The Matrix Matters: Effective Isolation in Fragmented Landscapes

Taylor H. Ricketts*

Department of Biological Sciences, Stanford University, Stanford, California 94305-5020

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ABSTRACT: Traditional approaches to the study of fragmented landscapes invoke an island-ocean model and assume that the nonhabitat matrix surrounding remnant patches is uniform. Patch isolation, a crucial parameter to the predictions of island biogeography and metapopulation theories, is measured by distance alone. To test whether the type of interpatch matrix can contribute significantly to patch isolation, I conducted a mark-recapture study on a butterfly community inhabiting meadows in a naturally patchy landscape. I used maximum likelihood to estimate the relative resistances of the two major matrix types (willow thicket and conifer forest) to butterfly movement between meadow patches. For four of the six butterfly taxa (subfamilies or tribes) studied, conifer was 3–12 times more resistant than willow. For the two remaining taxa (the most vagile and least vagile in the community), resistance estimates for willow and conifer were not significantly different, indicating that responses to matrix differ even among closely related species. These results suggest that the surrounding matrix can significantly influence the "effective isolation" of habitat patches, rendering them more or less isolated than simple distance or classic models would indicate. Modification of the matrix may provide opportunities for reducing patch isolation and thus the extinction risk of populations in fragmented landscapes.

Keywords: fragmentation, landscape ecology, matrix, dispersal, butterflies, maximum likelihood.

Because many species inhabit patchy landscapes, the effects of landscape pattern on population and community dynamics is of central interest to ecologists (e.g., Wiens 1995; Tilman and Kareiva 1997). In addition, as human activities increasingly fragment native habitats, understanding the effects of this fragmentation on native biotas has become essential to their conservation (Saunders et al. 1991; Bierregaard et al. 1992; Robinson et al. 1992).

The study of fragmented landscapes has been dominated by two classical paradigms, island biogeography and metapopulation dynamics, which supply theoretical frameworks for both ecological research and conservation efforts (MacArthur and Wilson 1967; Ehrlich and Murphy 1987; Harrison et al. 1988; Soulé et al. 1992; Hanski 1998). Both these theories assume a binary landscape of "habitat" and "matrix" (i.e., the nonhabitat surrounding the native habitat patches of interest) and focus almost exclusively on the former. The matrix is assumed to be uniform, like the ocean in island archipelagoes, and isolation, a crucial parameter to the predictions of both models, is measured simply as the distances among patches (Doak et al. 1992; Thomas et al. 1992). Terrestrial habitat patches, however, are often surrounded by a complex mosaic of other land cover types, which may differ in their resistance to the movement of individuals among the patches. Therefore, patches may be more or less effectively isolated than simple distance would indicate, depending on the type of intervening matrix.

The notion of effective isolation was perhaps first articulated by Darwin. In considering the biogeography of the Galápagos Islands, he noted that patterns of ocean currents rendered some islands "far more effectually separated from each other than they appear to be on a map" (Darwin 1859, p. 401). Despite this early mention in the literature, the effects of a heterogeneous matrix have only recently been incorporated into the study of habitat fragmentation, as ecologists pay increased attention to the ways in which the matrix may influence the distribution and population dynamics of organisms inhabiting patchy landscapes (e.g., Hobbs et al. 1993; Wiens 1995; Gascon et al. 1999; Daily et al. 2001). Several authors have discussed the idea that the "connectivity" of a landscape depends not only on the distance between habitat patches but also on the presence of movement corridors or stepping stones of natural habitat between fragments and the resistance of the matrix to interpatch movement by individuals (e.g.,

* E-mail: ricketts@stanford.edu.

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Taylor et al. 1993; Fahrig and Merriam 1994; Rosenberg et al. 1997).

While corridors and stepping stones have received much recent empirical investigation and public attention (e.g., Sutcliffe and Thomas 1996; Schultz 1998; Haddad 1999*b*; Laurance and Laurance 1999), the resistances of the matrix types themselves have been much less well studied. A few authors have developed models to simulate the effects of heterogeneous matrix on movement patterns and population persistence in hypothetical landscapes, using arbitrarily assigned values for matrix characteristics (Gustafson and Gardner 1996; Schippers et al. 1996). Others have tested whether patterns of patch occupancy are consistent with the hypothesis that resistances to interpatch dispersal differ among matrix types (Lomolino 1994; Aberg et al. 1995; Moilanen and Hanski 1998).

To date, however, few studies have measured matrix resistances directly by examining the rates of individual movement across different matrix types. Hokit et al. (1999) observed individual lizard behavior in experimental arenas of different vegetation types. They found that, although movement rates were significantly lower across matrix vegetation than across native habitat, the matrix types did not differ significantly in resistance to individual movement. Pither and Taylor (1998) used mark-recapture methods to compare the movement abilities of two sympatric damselfly species through two differing matrix types: forest and pasture. They found that one species moved significantly more readily through pasture than through forest but found no such difference in the other species. These studies indicate that the matrix can affect rates of interpatch movement, but these effects will likely differ among even closely related taxa (Robinson et al. 1992).

In this study, I tested whether the matrix can contribute significantly to patch isolation, using a butterfly community inhabiting meadow patches surrounded by two contrasting matrix types: conifer forest and willow thicket. Although not a human-fragmented landscape, this natural system provides an opportunity to investigate the matrix characteristics that may affect connectivity in any system of habitat patches or fragments (Roland et al. 2000). I used mark-recapture methods to measure butterfly movement among meadow patches and used maximum likelihood to estimate the relative resistance of each matrix type. Such field-derived estimates of matrix resistance may be useful in parameterizing simulation models like those discussed above (e.g., Gustafson and Gardner 1996) and may be incorporated into existing analytical models to improve their predictive ability in landscapes with heterogeneous interpatch matrix (Moilanen and Hanski 1998).

Field Methods

Study Site

I conducted this study in the Copper Creek Valley (3,050 m a.s.l.) near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. In this valley is a system of 14 meadow sites embedded in a matrix composed primarily of willow thicket and conifer forest (fig. 1). All meadow sites except two were approximately 2,200 m^2 in area, either incorporating an entire meadow patch or comprising a rectangular plot within a larger meadow. The two remaining sites (G and H) were approximately one-third the size of the others but were included nevertheless to allow short matrix routes between sites that were otherwise not available. Willow thickets were dominated by *Salix* spp., which grow to 2–4 m in height. Conifer forests were dominated by Engelmann spruce (*Picea engelmanni*), which grow to 8–14 m and are characterized by sparse, heavily shaded understories. Both matrix types contained occasional and small (5–50 m^2) openings with herbaceous vegetation.

