Compensatory behavior of *Ensatina eschscholtzii* in biological corridors: a field experiment

Daniel K. Rosenberg, Barry R. Noon, John W. Megahan, and E. Charles Meslow

Abstract: Despite the general lack of theoretical or empirical support, biological corridors are assumed to mitigate the detrimental effects of habitat fragmentation by increasing landscape connectivity. To test the hypothesis that mechanisms which affect immigration rates from a source to a target patch are affected by the presence of a corridor in an otherwise unsuitable matrix, we created two strongly contrasting pathways in replicated field experiments. One pathway type included only bare mineral soil, the other included a potential corridor. We conducted these experiments with *Ensatina eschscholtzii*, a salamander in the family Plethodontidae. Pathways with surface organic material removed provided a harsh environment for *E. eschscholtzii*, which was reflected by lower selection, shorter residency time, and higher movement rates than on pathways that contained vegetation (corridor pathways). However, the numbers of *E. eschscholtzii* reaching target patches connected by corridor pathways were greater than those reaching target patches connected by bare pathways only in plots in which the matrix environment seemed most severe. Our results suggest that identifying candidate corridor areas on conservation maps might be difficult because animals may show compensatory behavioral responses to different types of habitat separating source and target patches. We argue that knowledge of a species' habitat-specific dispersal behaviors is critical to reliably designating corridors as functional components of reserve design.

Résumé : En dépit de l'absence de preuves théoriques ou empiriques, on attribue aux corridors biologiques des propriétés atténuantes sur les effets néfastes de la fragmentation de l'habitat parce qu'ils accroissent la connectivité entre les paysages. Pour éprouver l'hypothèse selon laquelle les mécanismes qui affectent les taux d'immigration d'un terrain source à une destination cible seraient affectés par la présence d'un corridor sur un substrat généralement hostile, nous avons créé deux types de parcours très différents au cours d'expériences répétées, l'un exclusivement sur du sol minéral nu, l'autre comportant un corridor potentiel. Une salamandre de la famille des Plethodontidae, *Ensatina erchscholtzii*, a servi d'animal expérimental. Les parcours à surface dénudée de matière organique constituaient un milieu très hostile pour les salamandres; ces parcours étaient peu fréquentés, les salamandres n'y restaient que pour de courtes périodes et leurs taux de déplacement y étaient plus élevés que le long des parcours garnis de végétation (corridors). Cependant, il n'y a que dans les milieux extrêmement hostiles qu'un plus grand nombre de salamandres ont atteint les terrains cibles réunis par des corridors. Nos résultats démontrent que la reconnaissance de corridors potentiels sur des cartes de conservation est un excercice difficile parce que les animaux manifestent parfois des comportements de compensation lorsqu'ils se retrouvent en présence d'habitats différents entre un terrain source et une destination cible. La connaissance préalable des comportements de dispersion d'une espèce dans des habitats spécifiques est indispensable à la création de corridors adéquats dans l'aménagement des réserves.
[Traduit par la Rédaction]

Introduction

Habitat fragmentation, the reduction of total habitat area and connectedness, is commonplace in landscapes throughout the world and is one of the greatest threats to biological diversity (Harris 1984; Wilcox and Murphy 1985; Temple and Wilcox 1986; Wilcove et al. 1986). The principles of island biogeography (e.g., MacArthur and Wilson 1967), models of demographic stochasticity (e.g., Shaffer 1981; Soulé 1987) and inbreeding depression (Schonewald-Cox et al. 1983; Mills and Smouse 1994), and metapopulation theory (Levins 1970; Taylor 1990; Hanski and Gilpin 1991) lead to predictions that small isolated populations, such as those that may result from habitat fragmentation, will have high local extinction rates. Empirical evidence supports this contention (Simberloff and Wilson 1970; Smith 1974,1980; Simberloff 1976; Gill 1978; Fritz 1979; Schoener and Spiller 1987; Harrison et al. 1988;

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Soulé et al. 1988). As relatively homogeneous environments are fragmented, panmictic populations may become a composite of metapopulations or discrete, isolated populations (Hanski and Gilpin 1991), depending upon the rate of exchange of individuals among populations.

In fragmented landscapes, high resistance to movement across unsuitable habitat would be expected to isolate populations and elevate extinction rates. Decreasing either the degree of fragmentation or the resistance to movement between patches would be expected to increase exchange among populations and may reduce local extinction rates (reviewed by Sjögren 1991). The concept that connectivity among patches of fragmented habitat decreases the probability of local extinction of populations and ultimately maintains biological diversity has become a paradigm in conservation biology (Doak and Mills 1994). Linear patches of natural vegetation ("corridors") have been advocated as a means to facilitate connectivity of fragmented landscapes (Noss 1983, 1987; Harris 1984, p. 141; Soulé et al. 1988; Bennett 1990). Indeed, inclusion of corridors in habitat-conservation plans has gained wide acceptance as an essential component of conservation planning (Noss 1987; Saunders and Hobbs 1991; Mann and Plummer 1993; Noss and Cooperrider 1994). However, the value of corridors has been challenged (e.g., Simberloff and Cox 1987; Simberloff et al. 1992; Rosenberg et al. 1997). The controversy is caused largely by a lack of empirical studies on the efficacy of corridors in linking otherwise isolated habitat patches and, ultimately, on the resultant local and regional population-extinction rates (Simberloff 1988; Rosenberg et al. 1997).

Few studies have been conducted on the means by which corridors facilitate animal movement through fragmented landscapes, despite the assumed importance of corridors in conservation biology. Recently, several experimental studies of corridors have been conducted (reviewed in Rosenberg et al. 1997). La Polla and Barrett (1993), Andreassen et al. (1996), and Coffmann (1997) tested the efficacy of biological corridors in facilitating movements of voles (*Microtus* spp.), Haddad (1997) tested the effects of corridors on butterfly movement patterns and density, and Machtans et al. (1996) tested effects on landbirds in a quasi-experimental design. These studies typically demonstrated that for some species and in some landscape contexts, corridors increased movement rates among patches, but were not essential for movement to occur (Rosenberg et al. 1997). Observational studies support these findings and have often been cited as evidence of corridors facilitating movement among habitat patches (e.g., MacClintock et al. 1977; Bennet 1990). The observational studies have often been criticized as unsubstantiated (Nicholls and Margules 1991; Simberloff et al. 1992; Rosenberg et al. 1997). Further, few species and environmental contexts have been studied, thus the hypothesis that corridors effectively connect otherwise isolated populations and thereby increase regional persistence remains relatively untested (Nicholls and Margules 1991; Simberloff et al. 1992).

