distance over which edge behavior altered movement distances.

Previous authors have found simultaneously estimating correlation and bias to be problematic (Turchin 1998). We built a simple model that assesses the relative influences of the “correlated” and “biased” components (Fig. 3). If movement were only correlated (not biased), the expected direction \( E(\theta_{i+1}) \) would be that of the previous move:

\[
E(\theta_{i+1}) = \theta_i
\]

where \( \theta_i \) is the direction of move \( i \) in a path. We defined bias as the tendency for the expected direction of movement to be the straightest “beeline” to the nearest habitat patch, rather than the direction of the previous move. If movement at lupine edges were perfectly biased the expected direction \( E(\theta_{i+1}) \) would be

\[
E(\theta_{i+1}) = \theta_{\text{lupine}}
\]

where \( \theta_{\text{lupine}} \) is the direction toward the nearest part of the nearest lupine patch. (This is one of many possible ways in which butterflies could bias their movement directions, chosen because it seemed to match earlier visual observations of behavior. For further discussion, see Morris and Kareiva 1991). To allow imperfect bias, we assumed that the net expected direction of movement was a weighted mean of the two directions:

\[
E(\theta_{i+1}|\leq d_{\text{bias}} \text{ meters outside lupine}) = \text{bias} = \theta_{\text{lupine}} = \theta_i\]

\[
E(\theta_{i+1}|>d_{\text{bias}} \text{ meters outside lupine}) = b\theta_{\text{lupine}} + (1 - b)\theta_i,
\]

\[
E(\theta_{i+1}|\text{inside lupine}) = \theta_i,
\]

where \( b \) is a fitted parameter (ranging from 0 to 1) that weights the relative influences of bias and correlation on movement direction, and \( d_{\text{bias}} \) is a fitted parameter denoting the spatial distance over which movement is biased toward the nearest lupine patch. Thus we had nested models that allowed for testing the statistical significance of bias; if \( b \) were significantly different from 0, then bias would be statistically significant.

The final important parameter describing movement behavior is how much butterflies deviated from expected direction in turning angle (the “random” component of biased, correlated random walk). Because turning angles are circular they are not normally distributed. Thus, choosing an appropriate statistical distribution was a crucial first step in analysis (Turchin 1998). A variety of distributions have been suggested for circular data (Batschelet 1981, Fisher 1993). Many of these are most useful when data are mostly clumped at one part of the circle, which was not the case for our data (see Results). We initially chose two distributions of deviations that might be appropriate for
these butterflies; a wrapped normal distribution and a scaled beta distribution. Both assume that deviations from the expected directions are symmetric (i.e., butterflies are equally likely to turn right or left). Use of these distributions was based on previous studies that indicated there was no tendency for turns in any absolute directions (Schultz 1998a) and on the fact that maximum likelihood estimates of two-parameter models that were not constrained to be symmetric were close to symmetric anyway (E. Crone, unpublished analyses). In plain language, the wrapped normal distribution is exactly what it sounds like—what would result if one took the infinite tails of a normal distribution, wrapped them around a circle, and took the sum of all wrapped layers as the net probability of each particular value. For example, for wrapped normal distributions with high variance, reversals in movement direction could come about because butterflies turn only 0.5 times, or because they pirouette 1.5, 2.5, or more times around the circle. In contrast, the symmetric beta distribution does not have infinite tails. Therefore all turns resulting in direction reversal are assumed to be due to half turns (π radians or 180°). In spite of these differences, both distributions led to similar results for the Fender’s blue butterfly. We present results based on the symmetric beta distribution (Fig. 2b), which is somewhat more widely described in probability and statistics texts (e.g., Gelman et al. 1995).