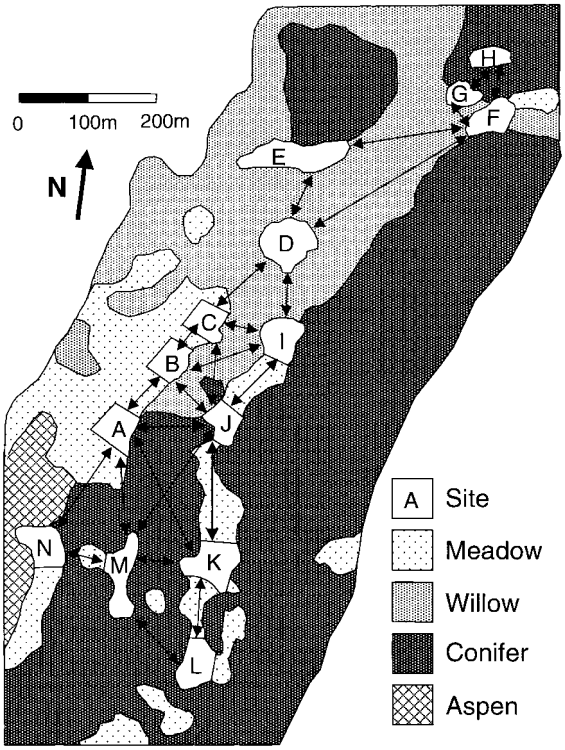

Figure 1: Map of 14 study sites with surrounding matrix vegetation. Connecting arrows indicate movement routes considered in the analyses. Map is not drawn precisely to scale and covers only the valley floor; steep valley walls are not shown. For simplicity, all features (e.g., forest gaps) smaller than approximately 1,000 m^2 are not shown.

Butterfly Mark-Release-Recapture

In these 14 sites, I conducted a mark-release-recapture study on 21 butterfly species (table 1). All the butterfly species treated here are meadow obligates, requiring meadow vegetation for both larval host plants and adult nectar sources. Previous butterfly surveys confirm that these 21 species are almost never found outside of meadows (T. H. Ricketts, G. C. Daily, and P. R. Ehrlich, unpublished data).

I sampled the meadow sites in rotation throughout the summer flight seasons (mid-June through late August) of 1998 and 1999. I conducted a time-constrained search in each site (usually 40–60 person min), marked each new individual with a unique number using a felt pen, recorded recaptures, and released all butterflies at the center of the site. For four species in which sex could be identified quickly (*Euchloe ausonia*, *Chlosyne palla*, *Phyciodes campestris*, and *Lycaena heteronea*), I recorded the sex for each individual captured. Typically, I sampled between seven and 14 sites each day, so that each site was visited every 1–2 d. Sampling was suspended on rainy and heavily overcast days, when butterflies were relatively inactive. Sampling effort (the number of person minutes), time of day, and weather conditions (cloud cover, temperature, and wind speed) were monitored to ensure equivalence among sites for each sampling rotation and throughout both sea-

Table 1: Butterfly species included in the study and the six taxa used for analysis

Species	Marks	Recap. rate	Wing length (mm)	Stay rate	Meadow rate	Matrix rate
Satyrinae (Nymphalidae):			21.5	.36	.27	.36
Cercyonis sthenele	43	.23				
Coenonympha tullia	72	.26				
Oeneis chryxus	458	.38				
Erebia epipsodea	525	.34				
Melitaeini (Nymphalidae):			19.1	.42	.21	.37
Phyciodes campestris	340	.23				
Chlosyne palla	397	.17				
Argynnini (Nymphalidae):			26.8	.44	.09	.47
Speyeria atlantis	536	.26				
Speyeria mormonia	1,039	.28				
Pierinae (Pieridae):			22.3	.27	.29	.43
Pieris callidice	37	.22				
Pieris protodice	127	.28				
Euchloe ausonia	164	.16				
Polyommatini (Lycaenidae):			14.0	.56	.11	.33
Plebejus acmon	40	.23				
Glaucopsyche lygdamus	50	.08				
Everes amyntula	196	.04				
Plebejus saepiolus	352	.21				
Plebejus glandon	377	.24				
Plebejus melissa	494	.15				
Lycaenini (Lycaenidae):			15.4	.59	.20	.20
Lycaena rubidus	95	.41				
Lycaena helloides	215	.20				
Lycaena nivalis	221	.30				
Lycaena heteronea	495	.23				
Total	6,273	.25				

Note: Mark-release-recapture data are summarized for each species, with mean wing length and frequencies of movements of different types reported for each taxon (see "Discussion"). Nomenclature follows Scott (1986). Marks = number of marked individuals; recap. rate = proportion of marked individuals recaptured at least once. Wing length = mean wing length for each taxon, using only the species included in this study. For 12 species, wing lengths were measured in the field from three to 10 specimens each; for nine species, wing lengths were measured from plates in Scott (1986; a crude method, but sufficient for this purpose). Taxon values are unweighted means across member species. Stay rate, meadow rate, and matrix rate are the fractions of total recaptures that represent no movement (i.e., same site), movement within a single meadow (e.g., from site C to site B; see fig. 1), and movement over matrix, respectively.

sons. Because the periods of peak flight during the season differed among species, butterflies were rarely so abundant as to prevent me from attempting to capture all individuals seen. Therefore, conducting the study on all species did not substantially decrease effort spent on any one species.

Matrix Composition

To characterize matrix composition, I walked three parallel, equally spaced transects between each pair of butterfly sampling sites. I recorded the type of vegetation cover every 5 m along each transect and used this sample to estimate the percentage composition of the matrix "routes" between sites. Although small aspen stands, a creek, and talus slopes were present in the matrix, the vast majority of it was composed of willow, conifer, or small meadow openings. I therefore restricted estimates of matrix composition to these three vegetation types (willow, conifer, and meadow). I used the length of the shortest transect as the distance between sites.

Site Boundaries and Meadow Quality

The composition of site boundaries may also influence movement rates of butterflies among patches by affecting the likelihood that a butterfly would emigrate from a patch (Kuussaari et al. 1996). To examine this possibility, I measured the perimeter of each site, categorizing the vegetation at the boundary as conifer, willow, or meadow. I then calculated percentage composition of the perimeter in terms of these three types.