We created "microlandscapes" (sensu Johnson et al. 1992) with two strongly contrasting pathways to test the hypothesis that immigration to a habitat patch is increased by the presence of a corridor in an otherwise unsuitable habitat matrix. Such an approach allows direct testing of the mechanisms that may be responsible for differences in movement patterns, but may be limited in terms of the general applicability of the findings to real landscapes. We view this study as an initial investigation of the difficult task of understanding movement patterns of vertebrates in heterogeneous landscapes.

We chose *Ensatina eschscholtzii*, a salamander in the family Plethodontidae, as a test organism because of individuals' small home ranges, high density, activity near the soil surface, where they can be captured and monitored, and known microhabitat requirements (Stebbins 1954). These characteristics make them suitable subjects for this study because (*i*) small landscapes could be created in which the populations were tractable but sufficiently large numbers of individuals could still be monitored, (*ii*) dispersal events could be created by increasing the densities of animals above normal levels, and (*iii*) habitat could be manipulated relatively easily because of the animals' sensitivity to microclimatic variation.

Natural history of *E. eschscholtzii*

Ensatina eschscholtzii are found in forests from southwestern British Columbia to southern California along the Pacific coast inland to the Cascades and Sierra Nevada. They occupy many moist forest conditions (Bury 1983; Gomez and Anthony 1996) and are most abundant in forests with deep organic soils and abundant woody debris. Densities may reach 1300/ha in high-quality habitat (Stebbins 1954, p. 74). Movement is primarily nocturnal and occurs doing moist conditions (Stebbins 1945, 1954). *Ensatina eschscholtzii* are almost always found under cover during daylight.

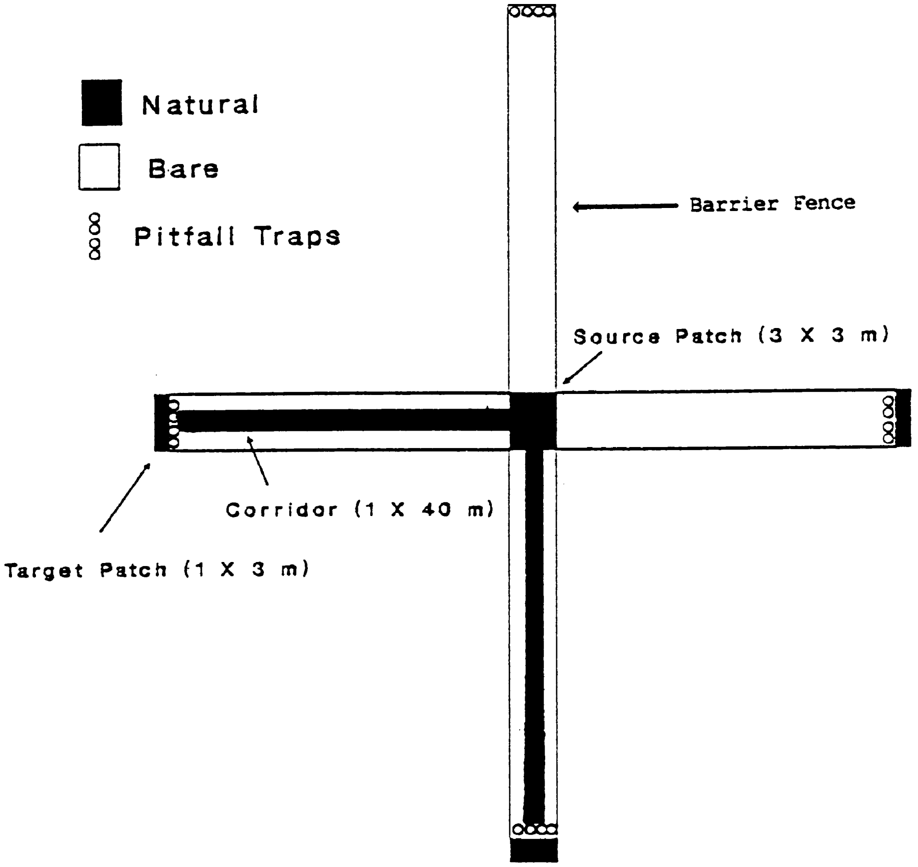
Ensatina eschscholtzii are relatively sedentary. Stebbins (1954) found that adult males typically move greater distances between successive (diurnal) locations ($\bar{x}$ = 10.0 m) than females ($\bar{x}$ = 5.3 m) and juveniles move approximately one-third the distance of adults. Similar patterns in males and females were reported by Staub et al. (1995): the maximum distance moved between recaptures was 60 and 120 m for females and males, respectively. Stebbins (1954) estimated mean home-range diameters of 10.0 m for females to 19.5 m for males. Territorial behavior of *E. eschscholtzii* has not been reported, although it has been documented in several related (plethodontid) species (Jaeger 1979; Jaeger et al. 1986; Hairston 1987; Nishikawa 1990).

Study areas

We established 5 experimental plots (Fig. 1) in Douglas-fir (*Pseudotsuga menziesii*) stands in the Coast Ranges of western Oregon; 3 were located in Lincoln County (plots A, B, and C) and 2 were in Benton County (plots D and E). Plots D and E were approximately 200 m apart (center to center); the remaining plots were ≥2 km apart. Study sites were characterized by a mild climate with small diurnal fluctuations in temperature (6–10°C), with wet, mild winters and relatively cool, dry summers. Precipitation occurs mostly as rain (150–300 cm annually), with 75–85% occurring between 1 October and 31 March and only 6–9% during summer (Franklin and Dyrness 1973). Precipitation decreases from the Pacific coast inland towards the Willamette Valley because of the influence of rain shadows (Franklin and Dyrness 1973). Therefore, the 2 interiormost study plots (D and E) typically receive less precipitation than the more westerly plots (A–C).

Although the study sites lie within the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1973, p. 70),

Fig. 1. Design of the experimental plots. Each plot contained 2 pathways (3 × 40 m) with natural vegetation ("corridor") and 2 with only a bare mineral soil surface remaining ("bare"). A barrier fence was installed around the perimeter of the plot. The study included 5 plots with the treatments (corridor, bare) applied randomly among the 4 pathways extending from the source patch to the target patches of each plot. To facilitate presentation, pitfall traps are illustrated as being outside of the target patches; however, they were placed at the edge of the linear patches embedded inside the target patches, arranged in a row of approximately 16 in each target patch.



