

The Dispersal System of a Butterfly: A Test of Source-Sink Theory Suggests the Intermediate-Scale Hypothesis

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ABSTRACT: Theory predicts source-sink dynamics can occur in species with the ideal preemptive distribution but not with the ideal free distribution. Source-sink dynamics can also occur in species with passive dispersal, in which a fixed fraction of the population disperses each generation. However, in nature, dispersal often approximates random diffusion rather than ideal choices or fixed probabilities. Here, I ask which dispersal system occurred in a butterfly (*Euphydryas editha*) known to have source-sink dynamics. The study used 13 experimental sites, where vacant and occupied habitat patches were juxtaposed. I estimated movement during the flight season and tested hypotheses about the type of dispersal system. Ideal free and ideal preemptive models were rejected because per capita movement rates were density independent. Passive dispersal was rejected because per capita rates were related to patch area and habitat preference. The diffusion model best explained the data because it predicted both the area relationship and an odd feature of the habitat preference: immigration was not higher in preferred habitat; rather, emigration was lower. The diffusion model implied that source-sink dynamics were driven by diffusion from areas of high to low population density. Existing source-sink theory assumes fine-scale patchiness, in which animals have perfect knowledge and ease of mobility. The results from the butterfly suggest that source-sink dynamics arise at coarser spatial scales, where diffusion models apply.

Keywords: source sink, dispersal, habitat, diffusion, ideal free distribution.

A premise of most ecological studies is that populations occur in a habitat that is suitable for their persistence (e.g., Verner et al. 1986). The premise is based on Hutchinson's (1958) concept of the fundamental niche, defined as the range of environmental conditions in which a species has fitness of at least 1. The niche concept is a cornerstone of

ecology (Real and Levin 1991), and introductory texts usually argue that species do not persist in a habitat outside their fundamental niche (e.g., Begon et al. 1986; Pianka 1988). In the past decade, source-sink theory has questioned this premise (Pulliam 1988; Dias 1996). The essential feature of source-sink systems is a sustained flow of organisms out of some habitats (sources) and into others (sinks). Because sinks continually receive immigrants, they can lie outside the fundamental niche and yet have populations that persist indefinitely. Theoretically, it is possible for more organisms to be found in sinks than in sources (Pulliam 1988; Pulliam and Danielson 1991). If such cases were common, then assuming a "hand-in-glove" relationship between a species and its fundamental niche (Pulliam 1997) would tend to mislead conservation strategies. In both theory and practice, biologists need to know when to expect the occurrence of source-sink systems.

By definition, emigrants must outnumber immigrants in sources, with the reverse case in sinks. To maintain the flow over time, births must outnumber deaths in sources, with the reverse case in sinks. To test the theory, empirical studies have focused on habitat differences in birth and death rates but have obtained mixed results. Diffendorfer (1998) reviewed studies of 25 vertebrates and three plants and claimed that only the plant studies showed clear evidence for source-sink dynamics (the studies are Keddy 1981; Watkinson et al. 1989; Kadmon and Shmida 1990). Four vertebrates showed evidence for the competing "balanced-dispersal" theory (Doncaster et al. 1997; Diffendorfer 1998), which predicts zero net flow. The other studies were ambiguous by his criteria. One reason for the ambiguity was noisy data—demographic data tend to be highly variable and difficult to gather. Direct estimates of births and deaths, with statistical significance between habitats, are rarely obtained. Diffendorfer (1998) concluded that the evidence for source-sink dynamics was weak, and the importance of the theory is still an open question.

Dispersal systems are a key to resolving this question, but first, it is necessary to draw a distinction between true sinks and pseudosinks (Watkinson and Sutherland 1995).

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Both are sinks in that they consistently receive immigration from nearby sources. Here is the distinction: true sinks are habitats outside the fundamental niche. If net immigration stops, their populations go extinct. In contrast, pseudosinks are within the fundamental niche. Immigration maintains the population above the carrying capacity, and deaths outnumber births by way of density-dependent mechanisms. If immigration stops, the population declines but only to carrying capacity, where deaths and births are equal. It does not go extinct. Both true sinks and pseudosinks have been found in nature (Keddy 1981; Watkinson et al. 1989; Kadmon and Schmid 1990; Thomas et al. 1996; Boughton 1999).

Dispersal Systems and Source-Sink Dynamics

The type of dispersal system is a key determinant of source-sink dynamics for two reasons: first, dispersal behavior directly affects the flow of organisms between habitats. Second, dispersal behavior indirectly affects birth and death rates in each habitat, by way of density-dependent competition. For example, a preferred habitat may attract so many animals that they exceed its carrying capacity and the habitat becomes a pseudosink.

A dispersal system that leads to source-sink dynamics is something of an evolutionary enigma. The reason is that organisms are consistently moving from a population where mean fitness is high to one where mean fitness is low. Evolution is not likely to produce such a system, unless some sort of constraint prevents optimal habitat selection. Such constraints are expected in plants because seed dispersal is performed by independent agents such as frugivorous animals or the wind. One might predict random diffusion from areas of high to low plant density. But constraints are not so likely in animals because they can actively move, assess the environment, and make choices that are at least approximately optimal (Krebs and Kacelnik 1991; Rosenzweig 1991). However, Pulliam and Danielson (1991) identified at least one possible constraint in animals: the ability of some animals to preempt the best habitat, preventing others from using it. This constraint occurs in many territorial species.