For the symmetric beta distribution, scaled from −180° to 180°, the probability density function of the deviation from expected direction, \( q = E(\theta) - \theta \), is

\[
\Pr(q | \text{inside lupine}) = \frac{\Gamma(2a_{\text{inside}})}{2\Gamma(a_{\text{inside}})} \left( \frac{q + 180}{360} \right)^{a_{\text{inside}}-1} \left[ 1 - \left( \frac{q + 180}{360} \right)^{a_{\text{inside}}-1} \right]
\]

\[
\Pr(q | \leq d_{\text{edge}}, \text{outside lupine}) = \frac{\Gamma(2a_{\text{edge}})}{2\Gamma(a_{\text{edge}})} \left( \frac{q + 180}{360} \right)^{a_{\text{edge}}-1} \left[ 1 - \left( \frac{q + 180}{360} \right)^{a_{\text{edge}}-1} \right]
\]

\[
\Pr(q | > d_{\text{edge}}, \text{outside lupine}) = \frac{\Gamma(2a_{\text{outside}})}{2\Gamma(a_{\text{outside}})} \left( \frac{q + 180}{360} \right)^{a_{\text{outside}}-1} \left[ 1 - \left( \frac{q + 180}{360} \right)^{a_{\text{outside}}-1} \right]
\]

where \( E(\theta) \) is the expected direction of move \( t \), \( \theta \), is the actual direction of move \( t \), \( q \) is the actual difference between these directions (in degrees), \( d_{\text{edge}} \) is the spatial distance over which the predictability of butterfly movement varies at patch edges, \( a \) is the parameter the scales the magnitude of expected deviations from the expected move direction (i.e., the variance in deviations from expected is \( 2a[(2a)^2/(2a + 1)] \)), and \( \Gamma \) is the gamma function (see Gelman et al. 1995). The term \( (q + 180)/360 \) rescales the deviation to \([0, 1]\), which is the domain of the unscaled beta distribution.

To assess statistical significance we used likelihood ratio tests to evaluate nested sets of models (Table 1).

<table>
<thead>
<tr>
<th>Move length, ( l ) (m)</th>
<th>Parameters estimated</th>
<th>Full model</th>
<th>Heterogeneous habitat</th>
<th>Identical sexes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inside lupine</td>
<td>M</td>
<td>X</td>
<td>X</td>
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<td></td>
<td>F</td>
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<td></td>
<td>M + F</td>
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<td>Outside lupine</td>
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<td>M + F</td>
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<tr>
<td>Lupine edge</td>
<td>M</td>
<td>X</td>
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<td>F</td>
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<td>M + F</td>
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<td>Edge width</td>
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<td>M + F</td>
<td>X</td>
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<tr>
<td>Bias, ( b ) (%)</td>
<td>Lupine edge only</td>
<td>M</td>
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<td>Edge width</td>
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<td>M + F</td>
<td>X</td>
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<tr>
<td>Deviation in turning angle, ( q ) (degrees)</td>
<td>Inside lupine</td>
<td>M</td>
<td>X</td>
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<td></td>
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<td>Outside lupine</td>
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<td>Lupine edge</td>
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<td>Edge width</td>
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<td>M + F</td>
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</table>

Note: “M + F” refers to models in which male and female data were pooled.

For move length and deviation from expected direction, the full model consisted of separate parameters for inside lupine, lupine edge, and outside lupine, plus the edge width, estimated separately for each sex (4 x 2 = 8 fitted parameters). For bias, the full model consisted of only the magnitude of bias and the edge width (we assumed no bias inside lupine or outside the edge; 2 x 2 = 4 fitted parameters). For each move component (move length, deviation, and bias), we compared this model to two nested submodels. In the first, parameters were estimated for sexes combined (4 x 1 = 4 fitted parameters for move length and deviation, 2 x 1 = 2 fitted parameters for bias). In the second, we included habitat heterogeneity (parameters which differ inside
of parameters for move length, directional bias, and number of butterfly paths. We estimated a unique set
ify that our results were not being driven by a small
edge widths, we performed additional analyses to ver-
above.
paths or individual butterflies) were used as the unit of
from all paths were pooled and “moves” (rather than
parameters (move lengths and turning angles, inside
1.3 times. In addition, variance in four key behavioral
other words, each butterfly was watched, on average,
mapped 156 Fender’s blue flight paths (56 female paths
1996 (Schultz 1997). In
and 100 male paths), and there were 122 Fender’s blue
butterflies during our observations, and statistically
differ substantially in movement behavior (Turchin
constantly estimated from a constant
maximum likelihood methods for model comparison, be-
edge behavior (lupine edge habitat or scaling for edge
parameter estimates were performed using Systat version
lupine and outside lupine) and sex differences, but no
effect (lupine edge habitat or scaling for edge
width; \(2 \times 2 = 4\) fitted parameters for move length
and deviation, no fitted parameters for bias).