Douglas-fir predominates; in stands that were regenerated with nursery stock (plots D and E), only Douglas-fir seedlings were planted. The study sites were characterized by almost continuous canopy cover, dense shrub cover, and relatively little herb cover, characteristics typical of this region (Franklin and Dyrness 1973, p. 76). Shrubs and ferns included *Berberis nervosa*, *Polystichum munitum*, *Pteridium aquilinum*, *Gaultheria shallon*, *Vaccinium* spp., *Cornus nuttallii*, and *Acer circinatum*. An almost continuous ground cover of moss existed in all plots.

Materials and methods

Plot design and construction

We designed study plots to represent landscapes with and without corridors in which the matrix, i.e., the environment in which habitat patches and corridors are embedded, was composed of poor-quality habitat. To create the matrix we removed organic matter from the soil surface. This very labor-intensive effort limited the spatial scale of the study and motivated us to establish fenced pathways in which animals were forced to choose alternative pathways for movement rather than creating a large area of matrix habitat in which they could move freely.

Each plot consisted of a central source patch (3 × 3 m) and 4 target patches (1 × 3 m) of unmodified habitat connected to the source patch by fenced pathways (3 × 40 m; Fig. 1). To facilitate description, we refer to the pathways with natural vegetation (described below) as corridor pathways and those without vegetation as bare pathways. From 14 to 16 adjacent pitfall traps (Corn and Bury 1990) were placed at the end of each pathway along the boundary with the adjacent target patch (Fig. 1); these traps were used to score the number of successful movements from source to target patches. Aluminum flashing (25 cm above and below ground) was installed around the perimeter of the entire plot to contain the salamanders. To restrain *E. eschscholtzii* from climbing out of the enclosures, we bent the top 5–7 cm of the fence towards the enclosure at a 90° angle. In an effort to eliminate possible confounding effects of naturally occurring salamanders, we operated pitfall traps for 18–24 days at 5-m intervals along both sides of corridor pathways prior to each experiment. The pitfall traps were not placed at the sides of the bare pathways because we believed that the traps would provide habitat (along the sides and underneath the trap) in an otherwise poor-quality environment.

In each plot, we manipulated the microhabitat in the pathways. We created bare pathways in 2 randomly selected pathways of each plot. In these pathways, we removed organic material (e.g., stumps, litter, woody debris, and vegetation <5 cm diameter at breast height), leaving a surface of mineral soil. In the remaining 2 pathways of each plot we created corridor pathways: organic matter was removed only from the outer 1 m at each side; we left the central 1 m in a natural condition (Fig. 1). Before each experiment, bare areas were re-treated to ensure that organic matter was largely absent from the soil surface; we also removed organic matter from approximately 30 cm along the outside perimeter of each plot.

Monitoring movements

We marked *E. eschscholtzii* with radioisotopes (Ta^{182}) for detection and by toe-clipping for individual identification. We anesthetized them with a 0.3 g/L solution of tricaine methanesulfonate (MS 222) buffered with 2.2 g/L of sodium bicarbonate. *Ensatina eschscholtzii* remained in this aqueous bath until they were completely immobile, which took approximately 5 min. We used a hypodermic needle (26 gauge) to create an opening in the abdominal cavity into which we inserted a 20-μCi (1 Ci = 37 GBq) Ta^{182} wire (approximately 0.4 × 2 mm), following the methods of Madison and Shoop (1970). *Ensatina eschscholtzii* resumed activity within 10 min of this procedure. A scintillation survey meter (Model 3, Ludlum Measurements, Inc., Sweetwater, Tex., U.S.A.) and a gamma scintillator (Model 44-10, Ludlum Measurements, Inc.) attached to a wooden pole were used to monitor the location of Ta^{182}-marked *E. eschscholtzii*. The detection limit was approximately 2 m on the surface and up to 0.5 m underground.

Collection site and handling

Ensatina eschscholtzii were collected during a visual search in and under litter and woody debris in October 1992 (expt. 1) and April 1993 (expt. 2) from a young (approximately 40–60 years old) Douglas-fir plantation located approximately 18 km northwest of plots D and E and ≥12 km northeast of plots A–C. The stands at the collecting site were similar in age and structure to those where the plots were located. Following capture, *E. eschscholtzii* were kept in 26 × 13 × 33 cm plastic containers in a thermally regulated environment (11–16° C) with approximately 8 h of diffuse light per day. Water, in the form of mist, and fruit flies were added at approximately weekly intervals. Our procedures of care while the animals were confined away from the field site were similar to those used by Ovaska (1987) with *Plethodon vehiculum*.

Overview of experiments

We conducted two experiments. The objective in expt. 1 was to test how the presence of corridors affected movement patterns. Experiment 2 was conducted to evaluate how robust were the findings from expt. 1 to changes in two variables: (1) increased severity of the matrix habitat and (2) animal experience.

In expt. 1 we marked and released a total of 250 adult *E. eschscholtzii*. The 50 adults per plot included 31 males and 19 nongravid (ovarian eggs not externally visible) females. We considered *E. eschscholtzii* with a snout–vent length of >4.2 cm to be adults (Rosenberg 1995). We introduced *E. eschscholtzii* into each plot on successive days (one plot was initiated per day). *Ensatina eschscholtzii* were confined to the source patch during a 4-day acclimation period after which we removed the acclimation barriers and monitored salamander movements at approximately 24-h intervals from 14 November to 8 December 1993, a total of 21 days per plot. *Ensatina eschscholtzii* that reached target patches were removed from the study and later released following removal of the Ta^{182} wire.

Experiment 2 consisted of two trials, first (trial A) with juveniles and then (trial B) with adult males. Rain interfered with the completion of trial A during dry (i.e., harsh) conditions. We commenced trial B when conditions were likely to remain dry until the experiment was completed (Rosenberg 1995). In contrast to expt. 1, juvenile (trial A) and adult male (trial B) *E. eschscholtzii* that reached target patches before the end of the experiment were returned to the center of source patches for evaluation of the behavior of "experienced" individuals.

In trial A, we marked and released a total of 25 juvenile *E. eschscholtzii* into each plot. We extended the acclimation period from the planned 4 days while awaiting drier conditions. After the 12- to 15-day acclimation period, juveniles were monitored daily in each plot for 9 days, from 9 to 17 June 1993. During this period, rain interrupted the otherwise dry conditions. We curtailed trial A so that a new trial with adult males could be conducted during the brief period of drier conditions prior to the summer drought, when conditions would be too severe for *E. eschscholtzii* to survive the trials (Rosenberg 1995).