Meadow quality also might affect the likelihood that a butterfly would emigrate from, or immigrate to, a meadow site (Kuussaari et al. 1996). To account for this, in 1999 I estimated four aspects of meadow quality at each site: vegetation cover and composition, flower density, temperature, and presence/absence of butterfly host plants. To estimate vegetation cover and composition, I established four permanent transects in each site, totaling 200 m in length. At the beginning, middle, and end of the 1999 flight season, I placed a 1-m^2 quadrat every 10 m along each transect and estimated the percentage cover of grasses, forbs, woody plants, and bare ground. I averaged these 1-m^2 samples to estimate percentage composition for each site.

To estimate flower density (a commonly used but crude measure of nectar availability; Kuussaari et al. 1996; Schultz and Dlugosch 1999), I used the same transects as above. Every week during the flight season, I counted the number of open, nonwilted flowers within a 1-m strip along each transect. Because the butterfly species treated here are known to be nectar generalists but prefer Asteraceae as nectar sources (Sharp et al. 1974; C. Boggs, personal communication; P. R. Ehrlich, personal communication; T. H. Ricketts, personal observation), I recorded two counts for each transect: the total number of flowers and the total number of flowers from species in the Asteraceae. I excluded several flower species (e.g., *Ipomopsis aggregata*, *Delphinium* spp., and species in the Umbelliferae) that are known not to be nectar sources for butterflies (C. Boggs, personal communication; P. R. Ehrlich, personal communication). I divided the flower counts by the total length of the four transects to estimate density for each site.

To compare temperature among sites, I placed shaded temperature loggers 25 cm off the ground in the center of each site. Loggers recorded air temperature every 15 min, and I calculated the average temperature of each site during the hours of peak butterfly activity (i.e., 1000–1600 hours) over three sunny days.

Finally, I searched each site for all locally occurring host plants of each butterfly species. Host plant information was taken from Scott (1986) and Opler et al. (1995), and locally occurring species (typically a small subset of those utilized over the entire range) were identified using the Rocky Mountain Biological Laboratory's herbarium. I recorded a plant species as present if I found at least one individual in the site and absent if I spent 1 hr searching for it without success.

Analyses

Butterfly Taxa

Because butterfly species vary in vagility and flight behavior, analyzing movement patterns of each species separately would be ideal. However, recaptures were not numerous enough to allow separate analyses for each species. I therefore grouped the 21 butterfly species into six higher taxa and analyzed each taxon individually. I divided the community into subfamilies and then into tribes (for the subfamilies in which tribes are recognized), resulting in a relatively even distribution of species into the six taxa (table 1). I thus assumed that the species in each taxon have similar vagilities and tendencies to disperse out of meadow habitat relative to species in the other taxa. My field observations over 3 yr in the region, in addition to published reports (Scott 1975; Shreeve 1981), support this assumption.

Allowed Movement Routes

In the following analyses, I included only butterfly movements between neighboring sites. In figure 1, the 14 meadow sites are connected by arrows to their nearest neighbors in each direction (using compass sectors of approximately 30° and maximum distance of 300 m), re-

sulting in a total of 50 "allowed" routes (both directions along each of the 25 lines in fig. 1). If a butterfly was captured in a given site and next recaptured in a site on the other end of an allowed route, I assumed that the butterfly flew directly between the two sites along that route. Restricting my analyses to movements between neighboring sites minimized assumptions about the actual routes taken by the butterflies (e.g., a butterfly marked in site N and next recaptured in site J may have traveled over a variety of routes). Of all recorded butterfly movements, 70% were over allowed routes.

Matrix Resistance Estimates

I used maximum likelihood to estimate the resistances of the two different matrix types to butterfly movement (Hilborn and Mangel 1997). I modeled the frequency of butterfly movements as an inverse power function of the distance between sites:

$$T_{jk} = \frac{a}{(D_{jk})^z}, \tag{1}$$

where T_{jk} is the number of butterflies transferring from site k across route j, D_{jk} is the distance of the route, and a and z are fitted constants. Baguette et al. (2000) and Hill et al. (1996) found that inverse power functions described distributions of movement distances well for three different butterfly species. For two of these species, inverse power functions fit observed data better than did negative exponential functions (e.g., Hanski 1994). An inverse power function is thus a reasonable model on which to base the likelihood function.

To account for the resistances of different matrix types, I expanded the distance term, D_{jk}, in equation (1) into its meadow, willow, and conifer components, with each of the latter two multiplied by a resistance parameter. Thus, T_{jk} becomes

$$T_{jk} = \frac{a}{(D_{\mathrm{m},jk} + r_{\mathrm{w}} D_{\mathrm{w},jk} + r_{\mathrm{c}} D_{\mathrm{c},jk})^z}, \tag{2}$$

where $D_{\mathrm{m},jk}$, $D_{\mathrm{w},jk}$, and $D_{\mathrm{c},jk}$ are the distances of route j across meadow, willow, and conifer, respectively (calculated as the total distance of route j multiplied by the route's proportional composition of these three vegetation types), and r_{w} and r_{c} are the resistance parameters of willow and conifer matrix, respectively. In this formulation, the resistance parameters are normalized such that meadow resistance equals 1 and thus r_{w} and r_{c} describe the matrix resistances relative to meadow.

The probability of a butterfly leaving site k along route j, given that it left site k along some allowed route, is

$$p_{jk} = \frac{T_{jk}}{\sum_{i=1}^{h_k} T_{ik}}, \tag{3}$$

where h_k is the number of allowed routes leading from site k to other sites. (Note that eq. [3] is a ratio of two terms containing a, so a is eliminated and need not be considered further.) The pattern of butterfly emigration from sites can thus be described by a multinomial distribution, assuming that butterflies behave independently of each other but follow the same movement probabilities.

Based on this multinomial distribution, the likelihood of obtaining the observed counts of butterflies exiting site k over the h_k possible routes is

$$L_k\left(\vec{\mathbf{x}} \,\middle|\, r_{\mathrm{c}}, r_{\mathrm{w}}, z\right) = \frac{h_k!}{\prod_{j=1}^{h_k} x_{jk}!} \times \prod_{j=1}^{h_k} p_{jk}^{x_{jk}}, \tag{4}$$

where $\vec{\mathbf{x}}$ is the matrix of $\{x_{jk}\}$, or the observed numbers of butterflies leaving site k over route j. Equation (4) states that the likelihood of obtaining the observed data ($\vec{\mathbf{x}}$) given the three parameters, r_{w}, r_{c}, and z, is based on the expected probabilities of moving across each route (from eq. [3]) and the observed butterfly movements over those routes. Finally, the likelihood function for the entire data set (i.e., all 14 sites) is

$$L\left(\vec{\mathbf{x}} \,\middle|\, r_{\mathrm{c}}, r_{\mathrm{w}}, z\right) = \prod_{k=1}^{14} \left[\frac{h_k!}{\prod_{j=1}^{h_k} x_{jk}!} \times \prod_{j=1}^{h_k} p_{jk}^{x_{jk}}\right]. \tag{5}$$

I wrote a program in MATLAB4 to find the values of r_{w} and r_{c} that maximize equation (5) for each movement model and each butterfly taxon. The program evaluated equation (5) over values of r_{w} and r_{c} ranging from 0.1 to 14.0 (step unit = 0.01) and returned the maximum value over this likelihood surface. I then tested two null hypotheses in sequence.