Variation among butterfly paths

In studies of movement behavior, one would ideally
study several unique individuals, and compare variance
among individual animals as part of the analysis. This
is particularly important when researchers sample a
small fraction of the population, or when individuals
differ substantially in movement behavior (Turchin 1998). Because the Fender’s blue was a candidate for
listing as an endangered species at the time the study
was conducted, we were not able to mark individual
butterflies during our observations, and statistically
compare variance among individuals. However, we
mapped 156 Fender’s blue flight paths (56 female paths
and 100 male paths), and there were 122 Fender’s blue
butterflies at Bailey Hill in 1996 (Schultz 1997). In
other words, each butterfly was watched, on average,
1.3 times. In addition, variance in four key behavioral
parameters (move lengths and turning angles, inside
and outside lupine habitat [excluding habitat edges])
was substantially higher within paths than among path
means (E. Crone, unpublished analyses). Thus, data
from all paths were pooled and “moves” (rather than
paths or individual butterflies) were used as the unit of
replication in maximum likelihood analyses described
above.

After completing these analyses and, in particular,
after estimating maximum likelihood parameters for
edge widths, we performed additional analyses to ver-
ify that our results were not being driven by a small
number of butterfly paths. We estimated a unique set
of parameters for move length, directional bias, and
deviation from expected direction for each butterfly
flight path that was represented at least twice in a par-
ticular habitat type (inside, edge, and outside lupine).
In other words, if a path included five moves inside
lupine, and five moves outside lupine within 10 m of
habitat edge, we estimated move lengths and deviations
in lupine and at the habitat edge for that path, as well
as directional bias in edge habitat. If a female butterfly
path included seven moves outside habitat within 22
m of a lupine patch, but only one of those moves was
within 10 m of the patch, then we estimated only move
length and directional deviation at the habitat edge to
that path; we would not estimate directional bias for
this path because only one move was within the edge
area for directional bias (see Table 2 for estimated edge
widths). Parameters were fit to each path using maxi-
mum likelihood routines in Microsoft Excel identical
to those used for the aggregate data. Parameter esti-
mates were unconstrained, occasionally fell outside
of biologically likely ranges, and likely reflect substantial
estimation error as well as variance among individual
paths. It was not possible to fit the full model, including
edge widths, to individual butterfly paths using maxi-
mum likelihood methods for model comparison, be-
cause the sample size would vary with different edge
widths. Likelihood ratio tests and similar statistics for
model comparison (e.g., Akaike Information Criterion
statistics) assume models are estimated from a constant
number of data points.

After fitting unique parameters to each path, we then
analyzed move length, directional bias, and directional
deviation parameters for each path to corroborate max-
imum likelihood model comparisons. Comparisons of
fitted parameters were performed using Systat version
8.0 (SPSS 1998). We tested whether estimated direc-
tional deviations and move lengths differed among sex-