In trial B, we marked and released 22 adult male *E. eschscholtzii* into the source patch of each plot. After a 4-day acclimation period, we removed the barriers that confined *E. eschscholtzii* to the source patches, and monitored movements at approximately 24-h intervals beginning the day after the barriers were removed (26–28 June 1993) until 9–11 July 1993, a total of 14 days per plot.

Assessment pens

The relative physiological cost to *E. eschscholtzii* in the 2 pathway types (bare, corridor) in expt. 2 was estimated by assessing behavior, mass loss, and mortality of *E. eschscholtzii* placed in 1 × 3 m pens. We randomly selected a 1 × 3 m section in both bare and corridor pathways in each plot. These areas were fenced with aluminum flashing. We covered the tops with chicken wire to minimize the potential for high predation rates; the restricted and exposed area within the assessment pens and the frequency of our visits motivated us to take this precaution. In each assessment pen, we confined 5 (Ta^{182}-tagged) randomly selected *E. eschscholtzii* (juveniles and nongravid females) for 12–15 days before trial A and 5 nongravid females for 5 days prior to trial B. We located and weighed (to the nearest 0.05 g) each salamander daily for the first 5 days (trials A and B) and every other day for the next 7–10 days (trial A). Assessment pens and *E. eschscholtzii* were removed before *E. eschscholtzii* were released from source patches to initiate trials A and B.

Statistical analyses

We estimated 3 parameters that likely influence successful immigration and 1 parameter that provides an estimate of immigration rates: (1) selection: the number of *E. eschscholtzii* initially located in the 2 pathway types (corridor and bare); (2) movement velocity: (*a*) initial distance moved outside of source patches (i.e., metres moved on the first day) and (*b*) the total number of successive days spent within the first pathway entered; (3) physiological cost (expt. 2 only): percent mass loss in assessment pens; and (4) immigration rate: the number of *E. eschscholtzii* located in target patches.

We used a completely randomized block design (Petersen 1985, p. 7) in the analysis of variance (ANOVA) for all variables except mass loss. We conducted two general analyses: one on values from the initial pathway in which an individual was located and the other on values from the pathway that was entered after the animals were returned to the source following successful immigration to a target patch (expt. 2 only). Plots were treated as the experimental blocks; the main effects in the ANOVA model were sex (expt. 1 only) and treatment. The interaction of plot and treatment was used as the experimental error term for analyses of the main effects of treatment. We included sex in the ANOVA model for expt. 1 to control for possible sex effects; however, we report only the variation remaining due to treatment. The statistical significance of the plot (block) is an approximate value because the blocking classification was not replicated (Petersen 1985). Within a plot, we pooled data from pathways with a common treatment because of their lack of independence. In trial A of expt. 2, there were no observations of *E. eschscholtzii* in the bare pathways within plot D, therefore we excluded plot D from analyses of initial day, number of days, and distance. We transformed (ln + 1) number of successive days to improve normality but report untransformed means and standard errors. In trial B of expt. 2 (adults), we located 3 individuals that died in the first pathway in which they were observed; these individuals were not included in analyses of distance moved or number of successive days.

We compared mass loss (from the assessment pen study, expt. 2) between treatments with a multivariate repeated-measures ANOVA with day as the repeated factor and initial mass (i.e., mass when the animals were placed in the pens) as a covariate. The response variable

Table 1. Variation ($\bar{x}$ ± SE) among plots of the number of marked *Ensatina eschscholtzii* located outside of source patches, number located in target patches, initial day of movement, initial distance moved, and number of successive days animals were located in the first pathway entered during expt. 1, November–December 1992.

Plot	Outside[a]	Target[b]	Day[c]	Distance (m)	No. of days[d]
A	38	28	3.5±0.4	27.1±2.2	2.9±0.7
B	48	36	5.7±0.9	22.8±1.8	2.0±0.2
C	42	27	8.0±0.7	22.7±2.5	2.3±0.5
D	45	20	8.6±0.8	22.3±2.1	2.3±0.5
E	48	39	5.0±0.6	27.2±2.1	1.8±0.4
All[e]	221	150	6.2±0.3	24.4±1.0	2.2±0.2

[a] Number of *E. eschscholtzii* located at least once outside of source patches.

[b] Number of *E. eschscholtzii* located in target patches (i.e., “immigrants”).

[c] Initial day after release that *E. eschscholtzii* were located outside of source patches.

[d] Number of successive days on which *E. eschscholtzii* were located in the first pathway within which an individual was found.

[e] All individuals pooled.

was the percentage of mass loss from the initial mass. We tested the effect of treatment (bare, corridor) and day (which includes both the characteristics of the particular day and length of confinement) and the interaction of treatment and day. This interaction tests whether the effect of day on mass loss differed between treatments. For the mass loss data from trial A, we restricted the analyses to the first 4 days because the sample size (number of salamanders and number of plots) decreased after 4 days. We used linear regression to describe the relationship of mean percent mass loss (i.e, the mean for all animals in each pen) with number of days spent in the pen. We used logistic regression to test the null hypothesis that mortality in the pens was unaffected by mass loss recorded on the last observation; the significance of the predictor variable (percent mass loss) was assessed with the deviance statistic, which has a χ^2 distribution (Hosmer and Lemeshow 1989). Because mass loss was minimal in animals confined to pens in trial A, we used only data from trial B in the mortality analysis.

Results

Experiment 1

Of 250 *E. eschscholtzii*, 221 (88.4%) were located at least once outside of source patches, 8 (3.2%) were located only in source patches, and 21 (8.4%) were never located. Of the 221 animals located outside of source patches, 149 (67.4%) were located in target patches. The numbers of *E. eschscholtzii* located outside source patches ranged from 38 to 48 per plot (Table 1). *Ensatina eschscholtzii* first moved outside of source patches, on average, on the 6th day after initial release (Table 1). The plot into which *E. eschscholtzii* were placed did not account for a significant amount of the variation in initial distance moved or the total number of successive days spent in the initial pathway ($F_{[4,4]} \leq 0.8$, $P \geq 0.6$). The number and proportion of *E. eschscholtzii* that reached target patches were considerably lower in plot D than in the other 4 plots (Table 1), although plot did not account for a significant amount of the variation ($F_{[4,4]} = 1.5$, $P = 0.3$).