Four types of dispersal systems can be identified: passive dispersal, the ideal free distribution, the ideal preemptive distribution, and diffusion (Holt 1985; Pulliam and Danielson 1991; Holt 1996). Passive dispersal occurs when a fixed proportion of individuals disperse each generation (Holt 1985; McPeck and Holt 1992; Holt 1996). It produces source-sink dynamics when one population is consistently larger than the other. The sink may be either a true sink or a pseudosink. The ideal free and ideal preemptive distributions are models of optimal behavior (Fretwell and Lucas 1970). They pertain to animals who can

balance the costs of intraspecific competition with the benefits of high-quality habitat. The ideal free model assumes that animals cannot defend resources and predicts they will redistribute themselves until every animal has the same expected fitness. Neither true sinks nor pseudosinks are predicted (Pulliam and Danielson 1991). Instead, there is balanced dispersal between habitat patches within the fundamental niche and no dispersal to patches outside the niche. In contrast, the ideal preemptive distribution assumes that the first animal to use a reproductive site can preempt it. The reproductive surplus from high-quality habitats is ejected to low-quality habitats, producing source-sink dynamics.

The last model—diffusion—occurs when organisms do a random walk through space. A body of mathematics has been developed to describe diffusion in plants and animals (Turchin 1998). Of interest here is the theoretical prediction that immigration and emigration rates depend on the size of a habitat patch because of perimeter-to-area ratios (e.g., Kareiva 1985). Consider a circular patch within a landscape. If the landscape contains moving organisms, and if population size is standardized by patch area, then both the emigration rate and the immigration rate decrease as patch size increases (see fig. 1A, 1B). Notice that for the immigration case, MacArthur and Wilson (1967) predicted the opposite relationship. This is not surprising since they had rather different starting assumptions (straight-line movement; migrants from distant point sources; patch sizes unequal).

The diffusion model predicts an effect not just of patch size but also motility. Faster movement through a patch brings the organism to the edge of the patch more quickly and should cause a higher emigration rate. But what determines motility? Odendaal et al. (1989) and Turchin (1991) have shown that motility depends on the fine-scale characteristics of the animal's random walk (velocity, movement lengths, and turning angles). When motility differs between habitat types, emigration rate should differ as well. A border between two such habitats may develop a net flow of dispersing animals simply as a consequence of the different motilities (fig. 1C). A feedback loop is possible: differential motility causes net flow, which causes high population density in one habitat and low in the other (Turchin 1991). By way of density-dependent births and deaths, the population growth is negative in the first and positive in the second, and net flow is maintained over multiple generations. A source-sink system develops. Thus, diffusion models are highly relevant to source-sink dynamics, yet the relationship has received little attention.

Here, I examine the dispersal system of the butterfly *Euphydryas editha* at a site where it has source-sink dynamics (Thomas et al. 1996; Boughton 1999). The goal of the study is to experimentally determine the dispersal sys-

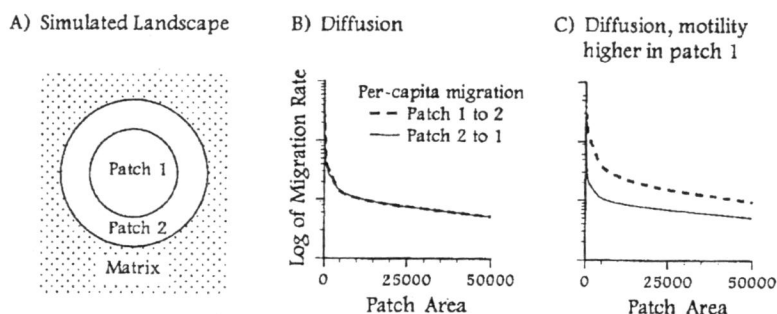


Figure 1: An illustration of diffusion concepts. A, Model landscape has two patches of equal area. Simulated organisms do a random walk through the landscape, moving freely between the patches and the matrix. B, As patch size increases, per capita movement rate decreases. The decrease is identical for the two patches. C, Motility was increased in patch 1 by restricting the turning angles of organisms (range $\pm 20^\circ$) and by increasing their velocity threefold. Patch 2 and the matrix kept the original motility (velocity = 1; range of turning angles $\pm 180^\circ$). The model landscape was 750×750 units, with "wraparound" boundaries. For each patch size, the landscape was populated with 5×10^4 butterflies and simulated for 10^4 time steps.

tem of the butterfly. The original characterization of source-sink dynamics was based on demographic criteria in two habitat types, replicated over multiple habitat patches (Boughton 1998, 1999). Here, dispersal is examined via a "natural experiment" that generated a series of vacant habitat patches. Other vacant patches were created experimentally (Boughton 1999).

Methods

Study Site

Edith's checkerspot butterfly (*Euphydryas editha*) is a nymphalid butterfly that occurs in the western United States, Mexico, and Canada. Populations tend to occur in discrete habitat patches, where the caterpillars feed on plants in the families Scrophulariaceae and Plantaginaceae. The study site is the General's Highway metapopulation, located in Sequoia National Forest of the Sierra Nevada, California. Here, habitat patches are embedded in a matrix of wet meadows, dense stands of *Pseudotsuga menziesii*, and barren granite domes. Adults spend most of their active life flying through the habitat searching for nectar, mates (in the case of males), and oviposition sites (in the case of females), sometimes leaving and entering individual habitat patches. The reproductive effort expended in any one patch probably correlates closely with the time spent in it. The butterfly populations occur in two types of patches—clearings and outcrops—and use different species of host plant in each. The two habitats are described in greater detail by Singer (1994), Thomas et al. (1996), and Boughton (1999).

Because of differences between the two habitat types, the system has complex source-sink dynamics (Thomas et

al. 1996; Boughton 1999). Clearings, when they have resident populations, act as sources, and the outcrops become pseudosinks. However, in clearings, the populations are more extinction prone in years with unusual weather (Singer and Thomas 1996; Thomas et al. 1996). Clearings, when they lack a resident population, act as true sinks and the outcrops become sources. The reason is that, in clearings, the host plant has begun to senesce by the time that butterflies arrive from other habitat patches. The colonists may lay eggs, but the plant nearly always dries out before the eggs hatch. As a result, the source-sink system has two locally stable states, summarized in figure 2 (Boughton 1999). The current study used sites in the second state, in which outcrops are sources, and clearings are true sinks.