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Female</th>
<th>90% confidence interval</th>
<th>n</th>
<th>Male</th>
<th>90% confidence interval</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Move length, (l (m))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inside lupine</td>
<td>2.1</td>
<td>(1.9–2.4)</td>
<td>259</td>
<td>5.12</td>
<td>(4.6–5.7)</td>
<td>290</td>
</tr>
<tr>
<td>Lupine edge</td>
<td>6.2</td>
<td>(5.2–7.5)</td>
<td>152</td>
<td>8.15</td>
<td>(7.2–9.3)</td>
<td>240</td>
</tr>
<tr>
<td>Outside lupine</td>
<td>8.8</td>
<td>(6.5–8.8)</td>
<td>36</td>
<td>14.50</td>
<td>(10.7–20.5)</td>
<td>39</td>
</tr>
<tr>
<td>Edge width (m)</td>
<td>14</td>
<td>(0–&gt;50)</td>
<td></td>
<td>16</td>
<td>(12–20)</td>
<td></td>
</tr>
<tr>
<td>Bias, (b (%))</td>
<td>0.38</td>
<td>(0.09–0.61)</td>
<td>113</td>
<td>0.29</td>
<td>(0.22–0.38)</td>
<td>192</td>
</tr>
<tr>
<td>Edge width (m)</td>
<td>10</td>
<td>(6–24)</td>
<td></td>
<td>14</td>
<td>(6–18)</td>
<td></td>
</tr>
<tr>
<td>Deviation in turning angle, (q) (degrees)†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inside lupine</td>
<td>49</td>
<td>(46–52)</td>
<td>259</td>
<td>46</td>
<td>(44–49)</td>
<td>290</td>
</tr>
<tr>
<td>Lupine edge</td>
<td>47</td>
<td>(43–50)</td>
<td>152</td>
<td>44</td>
<td>(41–47)</td>
<td>240</td>
</tr>
<tr>
<td>Outside lupine</td>
<td>23</td>
<td>(18–31)</td>
<td>22</td>
<td>41</td>
<td>(35–49)</td>
<td>39</td>
</tr>
<tr>
<td>Edge width (m)</td>
<td>22</td>
<td>(16–26)</td>
<td></td>
<td>16</td>
<td>(0–&gt;50)</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Bias only influences behavior in the lupine edge and is assumed to be zero inside and outside lupine. The width of
the edge was estimated independently for each of the three move parameters and was estimated to the nearest 2 m.
† Values are the square root of variance from the expected direction based on estimates from the beta distribution.

TABLE 2. Parameter estimates for full models with eight parameters. For example, the full model for move length includes
the three habitat types (inside lupine, outside lupine, and lupine edge) and edge width, each estimated separately for males
and females.
es and habitat types using factorial ANOVAs. We tested whether directional bias at habitat edges differed significantly among sexes using a two-sample t test, and whether estimated directional bias differed from no bias ($b = 0$) using a one-sample t test. Mean move lengths were lognormally distributed (Fig. 2), and were log transformed prior to analysis. Directional deviations (square root-transformed variance from scaled beta distributions of deviations for each path) and directional biases were approximately normally distributed without transformation (Fig. 2). Note the distinction between distributions of residuals among moves within each path (which were assumed to follow an exponential distribution for move lengths and a scaled beta distribution for directions) and distributions of residuals of mean parameters among paths.

**Patch residence time**

Given the best-fit model, we explored the potential ecological significance of edge behavior using computer simulations of long-term movement for individual butterflies. We simulated lifetime movement of butterflies, and predicted residence time, the amount of time butterflies spend in their natal patch, as a function of patch size, for butterflies born in isolated patches. We chose this metric for two reasons. First, residence time is directly related to the ability of isolated populations to persist, and therefore related to the potential effects of habitat fragmentation or restoration (see Crone and Schultz 2000). Second, we had independent data on residence times from a limited mark–recapture experiment (Schultz 1998b), that we could compare to output from our simulations as an independent test. We note that our usage of residence time refers to a transitory process of butterflies spending several days inside lupine, and many eventually leaving lupine. Therefore, descriptions of residence time that assume the population reaches an equilibrium distribution, such as Turchin’s (1991) “residence index,” are inappropriate to describe the spatial distribution of Fender’s blue butterflies (Turchin 1991).