Null 1. Meadow, willow, and conifer all have equal resistances to butterfly movement (i.e., $r_{\mathrm{w}} = r_{\mathrm{c}} = 1$). In this case, the model for butterfly movement is given by equation (1). If "null 1" was rejected, I then tested "null 2."

Null 2. Willow and conifer resistances may differ from meadow resistance but are equal to each other (i.e., $r_{\mathrm{w}} = r_{\mathrm{c}} = r$). In this case the model for butterfly movement is

$$T_{jk} = \frac{a}{(D_{\mathrm{m},jk} + rD_{\mathrm{w},jk} + rD_{\mathrm{c},jk})^z}. \tag{6}$$

To test these hypotheses, I determined whether the maximum likelihood estimates obtained from the general model

(eq. [2]) were significantly different from those obtained from the two constrained models (eqq. [1] and [6]) using likelihood ratio tests. In these tests, the likelihood of the general model (L_{gen}) is divided by the likelihood of the constrained model (L_{con}). The statistic, $-2\ln(L_{gen}/L_{con})$, is distributed approximately as χ^2, with degrees of freedom equal to the difference in the number of parameters between the two models (Hilborn and Mangel 1997).

Because relative matrix resistance is the focus of this article (and not the value of z), I simplified the analyses by assuming $z = 1$. Published estimates of z for butterflies range from 1.00 (Baguette et al. 2000) to near 1.20 (Hill et al. 1996; Baguette et al. 2000). To examine whether increasing z affected my results, I repeated the analyses assuming $z = 1.5$.

Site Boundaries and Meadow Quality

I also examined whether the rate of butterfly emigration from sites was related to the vegetational composition of site boundaries. Following Sutcliffe et al. (1997), I defined emigration rate (E) and immigration rate (I, to be used below) as

$$E = \frac{e}{e + r}, \tag{7}$$

$$I = \frac{i}{i + r}, \tag{8}$$

where e is the number of emigrants (individuals captured in a site and next recaptured in any other site), i is the number of immigrants (individuals recaptured in a site that had last been captured in any other site), and r is the number of residents (individuals captured in a site and next recaptured in that same site). I used backward stepwise regression to relate E for each taxon to the proportional composition of site perimeters in terms of conifer, willow, and meadow. All variables were arcsine transformed prior to regression analyses to improve normality.

I also examined how butterfly emigration and immigration rates were related to meadow quality. I used backward stepwise regression again to relate E and I for each taxon to seven habitat quality variables for each site: mean temperature during peak flight time (1000–1600 hours), mean and maximum density of all flowers over the eight weekly samples, mean and maximum density of composite flowers (Asteraceae) over the eight weekly samples, and mean percentage cover of bare ground and of forbs over the three monthly samples. Emigration rate, immigration rate, and percentage cover variables were arcsine transformed prior to regression analyses, all of which were performed using SYSTAT 7.0.1 (SPSS 1997).

Results

During the two field seasons, I marked 6,273 individuals of the 21 butterfly species and recorded 2,482 recaptures. Recapture rates varied among species, but overall, 25% of butterfly individuals were recaptured at least once (table 1).

Matrix Resistance Estimates

The likelihood function for each taxon displays a single smooth peak over the parameter space of r_w and r_c (fig. 2). On each panel in figure 2, the asterisk marks the point of maximum likelihood. The "×" marks the point $r_w = r_c = 1$ (representing null hypothesis 1: meadow, willow, and conifer resistances all equal). The diagonal black line represents $r_w = r_c$, and the circle marks the maximum point along this line (representing null hypothesis 2: willow and conifer resistances equal). These points are plotted for all taxa together in figure 3.

For four of the butterfly taxa (Satyrinae, Melitaeini, Pierinae, and Polyommatini), conifer is significantly more resistant to butterfly movement than is willow (fig. 3; table 2). The maximum likelihood estimates obtained with the general movement model (i.e., unconstrained r_w and r_c parameters) are significantly different than those obtained with either constrained model, and thus both null hypotheses are rejected. For these four taxa, conifer resistance is between three and 12 times higher than willow resistance (fig. 3).

The results for the two remaining taxa deviate from the above pattern in differing ways. For the Lycaenini, r_w and r_c are significantly >1 but are not significantly different from each other; therefore, the first null hypothesis is rejected but the second is not (fig. 3; table 2). This result suggests that, for the Lycaenini, the matrix is a significant filter to dispersal but that the two types of matrix—willow and conifer—do not differ in their relative resistances. For the Argynnini, r_w and r_c do not differ significantly from 1, so that neither null hypothesis is rejected (fig. 3; table 2). For this taxon, willow and conifer are no more resistant to movement than meadow habitat itself.

Repeating these analyses assuming $z = 1.5$ yields similar qualitative results (not shown). Estimates of r_w and r_c are smaller, as would be expected, but the results of all likelihood ratio tests are the same. Thus, the results appear robust to the range of z estimates reported for butterflies in the literature (Hill et al. 1996; Baguette et al. 2000).