Hypotheses and Study Design

The main question of the study is: Which of the four dispersal models best describes the movement of butterflies between habitat patches? The question was answered by estimating per capita migration rates in an experiment replicated at the level of the patch. The data were used to test predictions of the four models. The passive-dispersal model predicts that per capita emigration rate is constant, and thus independent of population density, habitat type, and patch area. The ideal free and ideal preemptive models predict that per capita rates (both immigration and emigration) are density dependent. The diffusion model predicts they are density independent and that they are related to patch area, and in the case of emigration rate, possibly to habitat type.

The study did not try to distinguish between the ideal free and ideal preemptive models because existing data do

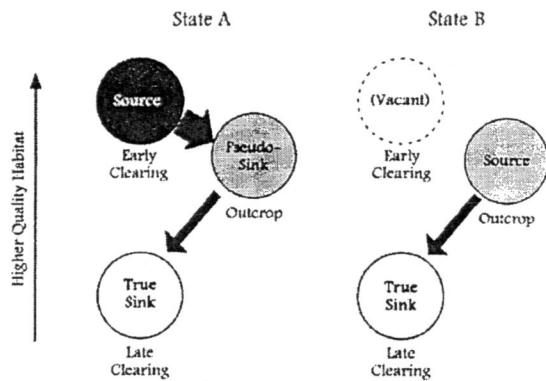


Figure 2: Two locally stable states of the General's Highway metapopulation. Arrows indicate the magnitude and net direction of dispersal. In one state (A), resident populations inhabit the clearings, occurring at two to 10 times the density of populations in outcrops. Dispersal from clearings to outcrops raises the population density in outcrops above the local carrying capacity, converting them into pseudosinks. However, unusual years of bad weather can drive the clearing populations to extinction without affecting the outcrop populations. The metapopulation then converts to the other state (B). This state persists over multiple years, but occasionally (one in 10 yr), a dispersing female will overcome the temporal barrier in the clearings and successfully reproduce. The population thus founded begins to grow and converts the site back to the first state. The details of these complex source-sink dynamics are described by Thomas et al. (1996) and Boughton (1999).

so already. The ideal preemptive model assumes that animals do not share reproductive sites, whereas the ideal free model assumes that they do. Thus, in the preemptive model, egg clusters would be overdispersed on host plants (reproductive sites), whereas in the free model they would be randomly dispersed or aggregated. Numerous data sets from the study site show that egg clusters are highly aggregated, implying that females readily share sites (Rausher et al. 1981; Moore 1987). Moreover, experiments show that female butterflies do not avoid ovipositing on plants that already have egg clusters (L. Ramakrishnan, unpublished data). Thus, the ideal preemptive model is rejected a priori.

The study was conducted in 1996 at a series of "target patches," six outcrops and seven clearings. Each target had no detectable population and was considered vacant. The clearings were vacant because of bad weather in 1992 (Singer et al. 1994), whereas the outcrops were vacant because insecticide was applied in 1995 (Boughton 1999). A portion of the nearest neighboring patch was identified as a "starting patch" (fig. 3A). Starting patches contained large resident populations of the butterfly. Virtually all immigrants to the target would have either originated in the starting patch or moved through it on their way to

the target. Thus, at the experiment's outset, each site had a vacant habitat patch (target) and a source of migrants (starting patch). The target could be a clearing or an outcrop; the starting patch was always an outcrop.

The size of the targets ranged from 0.030 to 5.58 ha, and the distance to the starting patch ranged from 0 to 30 m. For clearing targets, the variation in size and distance was naturally occurring. In the case of 0 m distances, the boundary between target and starting patch was simply the boundary between the clearing and the nearest outcrop. For outcrop targets, patches were designated to mimic the variation observed among the clearings. In the case of 0 m distances, this meant that the target outcrop was simply a subsection of a larger outcrop, in which the boundary was set by the experimenter. Likewise, starting patches were a subsection designated to have the same area as the target.

Dispersal was measured during the butterfly's flight period, which occurs once a year and lasts about 6 wk. During the first 20 d of the flight period, I repeatedly measured the density of butterflies in the target patches and starting patches. Each survey event measured a target and starting

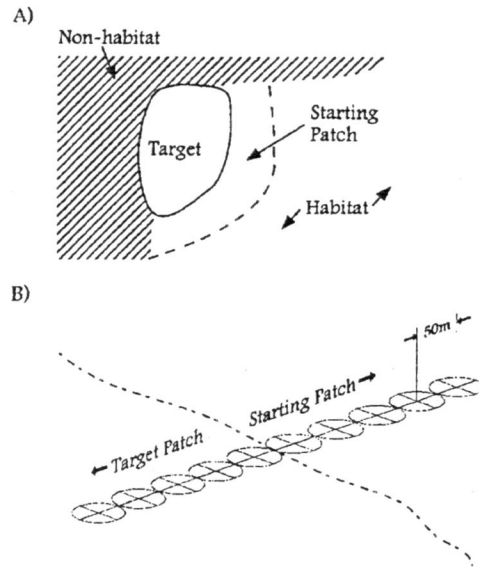


Figure 3: A, Schematic of a typical site in the study. At the beginning of the flight season, the target was vacant, whereas the starting patch was occupied. The starting patch is a portion of a larger patch and is assumed to have the same area as the target. The flow of butterflies between the site (target + starting patch) and the rest of the metapopulation is assumed to be approximately balanced in each direction. (These assumptions make the dispersal models mathematically tractable.) B, Layout of survey points at each patch pair. Circles indicate the maximum distance at which butterflies were counted.

patch simultaneously, using distance-sampling techniques (Buckland et al. 1993). The technique estimates population density for a snapshot in time.