The statistical model we fit provided parameter estimates for stochastic simulations of individual dispersal. At Willow Creek, butterflies emerge over 2–4 wk, and are out for 4–6 wk each year. Thus, we set 15 d as an approximate mean lifespan, (investigations based on life spans of 10–20 d led to qualitatively similar results; E. Crone, unpublished analyses). Based on time budget work (Schultz 1998b), we estimated that an average Fender’s blue was active for 6 hr on clear sunny days. Due to cool, wet weather in May, we estimated that during only ~45% of potential flight time was the weather adequate for butterfly activity (C. Schultz, unpublished analyses). We assumed that that butterflies lived up to 15 d and that 45% of the potential flight time was usable. From behavioral observations, flight moves took a mean of 70 s. Therefore, an average butterfly would have the opportunity for ~2100 moves/lifetime or ~140 moves/d. As an upper bound of dispersal, we simulated butterflies that moved 150 moves/d for 15 d. For each move, we calculated the expected move length and move direction, based on the butterfly’s history and location in the habitat, then drew an actual move length and deviation from expected direction from the appropriate exponential and beta distributions. For each scenario we simulated 3000 butterfly lifetimes, enough for mean output parameters to converge to within 2% of the mean values among replicate simulations from different random number seeds (E. Crone, unpublished data). All simulations started in circular patches. We chose eight patch sizes (0.1–8 ha) to span the range of existing Fender’s blue habitat patches and potentially restorable prairie fragments (see Hammond and Wilson 1993). Computer code for simulations was written in Pascal, using routines for probability distributions from Press et al. (1989).

To test simulation results against independent data, we used data from a limited mark–release–recapture study (Schultz 1998b). In May 1994, 74 butterflies were marked at the Main Butterfly area of Willow Creek, ~15% of the population in that year. Butterflies were recaptured daily for 26 d to evaluate daily survivorship. Using the methods of Hilborn and Mangel (1997), we estimated daily survivorship using a variety of models. The model best fitting the data assumes a constant daily survivorship and a constant daily recapture rate. Based on these survivorship estimates, we calculated the mean residence time of the butterflies in the Main Butterfly area. We tested predictions of the behavioral model by asking whether the 95% confidence limits for mean residence time based on the field estimates overlapped the mean residence time from the computer simulations. We limit extrapolation of movement behavior to residence time, and not other large-scale dispersal statistics, because residence time is the only measure with which we can directly compare our simulation results to independent field data.

Finally, we used simulations to investigate whether edge behavior altered how long butterflies spend in their natal patches. To investigate the influence of habitat heterogeneity and edge behavior on residence time, we simulated three versions of the model. First, we simulated butterfly dispersal as a correlated random walk in a homogeneous environment in which the whole landscape was a high quality patch. These simulations were the same as simple representations of dispersal behavior in which the habitat was assumed to be homogeneous. In the second model, we simulated butterfly dispersal as a correlated random walk in a heterogeneous environment. In this case, butterfly behavior changed as the butterflies crossed habitat boundaries, but the edge did not influence movement behavior. In the third case, we added edge behavior. Here we modeled butterfly dispersal as a correlated random walk inside lupine and outside lupine beyond the edge,
but butterflies were biased to return to lupine within the lupine edge.

RESULTS

Field results and parameter estimates

Nearly all estimated movement parameters differed significantly with butterfly location (inside lupine, outside lupine, and lupine edges, Table 2). Move lengths were shortest inside lupine, longer in lupine edge, and longest outside lupine (Fig. 4). Deviation in turning angle was highest inside lupine and lowest outside lupine. At lupine edges, butterflies were significantly more likely to turn toward lupine than would be expected due to correlation alone (\( b \) significantly greater than 0; Table 2), although the strength of bias was only about half as strong as the strength of correlation (\( b = 0.3, \) so \( 1 - b = 0.7 \)). Finally, models including edge behavior and habitat heterogeneity were significantly better than models with only habitat heterogeneity and no edge behavior (Table 3).

In addition, male and female butterflies behaved differently. Overall, models for move length and deviation in turning angle in which parameters were estimated separately for males and females were significantly better than models in which the sexes were combined (Table 3). Move lengths were about twice as long for male butterflies than female butterflies both inside lupine and outside lupine, but similar at lupine edge (Table 2). In contrast, deviation in turning angle was similar inside lupine and at lupine edge, but differed outside lupine.

The influence of the edge habitat on butterfly behavior extended from 10 to 22 m, depending on parameter and the error distribution used to estimate the parameters (Table 2). Bias influenced behavior over the shortest spatial scale, move length had an intermediate influence and deviation in turning angle had the longest influence—ffecting female butterflies’ behaviors 22 m from the lupine boundary. However, due to high variance in observed behavior and the rough scale of habitat mapping compared to the edge width, we had little ability to resolve edge width with great confidence for some parameters.