The presence of a corridor affected the number of *E. eschscholtzii* located, distance moved, and the number of successive days on which *E. eschscholtzii* were located in the initial pathway entered. Differences from the random expectation of 50% in the number that entered pathways with and without corridors ranged from 2.6 to 16.7% more in corridor than in bare pathways among the 5 plots. Overall, in corridors versus bare pathways, we located more *E. eschscholtzii* (26.8 ± 1.8 vs. 17.4 ± 1.2 (mean ± SE); $F_{[1,4]} = 16.5$, $P = 0.01$; Fig. 2), the initial distance travelled was shorter (19.5 ± 0.9 vs. 31.8 ± 2.4 m; $F_{[1,4]} = 16.1$, $P = 0.02$; Fig. 3), and more successive days were spent there (3.0 ± 0.4 vs. 1.1 ± 0.07; $F_{[1,4]} = 20.5$, $P = 0.01$; Fig. 4). There was only weak evidence that more *E. eschscholtzii* were located in target patches connected by bare pathways (17.4 ± 2.8) than in those connected by corridor pathways (12.6 ± 1.3; $F_{[1,4]} = 3.1$, $P = 0.15$; Fig. 5).

Experiment 2

Trial A: Juveniles

We located a total of 96 (76.8% of 125 released) *E. eschscholtzii* at least once outside of the source patches (Table 2), located 7 (5.6%) only in source patches, and 22 (17.6%) were never located. Of the 96 *E. eschscholtzii* located outside of source patches, 74 (77.1%) were located in target patches (Table 2). A total of 61 previously successful immigrants were located in pathways after being returned to source patches, and of these, 46 (75.4%) were located a second time in target patches.

The numbers of *E. eschscholtzii* located outside source patches after their initial release ranged from 14 to 24 per plot (Table 2). *Ensatina eschscholtzii* were first located outside the source areas typically between days 2 and 5 (2.7 ± 0.2). The number of *E. eschscholtzii* located in pathways and target patches, the initial distance moved, and the number of successive days spent in a linear patch did not vary significantly among plots ($F_{[3,3]} \leq 1.6$, $P \geq 0.3$; Table 2).

In corridor pathways versus bare pathways, greater numbers of *E. eschscholtzii* were located (12.4 ± 1.0 vs. 6.8 ± 1.8; $F_{[1,4]} = 6.7$, $P = 0.06$; Fig. 2), they had moved a shorter initial distance (28.4 ± 0.7 vs. 34.7 ± 2.5 m; $F_{[1,3]} = 8.3$, $P = 0.06$; Fig. 3), and they were found on more successive days (2.3 ± 0.3 vs. 1.3 ± 0.2; $F_{[1,3]} = 18.2$, $P = 0.02$; Fig. 4). However, the greater numbers of *E. eschscholtzii* (6.6 ± 1.0 vs. 5.6 ± 1.5; $F_{[1,4]} = 2.3$, $P = 0.2$; Fig. 2) and shorter distances moved (32.2 ± 0.5 vs. 34.2 ± 1.5 m; $F_{[1,3]} = 1.2$, $P = 0.3$; Fig. 3) were not evident for individuals returned to source patches following successful immigration, but we found a similar pattern of a greater number of days spent within corridor pathways (2.6 ± 0.3 vs. 1.1 ± 0.6; $F_{[1,3]} = 53.0$, $P = 0.005$; Fig. 4).

The numbers of immigrants were similar in target patches connected by corridor (8.4 ± 0.9) and bare (6.4 ± 1.4) pathways ($F_{[1,3]} = 1.5$, $P = 0.3$; Fig. 5). In plot D, the number of immigrants was much higher in target patches connected by corridors (Fig. 5); however, plot did not account for a significant amount of the variation, as described above. The similarity between treatment types was even greater for *E. eschscholtzii* that entered target patches a second time after having been returned to source patches (4.4 ± 0.8 vs. 4.8 ± 1.3; $F_{[1,3]} = 0.4$, $P = 0.8$; Fig. 5).

Assessment pens

The response of *E. eschscholtzii* that were confined to assessment pens before trial A was not affected by whether or not corridors were present. *Ensatina eschscholtzii* lost an average

Fig. 2. Percentages of *Ensatina eschscholtzii* located in corridor and non-corridor (bare) pathways. Values shown are from the initial pathway within which an individual was located during expt. 1 (*a*), trial A in expt. 2 (juveniles) (*b*), and trial B in expt. 2 (adult males) (*c*). Results from the second (i.e., after the animals were returned to a source patch following successful immigration) pathway entered are shown for trial A (*d*) and trial B (*e*) in expt. 2. Deviation from the value expected under the null hypothesis (50%) was used as a measure of corridor selection.