A series of dispersal models was developed for the purpose of testing hypotheses by fitting the models to the survey data. I used the approach of Hilborn and Mangel (1997), described by them as a Lakatosian viewpoint (Lakatos 1978). The approach is to develop alternative models based on competing biological theories and to use quantitative techniques to determine which one is better supported by the data. The first two models were used to ask whether emigration was density dependent. The third model was used to estimate per capita immigration and emigration rates in each vacant patch, so as to test for habitat-specific and area-specific emigration rates. The last model was used to check an assumption of the first three models—that mortality rate was small relative to migration rate and to the rate of adult emergence (rate of adult emergence is the number of pupae turning into adults, per unit time).

Distance Sampling

Snapshot-style estimates of butterfly density were made in each patch at repeated intervals for the first 20 d of the flight season. Estimation involved "distance sampling" (Buckland et al. 1993): an observer stands at a survey point and estimates the distances to organisms that he has detected. A detection function, which describes how the probability of detection declines with distance, is fitted to these data. Then the data and the function are used to estimate density in terms of organisms per unit area. The technique makes no assumptions about whether a population is closed or open.

Distance sampling had three critical assumptions that had to be met via appropriate study design. The first assumption is that the probability of detection close to the observer is 1. To meet this assumption, visual surveys were conducted only on calm sunny days, between 1200 and 1400 hours, when virtually all butterflies would be active and visible. The second assumption is that the organisms are immobile during the survey. Butterflies are clearly not immobile, so the survey method was tailored to validate the assumption: I divided each survey point into four quadrants and surveyed the quadrants one at a time, rotating by 90° until done. In each quadrant, I counted the butterflies and assigned them to discrete distance categories. The cut points between the categories were 2, 3, 4, 5, 7, 10, 15, and 20 m, with a maximum distance of 25 m. The method allowed the survey of each quadrant to take only a few seconds so that butterflies were effectively immobile. The third assumption of distance sampling is that the observer does not affect the organism's behavior.

Observations suggested that butterflies sometimes flee when a person is within ~2 m of them, so butterflies within 2 m of the census point were counted as I walked up to the point, before they had responded to my presence.

At each site, the point transects were laid out along a line crossing the border between the two patches (fig. 3B), with five points in each patch. They were laid out before the flight season and marked with green flags. Then, at each site, I conducted a survey every 3–6 d for the first 20 d of June 1996. I estimated my visual precision by randomly placing flags around one point transect, estimating distances, and then measuring actual distances with a tape. My error rate was 5%; all errors fell into classes neighboring the correct one ($n = 100$ flags).

Estimates of population density were computed using the program DISTANCE, available from its authors (Laake et al. 1994). I analyzed the data in two batches because the total data set exceeded the program's capabilities. Within each batch, the detection function was fit to pooled data, and separate density estimates were made for each survey of each patch. Pooling the data to fit the detection function was justified because all data were collected by the same observer under similar visual conditions. It is reasonable to assume they are all described by a single detection function. I followed the standard implementation of DISTANCE: its four key functions were each fit to the data, and the best fitting one was chosen via its Akaike Information Criterion score (Laake et al. 1994). Then, average density was computed for each survey of each patch.

Model Derivation

Four models were developed to test hypotheses and assumptions. Each is a variation on a basic model for day-to-day change:

$$\text{change in density} = \text{emergence} + \text{immigration} \\ - \text{mortality} - \text{emigration.} \quad (1)$$

The equations were developed using Mathematica 3.0 (Wolfram 1999).

Models of Density Dependence. The first two models were used to test for density-dependent dispersal into the colonized patch. For each survey interval, the change in the density is given by

$$\frac{\Delta C}{\Delta t} = \tau_{SC}S - \tau_{CS}C + W, \quad (2)$$

where S is density in the starting patch and C is density

in the target patch. The parameter r_{SC} is the per day, per capita rate of movement from the starting patch to the target patch, and the parameter r_{CS} is the rate in the opposite direction. Emergence rate in the target patch is 0, and mortality rate is assumed to be negligible. The parameter W is process error. Measurement error is assumed to be negligible relative to process error.

The density-dependent version of the equation (2) assumes that each rate has a constant component and a component that is a linear function of population density ($r_{SC} = r_0 + r_1S$ and $r_{CS} = r_2 + r_3C$, where $r_0 \dots r_3$ are constants). This gives

$$\frac{\Delta C}{\Delta t} = h + r_0S + r_1S^2 - r_2C - r_3C^2 + W, \quad (3)$$

where $\{r_0, r_2\}$ is the basic migration rate in each direction, and $\{r_1, r_3\}$ is the density-dependent component in each direction. The parameter h is a site effect. The density-independent version of the model is identical, except it assumes $r_1 = r_3 = 0$.

Model of Habitat Preference. The next model assumes density independence and is used to estimate instantaneous per capita migration rates in each patch. Although butterfly dispersal occurs at regular intervals (daily during the middle of the day), I used a continuous approximation of the process. The rate of change in each patch is

$$\frac{dC}{dt} = r_{SC}S - r_{CS}C \text{ and } \frac{dS}{dt} = b - r_{SC}S + r_{CS}C, \quad (4)$$

where r_{SC} and r_{CS} are the instantaneous rates of movement in each direction. The parameter b is the emergence rate of adults in the starting patch (per unit area of habitat). Assumptions are that mortality is negligible, and the two patches are equal in size. Assuming the three parameters to be constant and using the initial condition of $t_0 = C_0 = S_0 = 0$, integrating the equations gives

$$C = b \frac{-r_{SC}}{(r_{SC} + r_{CS})} \left[\frac{1 - e^{-(r_{SC} + r_{CS})t}}{(r_{SC} + r_{CS})} - t \right],$$

$$S = b \frac{r_{SC}}{(r_{SC} + r_{CS})} \left[\frac{1 - e^{-(r_{SC} + r_{CS})t}}{(r_{SC} + r_{CS})} - t \right] + bt. \quad (5)$$

The equations give the instantaneous density of adult butterflies in each patch, at time t after first appearance of butterflies. A new variable P is defined as $C/(C + S)$, the proportion of butterflies in the target patch (standardized by area). The variable P can be derived from the above equations as

$$P = m \left(\frac{e^{-tk} - 1}{tk} + 1 \right), \text{ where } m = \frac{r_{SC}}{r_{SC} + r_{CS}}$$

and $k = (r_{SC} + r_{CS}). \quad (6)$

The parameter m is the relative magnitude of r_{SC} versus r_{CS} , whereas the parameter k is the absolute magnitude of r_{SC} and r_{CS} taken together. Figure 4 shows the behavior of the variables S , C , and P as a function of time t , and the effect of m and k on the shape of the curve.