Patterns from the analysis of pooled data were consistent with results of parameters fit to individual paths. Move lengths differed significantly with sex and habitat and mean deviations differed significantly with habitat (see Table 4 and Fig. 5). Bias did not differ among males and females (\( t \) test, \( t = 0.355, df = 58, P = 0.72 \), but was significantly different from zero (one-sample \( t \) test, \( t = 5.22, df = 59, P < 0.0001 \))

Simulation results

Adding edge behavior increased residence time for both males and females (Fig. 6). For male butterflies, edge behavior increased mean residence time by less than half a day for all patch sizes investigated. For female butterflies, edge behavior increased mean residence time by more than a day. For example for a 2-ha patch, residence time increased by 46%, from 4.9

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Significance of full model relative to model with only heterogeneous habitat</th>
<th>Significance of full model relative to model with sexes identical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Move length, ( l ) (m)</td>
<td>( \chi^2 = 15.784 ), ( df = 4 ), ( P = 0.003 )</td>
<td>( \chi^2 = 119.28 ), ( df = 4 ), ( P &lt; 0.001 )</td>
</tr>
<tr>
<td>Bias, ( b ) (%)</td>
<td>( \chi^2 = 18.475 ), ( df = 4 ), ( P = 0.004 )</td>
<td>( \chi^2 = 1.517 ), ( df = 2 ), ( P = 0.468 )</td>
</tr>
<tr>
<td>Deviation in turning angle, ( q ) (degrees)</td>
<td>( \chi^2 = 15.381 ), ( df = 4 ), ( P = 0.004 )</td>
<td>( \chi^2 = 15.196 ), ( df = 4 ), ( P = 0.004 )</td>
</tr>
</tbody>
</table>
TABLE 4. Results of analyses of variation among butterfly paths.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Sum of squares</th>
<th>df</th>
<th>F ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Move length</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>24.41</td>
<td>2</td>
<td>28.07</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Sex</td>
<td>4.75</td>
<td>1</td>
<td>10.92</td>
<td>0.0011</td>
</tr>
<tr>
<td>Sex × Habitat</td>
<td>3.39</td>
<td>2</td>
<td>3.89</td>
<td>0.0222</td>
</tr>
<tr>
<td>Error</td>
<td>74.84</td>
<td>172</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deviation in turning angle</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat</td>
<td>2767.15</td>
<td>2</td>
<td>7.75</td>
<td>0.0006</td>
</tr>
<tr>
<td>Sex</td>
<td>31.26</td>
<td>1</td>
<td>0.175</td>
<td>0.6761</td>
</tr>
<tr>
<td>Sex × Habitat</td>
<td>302.68</td>
<td>2</td>
<td>2.249</td>
<td>0.1089</td>
</tr>
<tr>
<td>Error</td>
<td>288,554.91</td>
<td>160</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

FIG. 5. Box plots of analyses of variation among paths showing variation between sexes for bias (females, n = 24; males, n = 36); variation between sexes in different habitats for mean deviation in turning angle (females, edge, n = 26; females, inside lupine, n = 35; females, outside lupine, n = 4; males, edge, n = 41; males, inside lupine, n = 51; males, outside lupine, n = 9); and variation between sexes in different habitats for move lengths (females, edge, n = 26; females, inside lupine, n = 51; females, outside lupine, n = 7; males, edge, n = 52; males, inside lupine, n = 50; males, outside lupine, n = 9). Note that parameters fit in this analysis were unconstrained and occasionally fell outside biologically likely ranges due to small sample sizes. Constraining parameters resulted in consistent results (E. Crone, unpublished analyses).

FIG. 6. Mean residence time as a function of patch size for each sex estimated in the three dispersal models: homogeneous habitat, heterogeneous habitat, and heterogeneous habitat with edge-mediated behavior.

d to 7.2 d spent in habitat. For both sexes, adding only habitat heterogeneity reduced mean residence time in small patches, but had no effect in larger patches. Around these means, there was high variability among the simulated residence times of individual butterflies for all parameter combinations (e.g., Fig. 7). Because we ran simulations until means converged to within 2%, we know that differences among mean simulated residence times are real. However, movement, like any diffusion process, was highly stochastic and variable among individual paths.