Site Boundaries and Meadow Quality

Only one taxon showed any significant relationship between emigration rate and boundary composition of sites; emigration rate of the Lycaenini increased with the pro-

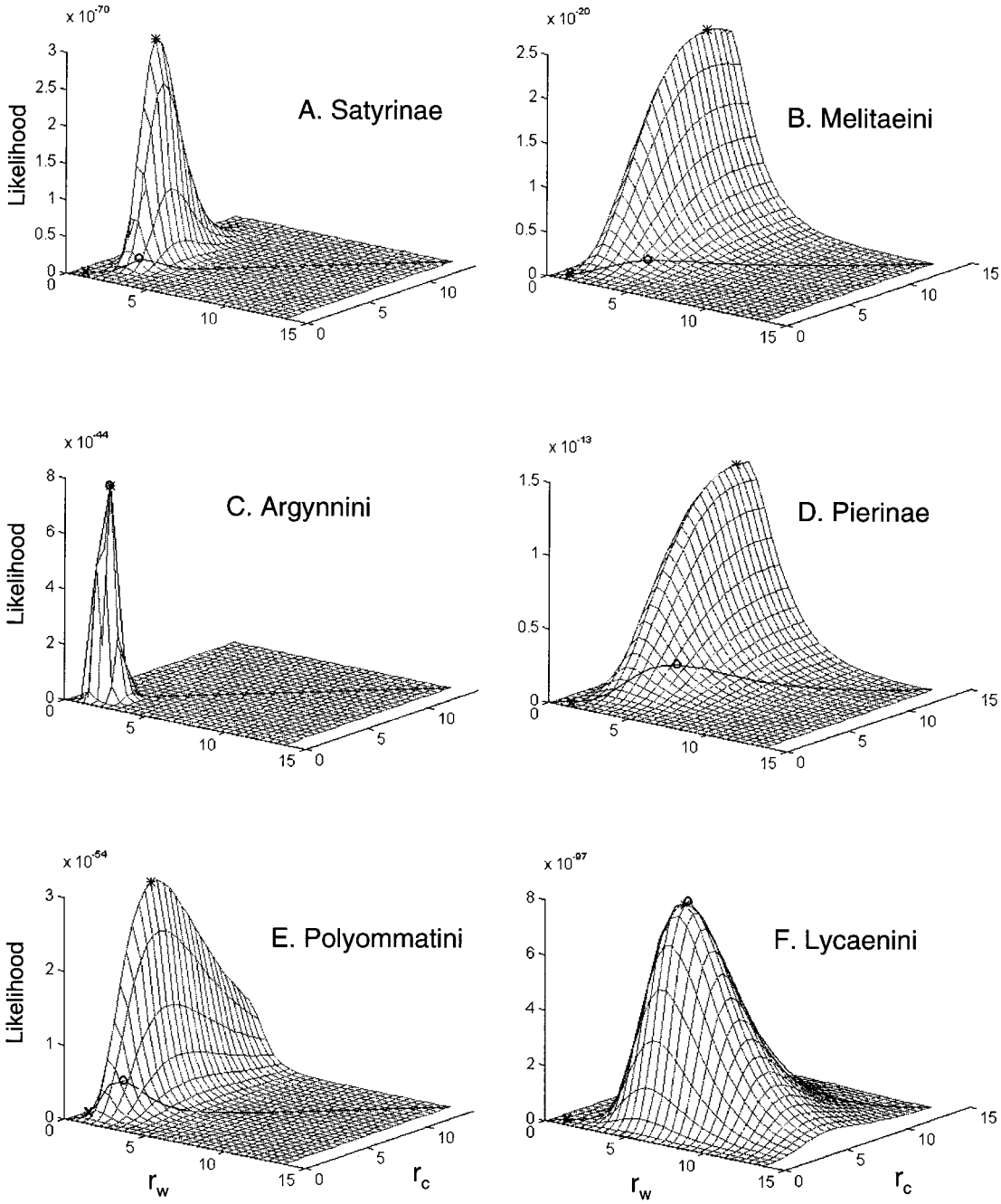

Figure 2: Likelihood surface plots for the six butterfly taxa (with $z = 1$)

portion of willow in site boundaries (fig. 4; $E = 0.237 + 0.648$ [willow]; $r^2 = 0.632$, $F = 18.912$, df $= 1$, $P = .001$). In this relationship, however, site D is an outlier with large leverage (fig. 4; Studentized residual $= 2.79$). Site D was almost entirely surrounded by willow and had an emigration rate of 100% for the Lycaenini, but this rate is based on only four recaptured individuals (none of which remained in the site) and is thus unlikely to be reliable. If site D is removed, the relationship is no longer significant ($P > .20$).

In examining the influence of habitat quality, I found no clear relationship between rates of emigration or immigra-

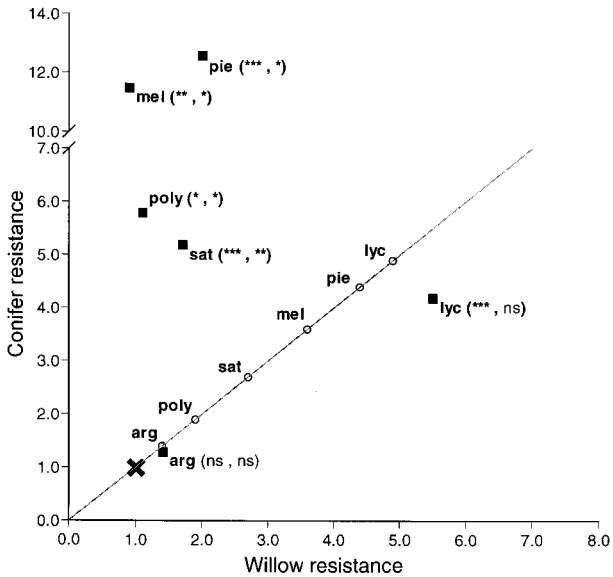

Figure 3: Resistance estimates for all taxa. This graph is equivalent to looking straight down onto the surface plots in figure 2. Filled squares mark the maximum likelihood estimates of r_w and r_c for each taxon. The "×" marks the location of $r_w = r_c = 1$. The diagonal line represents $r_w = r_c$, and open circles mark the maximum point for each taxon along this line. Taxon codes: *sat* = Satyrinae, *mel* = Melataeini, *arg* = Argynnini, *pie* = Pierinae, *poly* = Polyommatini, *lyc* = Lycaenini. The results of likelihood ratio tests for the two null hypotheses are in parentheses (null 1, null 2): $^{*}P < .05$; $^{**}P < .01$; $^{***}P < .001$; NS = not significant.

tion and the seven habitat quality variables (table 3). Although stepwise regression revealed significant relationships between some habitat quality variables and one of the two rates in certain taxa, no single variable had a consistent effect on more than one taxon. The sign of some relationships was actually opposite to expectation (e.g., maximum flower density was positively related to emigration rate in the Argynnini), and the results were in conflict at times (e.g., emigration rate in the Pierinae was positively related to maximum density of composite flowers but negatively related to the mean density of composite flowers). Indeed, with a Type I error rate (α) of 0.05 and 84 comparisons (seven variables × six taxa × two rates), one would expect four to five significant relationships due to chance alone. I found eight.

In addition, in every site I recorded at least one host plant species for every butterfly species except *Plebejus saepiolus* (Polyommatini). Host plants for *P. saepiolus* were present in about one-half of the sites (host plant data not shown).