The parameters m and k have a biological interpretation. The parameter m is a measure of mean habitat preference of the population and ranges from 0 to 1. A value of 0.5

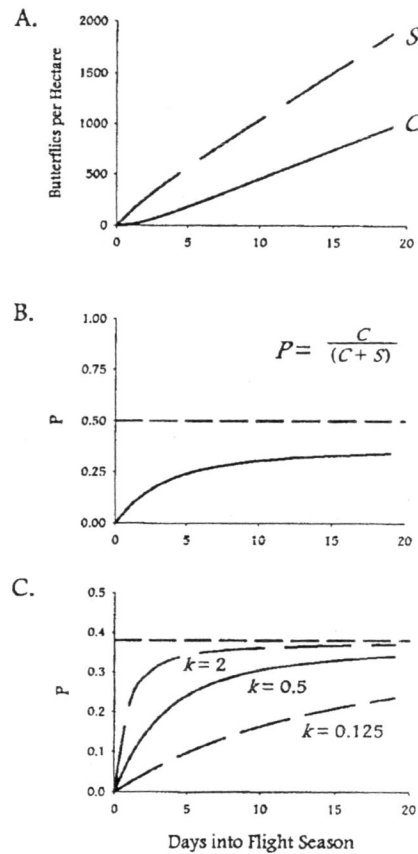


Figure 4: Some properties of the habitat-preference model. A, Density of adults in each habitat as a function of time, for the parameter values $b = 150$, $m = 0.38$, and $k = 0.5$. B, Behavior of the relative density P , for the same parameter values as in A. The curve's asymptote is $P = m$. The horizontal line is the asymptote of the H_0 , $m = 0.5$, interpreted as no habitat preference. C, Examples of the model in which m is held constant and k is varied. The horizontal line is the asymptote $P = m$.

indicates that r_{sc} and r_{cs} are equal, implying neutral preference. Values >0.5 indicate a preference for the target patch and values <0.5 , a preference for the starting patch. The parameter k is a measure of the absolute rate at which butterflies move between patches. Higher values of k imply that butterflies are crossing patch boundaries more frequently.

Mortality Assumption. The above models all assume that mortality rates are small relative to movement rates. To test this assumption, a model of total density was developed:

$$\frac{dN}{dt} = (b + Cr_{cs} - Sr_{sc} - Sq) + (Sr_{sc} - Cr_{cs} - Cq), \quad (7)$$

where $N = C + S$, and q is the mortality rate. The first set of parentheses encloses terms for the starting patch, and the second set encloses terms for the target patch. Simplifying and integrating over time gives

$$N = \frac{b}{q} (1 - e^{-qt}) \quad (8)$$

If mortality is small, total butterfly density is a linear function of time. If mortality is detectable, total density is a convex curve that asymptotes at $b = Nq$. This difference is used to test the small-mortality assumption of the first three models.

An important assumption of all the models is that males and females have similar dispersal behaviors. Mark-recapture studies at one site corroborate the assumption (Boughton 1998). Although there is evidence that females had higher individual variation (Thomas and Singer 1987; Boughton 1998), the population means of males and females were the same.

Model Fitting and Selection

Density Dependence. To test for density dependence, equation (3) was fit to the data. To make a robust test, two slightly different models were each used. In the full model, the parameters $r_0 \dots r_3$ were estimated from the data, along with parameters for site effects. In the simplified model with no habitat effect, the same parameters were estimated, but r_1 and r_3 were constrained to be equal. In other words, density dependence was assumed to operate identically in the two habitat patches at each site. Estimation was done in Statistica (Statsoft 1997), using the module for nonlinear curve fitting. Each survey interval was treated as an independent observation. The best-fit parameters were chosen using the least squares criterion.

The test asked the data which hypothesis it supported:

density dependence or density independence? The criterion for support was the sum of squares adjusted by the number of estimated parameters in the model (Efron and Tibshirani 1993; see Hilborn and Mangel 1997, p. 114–116). The model with the lowest value had the highest support.

Habitat Preference. To estimate habitat preferences and dispersal rates, equation (6) was fit to the data. Estimates were made separately for each site; thus, each site was treated as one sample of m and k . Otherwise, parameter estimation was the same as above. Estimates were only used when the curve-fitting procedure gave realistic values (i.e., $0 < m < 1$; unrealistic values occurred in three cases because the data gave too little information about asymptotic behavior). A test for habitat preference was made separately for clearing and outcrop sites. The test asked if m was significantly different from 0.5. Then, I tested the hypothesis that k was related to patch area, as predicted by the diffusion model. I estimated patch area by projecting aerial photos onto graph paper. The photos were obtained from the Hume Lake Ranger Station, Sequoia National Forest. The two hypotheses were tested with ANCOVA, using Statistica, release 5.

Mortality Rate. Last, to test the assumption that mortality rate was small, equation (8) was fit to the data, using the same estimation procedure as above. I tested the null hypothesis that $q = 0$. The magnitude of mortality relative to dispersal was quantified as $2q/(r_{sc} + r_{cs})100\%$.

Results

Distance Sampling

The best-fitting detection functions of the batches of data were similar (table 1). Over all sites, density ranged from 8.5 to 661 butterflies ha^{-1} , reflecting the waxing of the flight season.