The independent estimates of residence time confirmed the importance of edge behavior. Schultz (1998b) estimated a mean residence time of 8.8 d for females (n = 32 females, 95% confidence interval: 6.3–14.5 d) and of 10.4 d for males (n = 35 males, 95% confidence interval: 7.3–17.8 d) in a 2.3-ha patch. For females, only the mean residence times from the model with edge behavior and heterogeneous habitat overlapped the 95% confidence limits for mean residence time from mark–release–recapture data (Fig. 7). These estimates agreed fairly well quantitatively, as well; 7.2 d from simulations and 8.8 d from mark–release–recapture. For all other models of female movement, simulated mean residence times grossly underestimated actual residence times. For male butterflies, all of the simulated random walk models dramatically underestimated residence time. The model with edge behavior was perhaps best, because it predicted the longest residence time, but estimated means were far off (2.0 d from simulated data vs. 10.4 d from mark–release–recapture).
DISCUSSION

Fender’s blue butterfly dispersal behavior was significantly modified by habitat boundaries. In addition, adding edge behavior to the dispersal model had significant implications for making large-scale dispersal predictions based on small-scale observations (Fig. 6). Our habitat-based dispersal model suggests large-scale population patterns via residence time of female butterflies, a factor that directly influences the number and spatial distribution of eggs, and therefore the future number of butterflies (Crone and Schultz 2001). Because Fender’s blue butterflies only live a week or so, a change in residence time by a day markedly influences the distribution of eggs. Thus, at least for this species, it is necessary to consider both habitat heterogeneity and edge behavior to understand the potential effects of patch size on population dynamics. This represents a significant difference from many earlier modeling efforts with spatially uniform dispersal, an assumption which persists in many “canned” statistical packages for spatially explicit population viability analysis (see also discussion by Kindvall [1999]).

Behavior of Fender’s blue butterflies was distinctly different for the two sexes. The model of residence time was consistent with independent field estimates only for female butterflies. Since females are often the demographically important sex (Caswell 1989), we conclude that this dispersal model is a useful model from which to build models of larger scale processes such as metapopulation dynamics. In addition, there were a few likely reasons why our model did not capture the dispersal behavior of males. Male Fender’s blues landed in mud puddles more than 150 m from the lupine patch (C. Schultz, personal observation). Male butterflies land in mud puddles because wet mud provides key nutrients such as salts (Sculley and Boggs 1996). If males needed to search long distances from the habitat patch for key resources, they may have been more likely to leave a patch and return to it later. Events in which butterflies left host-plant patches and returned to them hours or days later would not be captured by short-distance observations. Extrapolations from short-distance observations such as these result in a consistent underestimate of residence time by models that
make larger scale predictions. Alternatively, while females were searching for host plants on which to oviposit, males may have been searching for females. Thus we did not expect male behavior to be as closely linked to plant resources as the females, especially over short distances. These details were apparent in our estimation of move parameters. For example, the deviation in turning angle was much smaller outside habitat for females than for males (Table 2).

A second, more subtle, difference between the fitted model and field data is the distribution of deviations of butterflies in edge habitat (see, e.g., Fig. 2), which was more leptokurtic than would be expected from the beta distribution. Statistically, this means our significance tests were conservative, (contrast the tails of the fitted curve and the distribution of deviations in Fig. 2). This would also be unlikely to change mean simulated residence times, because the distribution is bounded between 180° and −180°, although it might increase variance among individual paths. Biologically, the actual distribution of deviations implies that individual butterfly moves at the edge tended to be either very close to the predicted direction, or nearly random. It is tempting to speculate that butterflies choose to either move randomly, or return to lupine habitat. This speculation has two important caveats. First, the expected direction is a weighted mean of both the beeline direction to lupine and the previous move direction. Second, the distribution applies to moves, not individual butterflies or butterfly paths. In other words, each move would represent a decision to return vs. to forage randomly. The distribution of bias parameters among paths was approximately normal (Fig. 5).