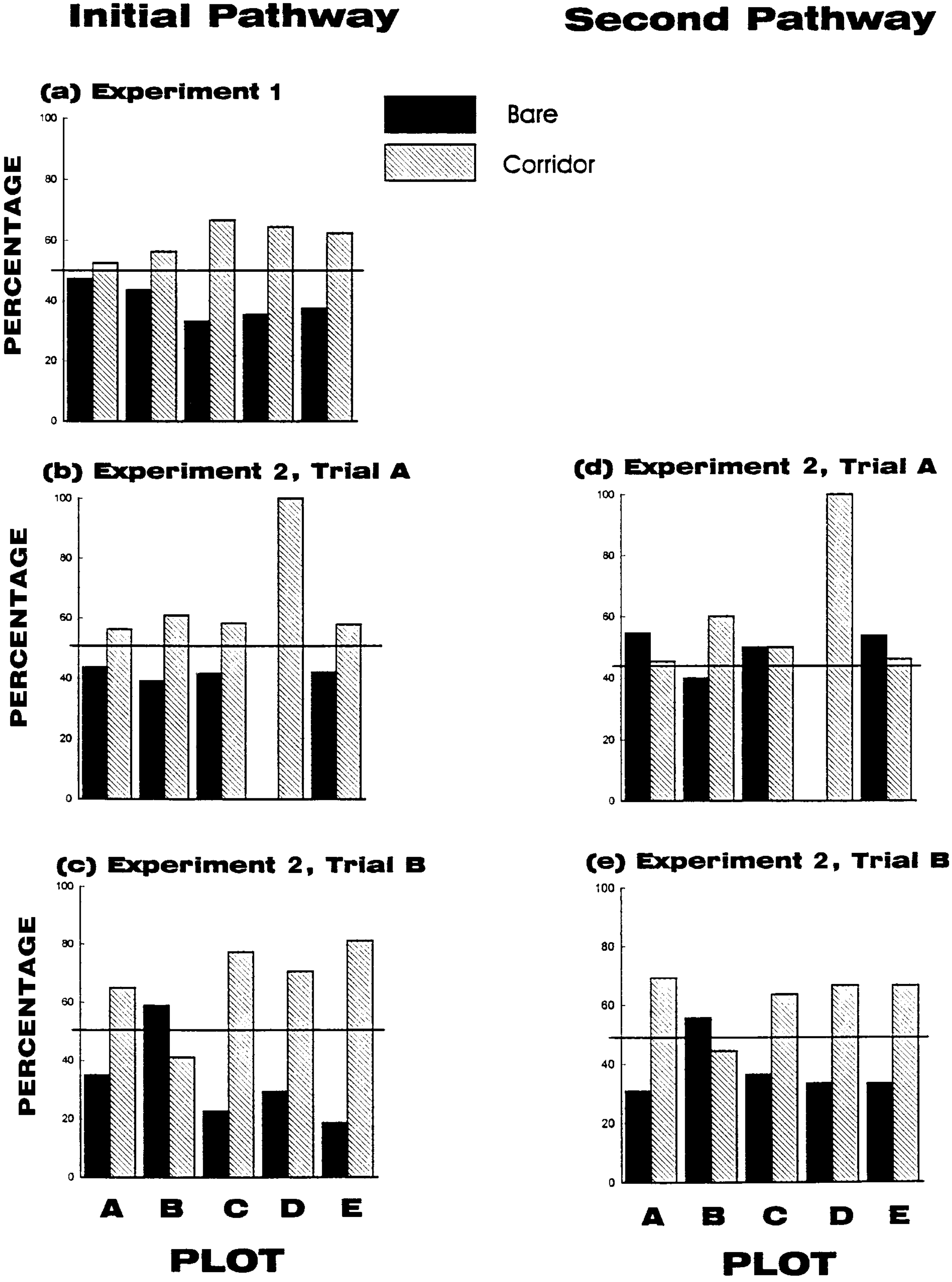


Fig. 3. Distances ($\bar{x}$ ± SE) from the source patches in which *Ensatina eschscholtzii* were first observed in corridor and non-corridor (bare) pathways. Values shown are from the initial pathway within which an individual was located during expt. 1 (*a*), trial A in expt. 2 (juveniles) (*b*), and trial B in expt. 2 (adult males) (*c*), and from the second (i.e., after the animals were returned to a source patch following successful immigration) pathway entered during trial A (*d*) and trial B (*e*) in expt. 2. No individuals were located in the initial or second pathway in plot D in trial A of expt. 2.

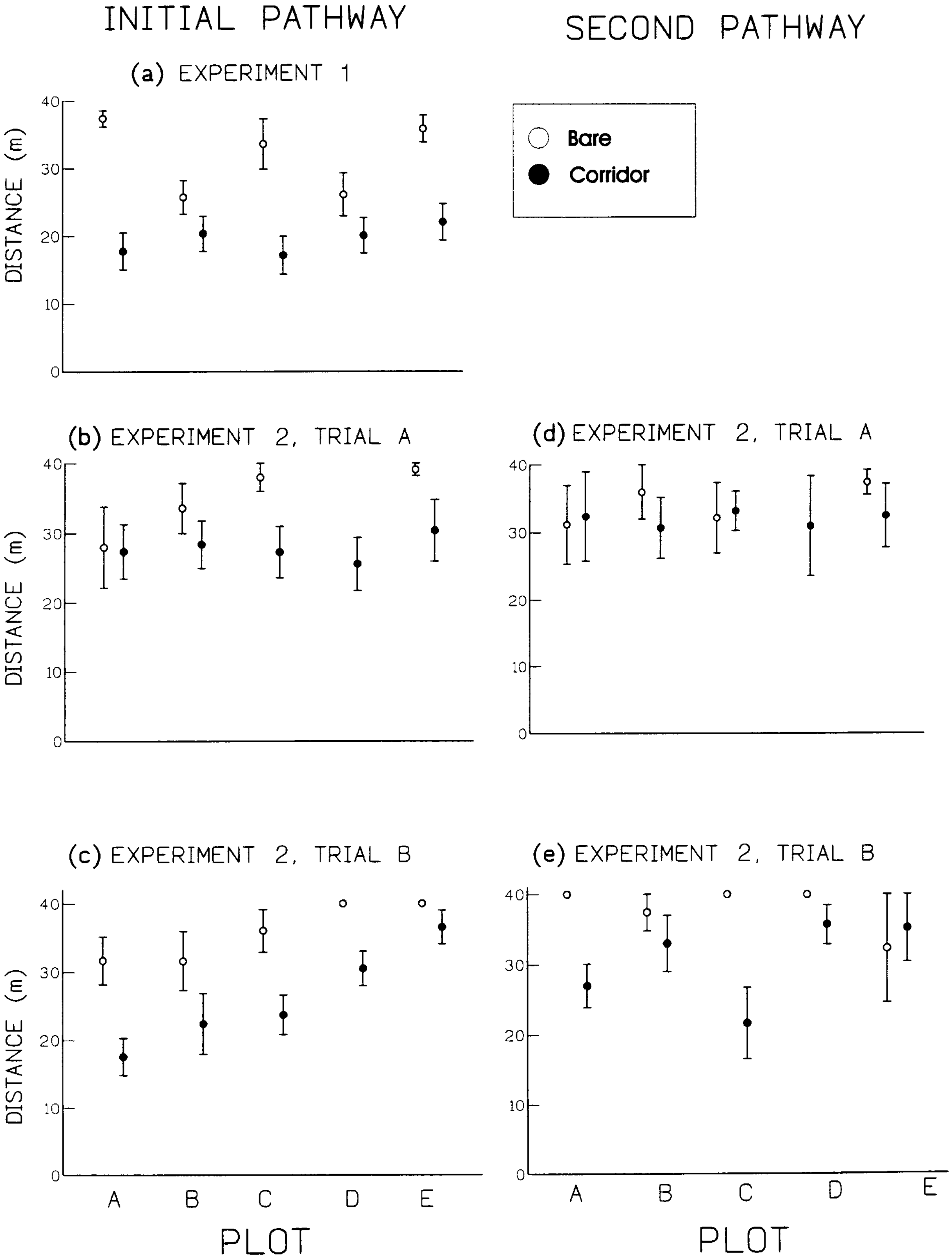


Fig. 4. Numbers ($\bar{x}$ ± SE) of successive days on which *Ensatina eschscholtzii* were located in corridor and non-corridor (bare) pathways. Values shown are from the initial pathway within which an individual was located during expt. 1 (*a*), trial A in expt. 2 (juveniles) (*b*), and trial B in expt. 2 (adult males) (*c*), and from the second (i.e., after the animals were returned to a source patch following successful immigration) pathway entered during trial A (*d*) and trial B (*e*) in expt. 2. No individuals were located in the initial or the second pathway in plot D in trial A of expt. 2.