Density Dependence

For both clearings and outcrops, in both the full and simplified models, density-independent dispersal was better supported by the test criterion (table 2). Thus, the test rejects the ideal free model. However, in general, the best-fit parameters explained a relatively low amount of the variation in the data—from about 25% to 50%, depending on the model. Plots of residuals against predictions showed no trend, and the residuals appeared normally distributed. The low fit is probably due to process error, which is to say day-to-day variation in the activity level of the butterflies. Although the surveys were only conducted on days

Table 1: Statistics for distance-sampling data and detection function fitted to them

	Clearing sites	Outcrop sites
Total patches ^a	18	12
Total surveys ^b	435	285
Total butterflies observed	1,630	932
Detection function and parameter estimates:		
Key function	$k(y) = 1 - e^{-(y/a)^b}$ (hazard rate ^c)	$k(y) = 1 - e^{-(y/a)^b}$ (hazard rate)
Slope of function at $y = 0$.0269 ± .0010	.0452 ± .0016
Parameter σ	6.514 ± .171	5.556 ± .132
Parameter b	3.847 ± .117	5.305 ± .211
Effective detection radius (m)	8.63 ± .15	6.65 ± .12
Probability of observing butterfly	.119 ± .004	.071 ± .0025
Mean density across surveys (butterflies ha ⁻¹)	160	187
Mean CV of density across surveys (%)	39	44

Note: Parameter estimates are given as estimate ± SE.

^a Two patches per site. The above data set had two sites with occupied clearings. The sites were used to fit the key function but otherwise were not part of this study.

^b The analysis omits surveys in which no butterflies were observed. Density was assumed to be 0 in these cases.

^c See Buckland et al. (1993) for details.

optimal for butterfly activity, intervening days were more variable in terms of wind, air temperature, and cloudiness. In contrast, the habitat preference and mortality models (below) could be integrated over time and tended to explain a much higher proportion of the variation.

The power of this test relied on variation in density "disparity." Disparity for a particular survey event is quantified as the mean density in the starting patch, minus the mean density in the target. Variation in disparity was high; mean and standard deviation was 82 ± 81 butterflies ha⁻¹ at outcrop sites ($n = 28$) and 86 ± 58 butterflies ha⁻¹ at clearing sites ($n = 42$).

Patch Area and Habitat Type

Estimates of m , which measures habitat preference, were significantly different for clearings and outcrops ($F = 17.32$, $df = 1, 10$, $P = .002$; ANCOVA) but were unrelated to patch area ($F = 0.48$, $df = 1, 10$, $P = .50$). These data were used to test for habitat preferences at the population level. For outcrops, the null hypothesis of neutral preference was not rejected ($H_0: m = 0.5$, $P > .05$, $n = 5$ sites). The result is in line with the expectation that butterflies would show no preference between vacant outcrops (the targets) and occupied outcrops (the starting patches). However, in clearings, a significant preference did occur ($H_0: m = 0.5$, $P < .0001$, $n = 7$ patch pairs). On a per capita basis, the butterflies were about twice as likely to fly from clearings to outcrops than the reverse. Estimates of k , which measure the magnitude of movement rates between patches, were significantly different for clearings and out-

crops ($F = 15.17$, $df = 1, 7$, $P = .006$) and showed a strong relationship with patch area ($F = 14.77$, $df = 1, 7$, $P = .006$). Dispersal rates into and out of the target patch tended to be higher the smaller the patch. For both m and k , the parallelism assumption (required by ANCOVA) was not rejected (m : $F = 0.000002$, $df = 1, 9$, $P = .999$; k : $F = 0.391$, $df = 1, 6$, $P = .555$).

The message of these data is most easily understood by examining dispersal rates into and out of the target patches. The rates are graphed in figure 5. Both the emigration and immigration rates decreased with increasing patch area. However, the parameter m , which is a function of these rates (see eq. [6]), is independent of patch area. The independence implies that the two dispersal-area relationships counterbalance each other. The diffusion model predicts exactly this result. In the diffusion model, patch size determines the rate at which animals encounter the boundary between habitat patches. However, their choice—the expression of preference at the boundary—is determined only by habitat type and not by patch size.

A second message is contained in figure 5. The habitat preference is expressed as the top regression line in figure 5A being lower than the top regression line in figure 5B. The line that stands out from the background is emigration rate from clearings; the immigration rate is similar to what is seen in the outcrop sites. Here is the simplest biological interpretation: the habitat preference for outcrops over clearings is caused not by a reduced immigration rate into clearings, but by an increased emigration rate out of them. In other words, dispersing butterflies do not avoid entering the clearings. But once they are in them, they are more

Table 2: Support for density-dependent versus density-independent models

Vacant patches/ model	Density dependence	No. of parameters	Estimate of r_1, r_3	R^2	Test criterion
Outcrops (6 sites):					
Full model	Allowed	10	$-7.5 \times 10^{-5}, 2.5 \times 10^{-4}$.504	645.8
	No	8375	542.4*
No habitat effect	Allowed	8	1.4×10^{-4}	.381	536.7
	No	7354	480.4*
Clearings (7 sites):					
Full model	Allowed	11	$-5.9 \times 10^{-4}, -3.0 \times 10^{-4}$.316	518.1
	No	9246	342.9*
No habitat effect	Allowed	9	-9.3×10^{-5}	.251	340.7
	No	8245	286.1*

* The better-supported criterion.

likely to leave (fig. 6). The pattern is consistent with a diffusion system in which motility is higher in clearings.