For the Fender’s blue, the scale of edge-mediated effects was 10–22 m (Table 2). Notably, the scale of the edge effect was different for different move components. These distances are similar to those from other insects for which the scale of edge behaviors has been measured. Root and Kareiva (1984) found that cabbage white butterflies (Pieris rapae) only modified their behavior within a few meters of their host plants. Haddad (1999) investigated the tendency of open habitat species to stray away from denser, wooded habitats. He observed butterfly behavior at the boundary between forest and newly cleared open habitat patch to detect dislike for leaving open areas and found that two open-habitat species, Phoebis sennae and Euurema nicippe, modified their behavior only within 8 m of the edge, the shortest distance category from the edge that was quantified. In contrast some other insects modified their behavior at only very short distances from the edge. Capman et al. (1990) found that skippers had a “surprisingly short” host-plant detection distance, a distance of <0.3 m. In observing flea beetle behavior, Kareiva (1985) concluded that the beetles did not orient toward the host-plant patch when released >2 m from the patch. Similarly, Fahrig and Paloheimo (1987) observed that cabbage white butterflies did not have a tendency to fly toward their host plants. They noted that “as far as we are aware, it has never been demonstrated that any butterfly can orient toward its host-plant from a distance of greater than 1 m” (Fahrig and Paloheimo 1987). Importantly, Morris and Kareiva (1991) remarked that if experimentalists misidentify the scale of an animal’s response to habitat boundaries, investigators may err and conclude that a search behavior was random when a behavior was actually an oriented search that was mediated by an edge.

Theorists familiar with diffusion models will not be surprised by the high variance among individual butterfly residence times in our simulations. However, readers not familiar with diffusion processes might be surprised at this result. This variability, in and of itself, has important implications. First, it would be extremely difficult to detect differences in residence time from experimental, rather than simulated, data. Second, in moderate-sized patches, substantial numbers of simulated female butterflies spend anywhere from hours to days to their entire lifetime in their natal lupine patch. For actual butterflies dispersing over a landscape of potential habitat patches, the search process would be similarly stochastic. Thus, we cannot divide butterflies into distinct classes of residents and emigrants. Furthermore, butterflies that disperse from one habitat patch to the next could spend a substantial fraction of their adult lifetime in their natal patch and/or between patches. This is different from the assumption of many spatially implicit (sensu Kareiva 1990) models of population dynamics, which assume dispersal is instantaneous.

In this paper, we have investigated the influence of edge-mediated behavior on one butterfly species, a species for which both habitat fragmentation and habitat restoration are ongoing processes (Schultz 1998b). Very few other studies (but see Kindvall 1999) have investigated the quantitative natural history of dispersal in the context of both edge-mediated behavior and population processes. Like Kindvall (1999), we found that edge-mediated behavior substantially influenced scaling up to large-scale processes. On one hand, this implies that making assumptions about dispersal that are not grounded in data, and using these assumptions to predict the effects of habitat fragmentation, is potentially dangerous—at least until we know more about “typical” behaviors at habitat edges. On the other hand, we emphasize that advances in statistical tools and computer simulation capability make it increasingly easy to quantify dispersal behavior and to test implications for population dynamics across a wide variety of taxa.

Finally, we note that ecologists often shy away from empirical field estimates of dispersal because dispersal data are considered difficult to collect and a very time-consuming task. Although we agree that empirical long-distance dispersal observations, on the scale of kilometers or tens of kilometers, are often difficult to
conduct, short-distance dispersal studies are considerably more feasible for many species. If they can capture relevant features of life history and behavior, and be combined with limited long-distance observations to groundtruth extrapolations, models in the correlated random walk context make dispersal possible to quantify for a much broader range of organisms.

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LITERATURE CITED


Anonymous. 2000. Endangered and threatened wildlife and plants; endangered status for Erigeron decumbens var. decumbens (Willamette Daisy) and Fender’s blue butterfly (Icaricia icarioides fenderi) and threatened status for Lupinus sulphurescens ssp. kincardii (Kincard’s lupine). Federal Register 65:3875–3890.