Pooling Years and Sexes

In the above analyses, I pooled both years of data and both sexes for each species. Thus, the analyses rest on two additional assumptions: that butterfly movement patterns were similar between the 2 yr and that males and females move similarly in the landscape. Sample sizes did not allow maximum likelihood estimates of matrix resistance for each year or each sex separately. I examined other aspects of movement patterns, however, to test these two assumptions.

To examine the similarity between years, I tested, across species, whether individual abundance, recapture rate, and emigration rate (E) were correlated between the 2 yr. I also tested, across sites, whether emigration rate (all species pooled) and abundance of each taxon, separately, were correlated between years. All correlations were significant (Spearman rank correlations, $P < .05$), and all but one were highly significant ($P < .01$), suggesting that simple community attributes (e.g., relative abundance) and movement patterns were similar in 1998 and 1999.

To examine the similarity between sexes, I compared the sex ratio of all recaptures to that of recaptures representing transfers between sites. For the four species for which I collected sex data, the sex ratios of transferring individuals did not differ significantly from those expected from the sex ratio of all recaptures (exact binomial tests, *Chlosyne palla*, *Phyciodes campestris*, and *Euchloe ausonia*, $P > .50$; *Lycaena heteronea*, $P > .10$). This suggests that males and females, at least in these four species, display the same tendency to move among sites at this scale (Shreeve 1981).

Table 2: Maximum likelihood estimates for matrix permeabilities (r_w and r_c) and results of likelihood ratio tests for the two null hypotheses (with $z = 1$)

Taxon ($z = 1$)	r_w	r_c	Null 1	Null 2	n
Satyrinae	1.7	5.2	31.29***	6.72**	231
Melitaeini	.9	11.5	12.59**	6.55*	51
Argynnini	1.4	1.3	2.70 NS	.09 NS	308
Pierinae	2.0	12.6	17.15***	4.30*	41
Polyommatini	1.1	5.8	7.41*	4.33*	80
Lycaenini	5.5	4.2	28.40***	.23 NS	111

Note: Null hypothesis 1: meadow, willow, and conifer resistances are all equal ($r_w = r_c = 1$); df = 2. Null hypothesis 2: willow and conifer resistances may differ from 1, but they are equal to each other ($r_w = r_c$); df = 1. NS = not significant.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

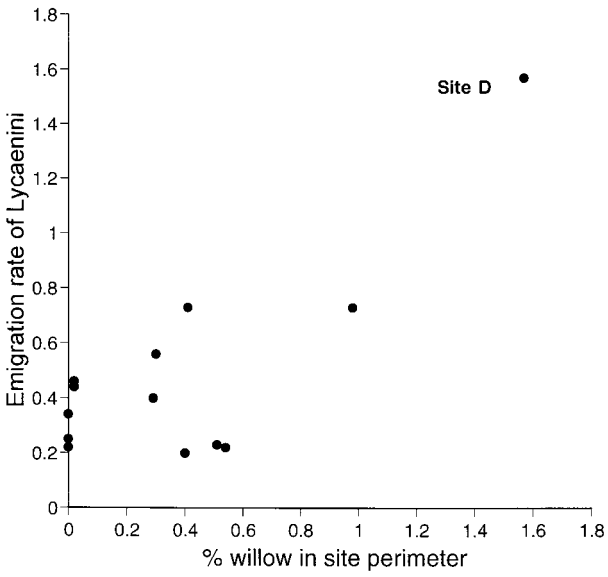

Figure 4: Relationship between willow composition of site perimeters and emigration rate of the Lycaenini. Both variables are arcsine transformed.

Discussion

Butterfly Movement Rates

The results presented here indicate that the type of intervening matrix can significantly influence the effective isolation of habitat patches. For four of the six butterfly taxa, the matrix matters: conifer is more resistant to butterfly movement than is willow (fig. 3), so sites separated by conifer are more effectively isolated than those separated by willow.

The two exceptions to this pattern are illuminating. The Lycaenini appear to move frequently within meadow habitat but are much less likely to leave the patches, regardless of the composition of the intervening matrix (fig. 3). The sedentary tendencies of the Lycaenini are corroborated by at least two other lines of evidence. This taxon has the second lowest mean wing length (a commonly assumed, although poorly tested, correlate of vagility; Van Dyke and Matthysen 1999) and the lowest rate of matrix movements (i.e., fraction of recaptures representing movement over matrix) of any taxon (table 1, "matrix rate"). On the other hand, the Argynnini appear to move across meadow and both matrix types with equal ease and thus perceive few barriers to movement in the landscape (fig. 3). Again, this result agrees with other evidence on vagility. The Argynnini have the highest mean wing length of the six taxa, the highest matrix movement rate (table 1), and are clearly the strongest (i.e., fastest) flyers (C. Boggs, personal communication; P. R. Ehrlich, personal communication; T. H. Ricketts, personal observation). Because these two taxa represent the extremes of vagility in this butterfly community, their distinct patterns of movement are not surprising, and they may be considered to support the rule reflected in the other four taxa: for species with intermediate levels of vagility, matrix type significantly affects rates of interpatch movement.

Although matrix composition appears to affect butterfly movement between sites (at least for most taxa), the composition of the site boundaries themselves does not seem to influence the rate at which butterflies exit sites initially. The emigration rate of only one taxon was related to any boundary composition variable, and even this relationship appears to be driven by a single outlying site (fig. 4). These results are somewhat counterintuitive, given the emphasis placed on boundary effects in fragmented landscapes (e.g., Kuussaari et al. 1996; Haddad 1999*b*). It could be simply that edge effects are not as important as the composition of the entire matrix in determining rates of butterfly movement in this system. Alternatively, the emigration metric used here, which relies on recapturing an individual elsewhere and aggregates movements in all directions, may not be sufficiently sensitive to detect the importance of boundary effects.

Movement among sites also does not appear to relate to differences in meadow quality; none of the seven habitat quality variables were consistently related to rates of emigration or immigration. Although this seems contrary to intuition and to previous field studies (e.g., Kuussaari et al. 1996), perhaps variation in meadow quality, while measurable, was not sufficient to influence butterfly movement patterns. Host plant presence/absence is also unlikely to have influenced butterfly movement strongly, as I found at least one host plant species in every site for every butterfly species except one (*Plebejus saepiolus*). It is possible, however, that some of these measures did not capture relevant aspects of habitat quality. For example, it would be preferable to measure nectar availability directly than to rely on flower density as a surrogate measure (Schultz and Dlugosch 1999), and one might expect butterflies to respond to the density of host plants in sites as well as simply their presence/absence (Baker 1984). Constraints on field time prevented these more meaningful measures.