Assumption of Small Mortality

Mortality rate was not significantly different from 0 in either type of site (clearing sites, $H_0: q = 0, n = 7, t = 1.1478, P = .15$; outcrop sites, $H_0: q = 0, n = 6, t = 1.2198, P = .14$). The magnitude of mortality relative to dispersal was 40% in clearings and 6% in outcrops. The large value for the clearing sites was due to one outlier at one site, the site's last observation of the season. Without this site, the relative magnitude for clearings was 6%. This site has been observed in other years to have a very short, steep period of emergence. The outlying datum was a plateau of density in the last survey of the site and is probably due to adult emergence stopping, rather than high mortality (i.e., emergence rate b abruptly went to 0). Experiments (not shown) with a model derived from equation (4), but in which the starting conditions assume $b = 0$, show that this stopping of emergence would not change the conclusions that were drawn in the previous section. At all the other sites, emergence rate appeared to be constant. It did not go to 0 until after the last survey, as intended by the study design.

Discussion

The study did not support the ideal free or ideal preemptive models. Instead, the data supported the diffusion model, with a higher motility in clearings than in outcrops. This was expressed at the larger scale as a habitat preference because the per capita rate of moving from clearing to outcrop was higher than the rate in the reverse direction.

Consequently, in this source-sink system the habitat preference and the net flow of butterflies were opposed (i.e., net flow was $S_{SC} > C_{CS}$, but per capita flow was $r_{SC} < r_{CS}$). The source-sink dynamics were thus driven by

diffusion from high population density to low population density, though dampened by habitat preference. In a sense, the dispersal system of the butterflies was somewhat "plantlike" because it was driven by density gradients. Of course, the metapopulation has another mode with net flow in the opposite direction (i.e., fig. 2A). In this mode, population density in clearings tends to be two to 10 times higher than in outcrops. Net flow would be driven by the habitat preference and the density gradient acting in concert.

The above interpretation is supported by data from other studies. In particular, density-independent movement is supported by mark-recapture data from one site (Boughton 1998). Data were collected in 2 yr, one in which the clearing had a resident population about twice as dense as the outcrop (Thomas et al. 1996) and one in which the clearing was vacant or nearly so (Boughton 1998; the outcrop population density was roughly the same for the 2 yr). These represent the extremes of density variation expected in the system, yet the per capita movement rates were virtually identical for the 2 yr, as were the rates for males and females ($n = 742$ butterflies). Habitat preference, however, was significantly different from neutral. Thus, the intensive study at one site is in accord with the current extensive study at 13 sites.

The diffusion model is congruent with data from three other studies. Mackay (1985), Parmesan (1991), and Parmesan et al. (1995) found that female butterflies at the study site searched for host plants more efficiently in outcrops than in clearings. Although they did not try to quantify motility, their results suggest that butterflies searched more intensively in outcrops and might have had lower motility there. Odendaal et al. (1989) and Turchin (1991) found that in the related species *Euphydryas anicia*, dispersal can be described by a random-walk model. They found that "residence index" (similar to motility) was different between areas with and without host plants and that this difference could be explained as a difference in fine-

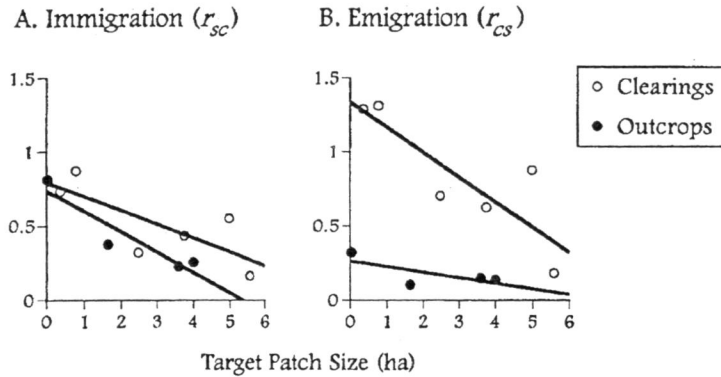


Figure 5: Dispersal rates into and out of the patches being colonized during the study. Immigration rates into clearings and outcrops were similar (A), but emigration rates were very different (B).

scale movements. Unlike the current study, dispersal seemed to be density dependent and differed for males and females. Density-dependent dispersal has also been found in the butterfly *Procllossiana eunomia* at fragmented sites in Belgium (Baguette et al. 1998).

The Intermediate-Scale Hypothesis

Over ecological time, source-sink dynamics occur if a constraint forces animals into sinks. Over evolutionary time, sinks may disappear either because the animals evolve the ability to avoid them (immigration rate decreases) or the animals adapt to them (birth rate increases or death rate decreases). For passive dispersal, an evolutionary model (McPeck and Holt 1992) predicts that rates will tend to evolve toward a balanced flow among patches within the fundamental niche. In short, pseudosinks were not evolutionarily stable (true sinks were not examined). Holt (1996) asked whether populations would adapt to true sinks by evolving an expanded niche. Passive-dispersal systems evolve if dispersal rates are high and fitness in the sink is not very low. Ideal preemptive systems evolve readily. A summary of these points is in table 3. Overall, the constraints do not seem to be evolutionarily stable, and source-sink systems based on them may be uncommon.

Another constraint is spatial structure, in which organisms are more likely to encounter resources that are closer to them in space. All animals have this constraint, but it is most relevant at certain intermediate scales defined by their mobility. If patchiness occurs at a fine scale relative to mobility, animals encounter many different patches. This increases the odds that they will encounter resources in proportion to their occurrence and that preferences will be expressed. If patchiness occurs at large scales relative

to mobility, most animals encounter just one patch during their life. Movements between patches will tend to be rare stochastic events. But, at some intermediate scale, movement between patches is probably similar to continuous diffusion. I would like to propose the "intermediate-scale hypothesis": source-sink dynamics are most likely to occur when patchiness is at the intermediate scale. The hypothesis assumes that spatial constraints are more evolutionarily stable than constraints on niche evolution or optimal behavior.