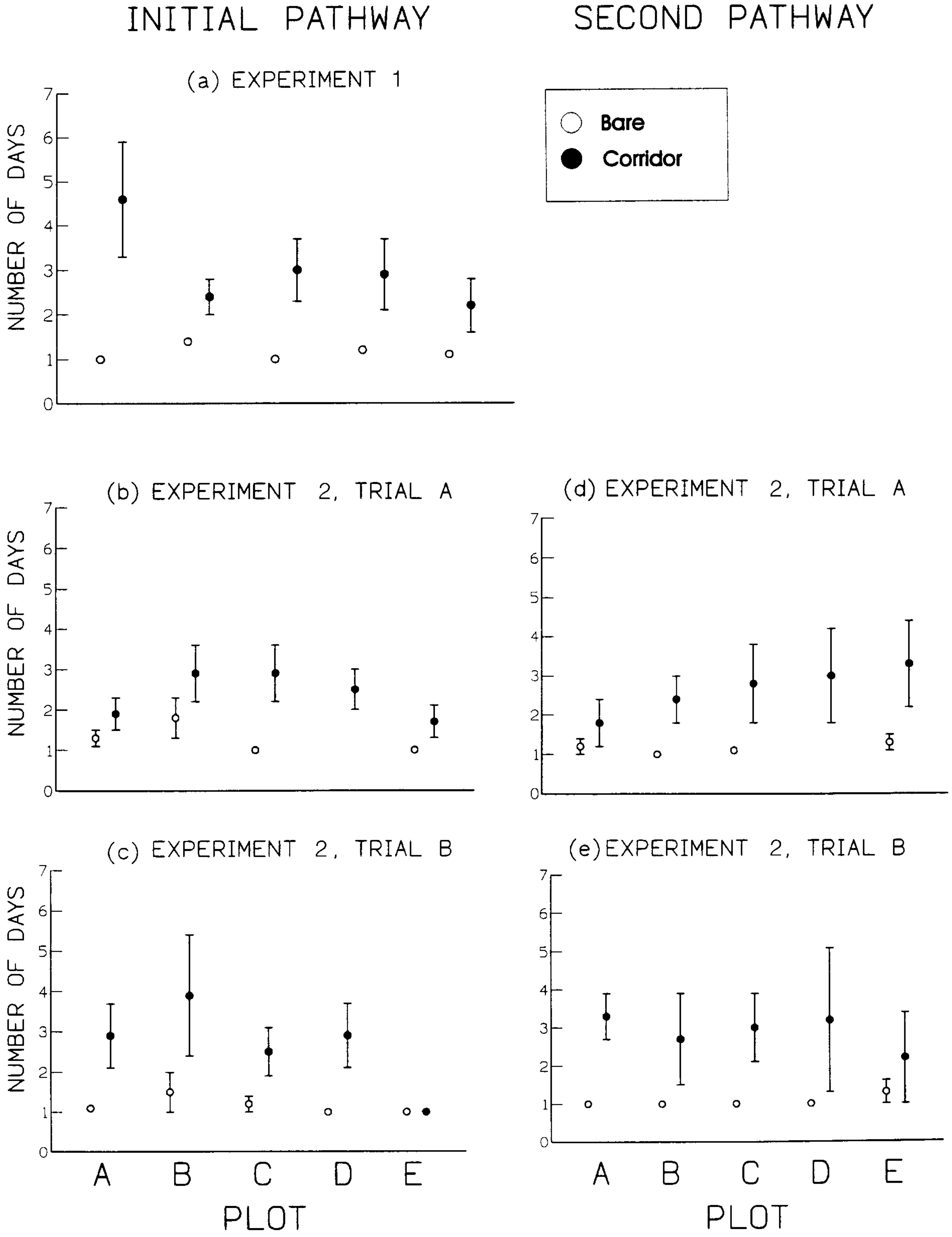


Fig. 5. Percentages of *Ensatina eschscholtzii* located in target patches connected to source patches by pathways with and without corridors. Values shown are from the initial target patch entered during expt. 1 (*a*) and trial A (juveniles) (*b*) and trial B (adult males) (*c*) of expt. 2. Results from the second (i.e., after the animals were returned to a source patch following successful immigration) target patch entered are shown for trial A (*d*) and trial B (*e*) of expt. 2. Deviation from the value expected under the null hypothesis (50%) was used as a measure of corridor selection.