The resistance estimates I report here probably apply to the movement of individuals within local landscapes, as opposed to long-distance dispersal or migration. Larger-scale movements are likely triggered by different behavioral cues (Baker 1984; Harrison 1989), and dispersing or migrating butterflies probably respond to landscape structure differently than those moving at smaller scales. Although none of the species considered here are migratory, some evidence suggests that at least some species occasionally move much larger distances than I was able to study in this landscape. Three butterfly individuals marked in my

Table 3: Results of multiple stepwise regression relating butterfly emigration rate and immigration rate to site-quality variables

Taxon	Temp	Mean flowers	Max flowers	Mean composites	Max composites	%cover bare	%cover forbs
Emigration rates:							
Satyrinae							
Melitaeini							
Argynnini			+				−
Pierinae			−	(−)	(+)		
Polyommatini							
Lycaenini							
Immigration rates:							
Satyrinae							
Melitaeini						+	
Argynnini	(−)	(+)					
Pierinae							
Polyommatini							
Lycaenini							

Note: Symbols in cells represent variables remaining in the model after backward elimination was completed. Plus sign represents a positive relationship, and minus sign represents a negative relationship. Symbols in parentheses: $.05 > P > .01$; symbols not in parentheses: $P < .01$. See methods for explanation of habitat quality variables.

sites were recaptured by other researchers 1.8 km away (two *Erebia epipsodia* and one *Speyeria mormonia*), and Boggs (1987) has documented movements of up to 1.7 km by *S. mormonia* in the same region. Although long-distance movements may be important to the population dynamics and genetic structure of some species (Hill et al. 1996), they are difficult to detect and thus difficult to study directly. Studying individual movement at intermediate landscape scales, where movement rates are high enough to analyze rigorously, may provide a useful link between these important large-scale processes and more abstract experimental systems at smaller scales (e.g., Wiens et al. 1997; Andreassen et al. 1998).

In addition to the mark-recapture technique used here, a behavioral approach would also be useful in comparing butterfly movement rates across different matrix types (Turchin et al. 1991). Several studies have quantified movement behaviors (e.g., step length and turning angle) of butterflies to examine edge-avoidance behavior (Haddad 1999*b*) and to parameterize correlated random-walk models (Turchin 1998). Such behavioral data provide a mechanistic understanding of movement that is missed by mark-recapture and would allow one to predict movement rates in any landscape configuration using simulation models (Doak et al. 1992; Schultz 1998). These predictions, however, involve large extrapolations from small-scale behaviors to landscape phenomena. Since many landscape models are phenomenological (e.g., metapopulation models that consider successful movement between patches), mark-recapture approaches, which measure the phenomenon directly, may be sufficient for estimating parameters such as matrix resistance. Nevertheless, the two approaches are clearly complementary.

Theoretical and Conservation Implications

The results presented here suggest that simple models assuming a homogeneous matrix ignore a potentially important aspect of patch isolation. This simplicity has been pointed out by landscape ecologists (e.g., Taylor et al. 1993; Fahrig and Merriam 1994), but the sheer complexity of real landscapes has hampered efforts to develop modeling frameworks that capture all important spatial features (Wiens et al. 1993; Wiens 1995). A promising start toward solving this problem may be to incorporate certain aspects of matrix heterogeneity into well-developed and relatively simple modeling approaches such as island biogeography or metapopulation dynamics (e.g., Moilanen and Hanski 1998). Because the rate of interpatch movement is a crucial parameter to the predictions of both models (Hansson 1991), adding parameters that describe the relative resistances of different matrix types may significantly improve their predictive power (Hokit et al. 1999).

The hypothesis that rates of interpatch dispersal differ among matrix types also generates a set of predictions, based on island biogeography and metapopulation theory (MacArthur and Wilson 1967; Hanski 1998), that are testable with field observations. For example, comparatively resistant matrix types should result in decreased species richness in isolated patches (Lomolino 1994; Aberg et al. 1995), lower patch occupancy within a metapopulation (Moilanen and Hanski 1998), and lower levels of gene

flow among isolated populations (Westerbergh and Saura 1994).

In addition to its theoretical applications, the idea of effective isolation also has important conservation implications. One of the central concerns regarding fragmented landscapes is the genetic and demographic risk of isolation (Meffe and Carroll 1994; Sutcliffe and Thomas 1996; Rosenberg et al. 1997; but see Simberloff et al. 1992). In efforts to increase the connectivity of fragmented landscapes (Taylor et al. 1993), conservation biologists have focused on the distribution of remnant fragments and the presence of stepping stones and corridors of natural or seminatural habitat (Doak et al. 1992; Sutcliffe and Thomas 1996; Schultz 1998; Haddad 1999*a*). It often may be more feasible, however, to reduce the effective isolation of fragments by altering management practices in the surrounding matrix than to reconnect them with restored corridors (Simberloff et al. 1992; Mann and Plummer 1995; Bowne et al. 1999). Models modified to incorporate matrix resistance may even allow landscape planners to compare the effects of alternative management strategies (e.g., agricultural production regimes) on the effective isolation of habitat remnants (Gustafson and Gardner 1996; Schippers et al. 1996).

How applicable are the results from this model system to other landscapes, particularly human-fragmented areas? In this study, matrix resistance was probably related to some combination of vertical vegetation structure, light environment, and temperature. Conifer forests are taller, darker, and colder than willow thickets (data not shown) and probably discourage butterflies more strongly from crossing them. Many human-fragmented landscapes are characterized by the opposite structural relationship between patch and matrix: forest remnants surrounded by more open agricultural land uses. Nevertheless, in these systems, the patches and matrix also differ markedly in thermal characteristics, and these factors will likely be important to butterflies in human-fragmented landscapes as well (Daily and Ehrlich 1996). In general, the resistance of a given matrix type will depend on the interaction between autecological traits of species and characteristics of the matrix (Dennis and Shreeve 1997; Henein et al. 1998; Gascon et al. 1999). Matrix resistance therefore may be expected to vary among differing species (e.g., homothermic vs. poikilothermic animals). Indeed, responses to the matrix differed even among butterfly taxa in this study, suggesting that the general effects of matrix on interpatch movement will be difficult to predict (Offerman et al. 1995; Daily and Ehrlich 1996; Wiens et al. 1997; Pither and Taylor 1998). Understanding the factors that determine this variability in matrix resistance may not only further our ecological understanding of fragmented landscapes but also improve our ability to conserve species inhabiting them.

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Literature Cited

Aberg, J., G. Jansson, J. E. Swenson, and P. Angelstam. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. Oecologia (Berlin) 103:265–269.