The optimality models—ideal free, ideal preemptive—usually apply to the fine-scale case because they as-

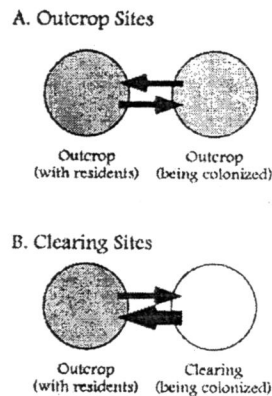


Figure 6: Interpretation of the data for habitat preference in figure 5. The size of the arrows indicates the magnitude of per capita dispersal in each direction. Butterflies fly into vacant clearings at about the same rate as into outcrops of the same size. The preference arises because they fly out of clearings at about twice the rate that they fly out of outcrops of the same size.

Table 3: Ecological and evolutionary stability of source-sink systems in theory

	Passive dispersal	Ideal free distribution	Ideal preemptive distribution
Source-sink dynamics?	Predicted if population sizes are different	Not predicted	Predicted when source habitat is saturated
Habitat preference?	No	Yes	Yes
Density-dependent dispersal?	No	Yes	Yes
Evolution of dispersal	Pseudosinks evolve to balanced dispersal; true sinks evolve to be avoided	Stable	Stable
Evolution of niche	True sinks evolve if dispersal rates are high and fitness in sink is not very low	Stable	Evolves

Note: Summarized from Johnson and Gaines (1990), Pulliam and Danielson (1991), Holt and Gaines (1992), McPeck and Holt (1992), Watkinson and Sutherland (1995), and Holt (1996).

sume that animals have a perfect ability to find and assess reproductive sites (Goss-Custard and Sutherland 1997). An exception is Bernstein et al. (1991), who modeled the effects of dispersal costs and patchiness on optimal behavior. They used the basic ideal free model as a starting point and standard of comparison. As the time costs of dispersal went up (i.e., as patches were made more distant), the distribution of foragers tended from ideal to random. Likewise, as patchiness became more coarse-grained relative to the mobility of the foragers, the foragers gained a less accurate knowledge of the environment. The distribution of foragers tended from ideal to random. In both cases, resource-dense areas were underused, and resource-sparse areas were overused. If the resource base were stable over multiple generations, this would tend to initiate the source-sink feedback loop. The predictions of this optimality model seem to be consistent with the intermediate-scale hypothesis.

To summarize the argument, at intermediate scales, source-sink dynamics would tend to be driven by net diffusion from areas where population density is high to areas where it is low. At other scales, source-sink systems in animals would tend to be rare—they are evolutionarily unstable at finer scales, and dispersal is too rare to have a quantitative impact at larger scales.

The hypothesis makes testable predictions. Source-sink systems will tend to be found at the scale where animal movement resembles a random walk and where there is a consistent spatial gradient in population density. Most tests of source-sink theory have focused on differences in habitat quality and in particular on the habitat-specific growth rate, λ . The parameter λ is the mean number of adults produced per adult per generation in a particular habitat patch (Pulliam and Dunning 1997). At equilibrium, $\lambda > 1$ in sources and $\lambda < 1$ in sinks. The interme-

diated-scale hypothesis predicts that population density N will be higher in sources than in sinks or, in other words, that λ and N are positively correlated among patches. Notice that the prediction is the opposite of classic density-dependent population growth, in which λ and N are negatively correlated. It is important to note here that N refers to animals per unit area, and not total population size, since it is density gradients that drive diffusion.

Source Sinks, Balanced Dispersal, and the Biodiversity Crisis

Source-sink models and balanced-dispersal models are competing theories (Doncaster et al. 1997). The crucial distinction is that only source-sink systems maintain a stable net flow over many generations. In the balanced-dispersal model, two patches may show net flow in any one season, but over several seasons, the net flow will average to 0. This situation would develop when temporal variation of habitat quality is high and uncorrelated among patches. High levels of dispersal tend to be evolutionarily stable in such a landscape (Johnson and Gaines 1990), so systems with balanced dispersal may be relatively common in nature. As argued above, source-sink systems may be relatively rare. Of course, the argument is evolutionary and may not apply in landscapes that have been so altered by human activity that they scarcely resemble the landscapes in which past evolution occurred.

Empirical studies on this question are important for two reasons that are relevant to the biodiversity crisis. The first concerns population regulation and persistence; the second has to do with the assumptions of many habitat models used in conservation planning.

Population regulation is often defined as population fluctuations within limits, with the lower limit >0 (Mount-

ford 1988; Murdoch and Walde 1989; Hanski 1990). The narrower the window in which the population normally fluctuates, the more tightly it is regulated. Long-term protection from extinction relies on regulation; population regulation in turn requires birth or death rates to have a density-dependent component. In Pulliam's (1988) original source-sink model, density dependence in births or deaths was assumed to be caused by density dependence in dispersal. Only at high densities, when source habitat became saturated, were some animals forced to move into sinks, thus lowering the growth rate of the population as a whole. Therefore, the ideal preemptive model of habitat selection was the means of population regulation in his theory of sources and sinks. In fact, population regulation via ideal habitat selection has broader relevance than source-sink theory. Hanski (1982), for example, compared population variability for a large number of bird and insect species. He found that birds tended to be more tightly regulated near carrying capacity, compared to insects. He attributed the difference to ideal habitat selection occurring in birds but not insects. The intermediate-scale hypothesis that I have advanced above suggests that most source-sink systems may be more insect-like than birdlike. Population regulation in source-sink theory may need to be reconsidered.

Increasingly, plans to protect biodiversity must integrate the protection of multiple species within a given landscape (Noss et al. 1997). To be effective and practical, these plans often use habitat as a surrogate for species (Noon 1999). The approach is validated and parameterized by quantitative studies of the associations between individual species and their habitats (Verner et al. 1986), but these associations rest on the crucial assumption that true sinks are rare in nature. According to Diffendorfer (1998), the data in most studies of source-sink systems were ambiguous with regard to true sinks. The intermediate-scale hypothesis may help inform this debate. It predicts that in species with neutral habitat preferences, true sinks will tend to occur where population density is consistently the lowest over many generations. Any sort of nonneutral, adaptive preference will only accentuate this pattern even further.

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