Andreassen, H. P., K. Hertzberg, and R. A. Ims. 1998. Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. Ecology 79:1223–1235.

Baguette, M., S. Petit, and F. Queva. 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. Journal of Applied Ecology 37:1–10.

Baker, R. R. 1984. The dilemma: when and how to go or stay. Pages 279–296 *in* R. I. Vane-Wright and P. R. Ackery, eds. The biology of butterflies. Academic Press, London.

Bierregaard, R. O. J., T. E. Lovejoy, V. Kapos, A. A. D. Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments: a prospective comparison of fragments and continuous forest. BioScience 42:859–866.

Boggs, C. L. 1987. Within population variation in the demography of *Speyeria mormonia* (Lepidoptera: Nymphalidae). Holarctic Ecology 10:175–184.

Bowne, D. R., J. D. Peles, and G. W. Barrett. 1999. Effects of landscape spatial structure on movement patterns of

the hispid cotton rat (*Sigmodon hispidus*). Landscape Ecology 14:53–65.

Daily, G. C., and P. R. Ehrlich. 1996. Nocturnality and species survival. Proceedings of the National Academy of Sciences of the USA 93:11709–11712.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: utilization of human dominated habitats by the avifauna of southern Costa Rica. Ecological Applications 11:1–13.

Darwin, C. 1859. The origin of species by means of natural selection. J. Murray, London.

Dennis, R. L. H., and T. G. Shreeve. 1997. Diversity of butterflies on British islands: ecological influences underlying the roles of area, isolation and the size of the faunal source. Biological Journal of the Linnean Society 60:257–275.

Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biology 41:315–336.

Ehrlich, P. R., and D. D. Murphy. 1987. Conservation lessons from long-term studies of checkerspot butterflies. Conservation Biology 1:122–131.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8:50–59.

Gascon, C., T. E. Lovejoy, R. O. Bierregaard, J. R. Malcolm, P. C. Stouffer, H. L. Vasconcelos, W. F. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91:223–229.

Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77:94–107.

Haddad, N. M. 1999*a*. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. Ecological Applications 9:612–622.

———. 1999*b*. Corridor use predicted from behaviors at habitat boundaries. American Naturalist 153:215–227.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

———. 1998. Metapopulation dynamics. Nature (London) 396:41–49.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89–104.

Harrison, S. 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. Ecology 70:1236–1243.

Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly *Euphydryas editha bayensis*: evidence for a metapopulation model. American Naturalist 132:360–382.

Henein, K., J. Wegner, and G. Merriam. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. Oikos 81:168–186.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, N.J.

Hill, J. K., C. D. Thomas, and O. T. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. Journal of Animal Ecology 65:725–735.

Hobbs, R. J., D. A. Saunders, and G. W. Arnold. 1993. Integrated landscape ecology: a Western-Australian perspective. Biological Conservation 64:231–238.

Hokit, D. G., B. M. Stith, and L. C. Branch. 1999. Effects of landscape structure in Florida scrub: a population perspective. Ecological Applications 9:124–134.

Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. Journal of Animal Ecology 65:791–801.

Laurance, S. G., and W. F. Laurance. 1999. Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. Biological Conservation 91:231–239.

Lomolino, M. V. 1994. Species richness of mammals inhabiting nearshore archipelagoes: area, isolation, and immigration filters. Journal of Mammalogy 75:39–49.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Mann, C. C., and M. L. Plummer. 1995. Are wildlife corridors the right path? Science (Washington, D.C.) 270: 1428–1430.

Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sinauer, Sunderland, Mass.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503–2515.

Offerman, H. L., V. H. Dale, S. M. Pearson, R. O. J. Bierregaard, and R. V. O'Neill. 1995. Effects of forest fragmentation on Neotropical fauna: current research and data availability. Environmental Reviews 3:191–211.

Opler, P. A., H. Pavulaan, and R. A. Stanford. 1995. Butterflies of North America. Northern Prairie Wildlife Research Center Home Page (http://www.npwrc.usgs.gov/resource/distr/lepid/bflyusa/bflyusa.htm), Jamestown, N.Dak.

Pither, J., and P. D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos 83:166–174.

Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. Science (Washington, D.C.) 257:524–526.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine

Parnassius butterfly dispersal: effects of landscape and population size. Ecology 81:1642–1653.

Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Biological corridors: form, function, and efficacy. BioScience 47:677–687.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18–32.

Schippers, P., J. Verboom, J. P. Knaapen, and R. C. van Apeldoorn. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. Ecography 19:97–106.

Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. Conservation Biology 12:284–292.

Schultz, C. B., and K. M. Dlugosch. 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia (Berlin) 119:231–238.

Scott, J. A. 1975. Flight patterns among 11 species of diurnal Lepidoptera. Ecology 56:1367–1377.

———. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, Calif.

Sharp, M. A., D. R. Parks, and P. R. Ehrlich. 1974. Plant resources and butterfly habitat selection. Ecology 55: 870–875.

Shreeve, T. G. 1981. Flight patterns of butterfly species in woodlands. Oecologia (Berlin) 51:289–293.

Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology 6:493–504.

Soulé, M. E., A. C. Alberts, and D. T. Bolger. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63:39–47.

SPSS. 1997. SYSTAT. Version 7.0.1. SPSS, Chicago.

Sutcliffe, O. L., and C. D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. Conservation Biology 10:1359–1365.

Sutcliffe, O. L., C. D. Thomas, and D. Peggie. 1997. Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. Oecologia (Berlin) 109:229–234.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Thomas, C. D., J. A. Thomas, and M. S. Warren. 1992. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. Oecologia (Berlin) 92: 563–567.

Tilman, D., and P. Kareiva, eds. 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, N.J.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer, Sunderland, Mass.

Turchin, P., F. J. Odendaal, and M. D. Rausher. 1991. Quantifying insect movement in the field. Environmental Entomology 20:955–963.

Van Dyke, H., and E. Matthysen. 1999. Habitat fragmentation and insect flight: a changing "design" in a changing landscape? Trends in Ecology & Evolution 14:172–174.

Westerbergh, A., and A. Saura. 1994. Gene flow and pollinator behaviour in *Silene dioica* populations. Oikos 71: 215–224.

Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1–26 *in* L. Hansson, L. Fahrig, and G. Merriam, eds. Mosaic landscapes and ecological processes. Chapman & Hall, London.

Wiens, J. A., R. L. Schooley, and R. D. Weeks. 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos 78:257–264.

Wiens, J. A., N. C. Stenseth, B. Van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369–380.

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