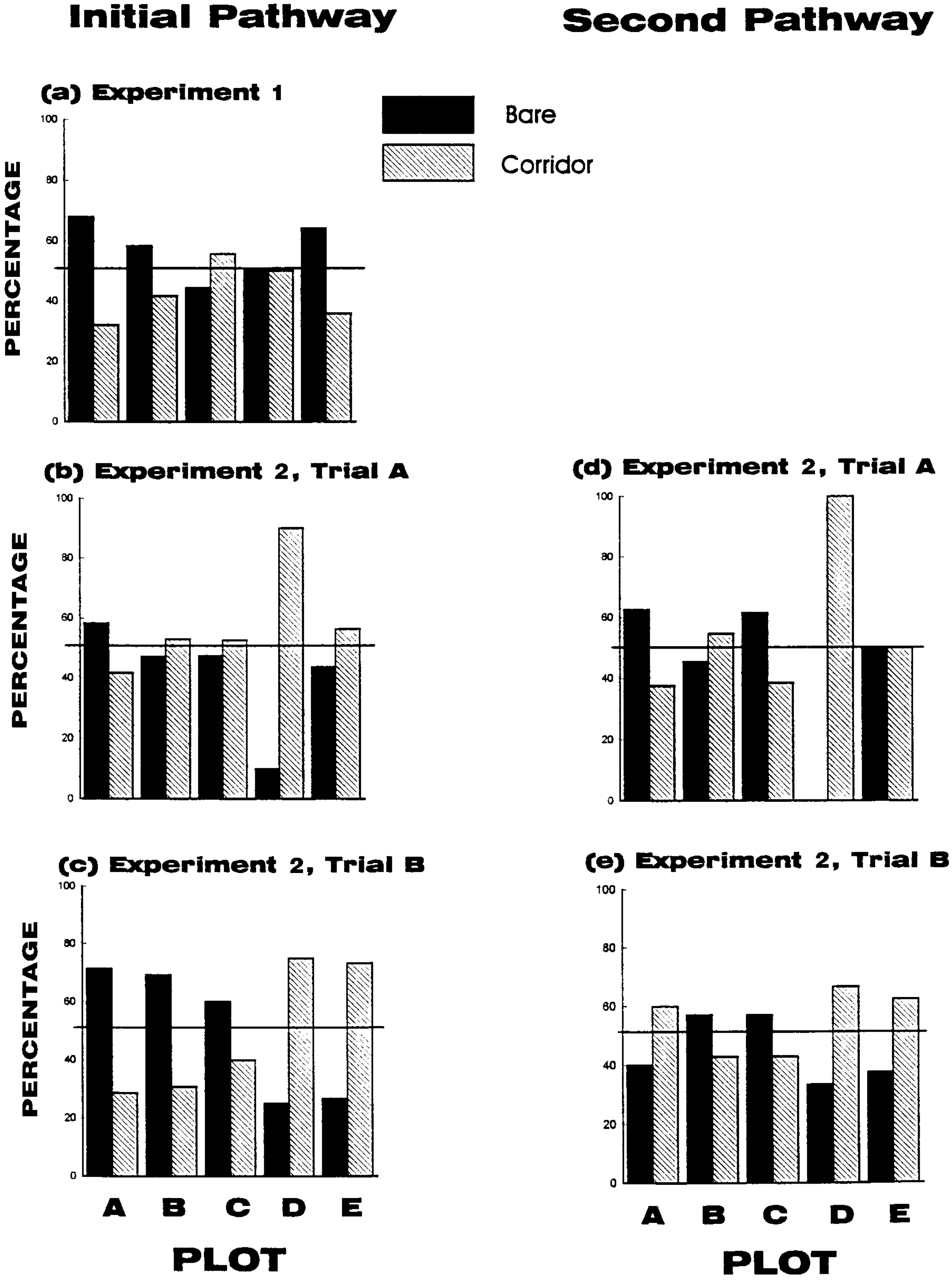


Table 2. Variation ($\bar{x}$ ± SE) among plots of the number of marked juvenile *Ensatina eschscholtzii* located outside of source patches, number located in target patches, initial day of movement, initial distance moved, and number of successive days animals were located in pathways entered during trial A of expt. 2, June 1993.

	Initial pathway					Second pathway[a]		
Plot	Outside[b]	Target[c]	Day[d]	Distance (m)	No. of days[e]	Outside[b]	Distance (m)	No. of days[e]
A	16	12	2.6±0.5	27.7±3.2	1.6±0.3	11	31.7±4.2	1.4±0.3
B	23	17	2.4±0.4	30.4±2.5	2.5±0.5	15	32.8±3.1	1.9±0.4
C	24	19	2.2±0.4	31.7±2.5	2.1±0.5	18	32.7±2.9	1.9±0.5
D	14	10	3.7±0.5	25.6±3.8	2.5±0.5	4	31.0±7.4	3.0±1.2
E	19	16	3.1±0.6	34.0±2.7	1.4±0.2	13	34.4±2.4	2.4±0.7
All[f]	96	74	2.7±0.2	30.3±1.3	2.0±0.2	61	32.8±1.5	2.0±0.2

[a] The pathway first entered after being returned to a source patch following successful immigration.

[b] Number of *E. eschscholtzii* located at least once outside of source patches.

[c] Number of *E. eschscholtzii* located in target patches (i.e., "immigrants").

[d] Initial day after release that *E. eschscholtzii* were first located outside of source patches.

[e] Number of successive days on which *E. eschscholtzii* were located in the first pathway within which an individual was found.

[f] All individuals pooled.

of 3.8 ± 0.9% of initial body mass by the 4th day following placement in the confined pens. There was no effect on mass loss of the presence of a corridor ($F_{[1,39]} = 0.2$, $P = 0.7$), nor was day a significant factor ($F_{[3,37]} = 0.9$, $P = 0.4$); the interaction of day and the presence of a corridor was weak ($F_{[3,37]} = 2.0$, $P = 0.14$; Fig. 6). The plot in which *E. eschscholtzii* were placed accounted for most (37%) of the variance between subjects ($F_{[4,39]} = 3.6$, $P = 0.01$); plot D had the lowest daily average mass loss (<2.5%) and plot C had the highest (7–11%). All *E. eschscholtzii* survived the first 4 days of confinement; for any single day, mean mass loss was <7%. Despite the lack of a difference in mass loss between patches with and without corridors, all marked *E. eschscholtzii* in assessment pens with corridors were observed (diurnally) 2–10 cm below the surface in organic matter in the 1 × 1 m area that contained moss; none were observed in the bare sections of the pens when organic matter was available.

Trial B: Adults

We located a total of 92 (83.6% of 110 released) adult *E. eschscholtzii* at least once outside of source patches (Table 3), located 3 (2.7%) only in source patches, and never located 15 (13.6%). Of the 92 *E. eschscholtzii* located outside of source patches, 69 (75.0%) were located in target patches (Table 3). A total of 48 previous immigrants were located in pathways after being returned to source patches (Table 3), and of these, a total of 35 (72.9%) were located in target patches. Only initial distance moved varied significantly among plots ($F_{[4,4]} = 8.4$, $P = 0.03$; Table 3). Initial day, number of days spent within the initial pathway, and number of *E. eschscholtzii* located in linear and target patches did not vary significantly among plots ($F_{[4,4]} \leq 0.2$, $P \geq 0.3$; Table 3).

We found differences between pathways with and without corridors in the number of adult *E. eschscholtzii* located, distance moved, and number of days spent within the initial pathway. Differences from the null expectation of 50% in the number that entered each pathway type ranged from 8.8% more in bare pathways to 31.3% more in corridor pathways (Fig. 2). We located more *E. eschscholtzii* (12.4 ± 1.6 vs. 6.0 ± 1.2; $F_{[1,4]} = 6.1$, $P = 0.07$; Fig. 2), at shorter initial distances (26.1 ± 3.3 vs. 35.9 ± 1.9 m; $F_{[1,4]} = 33.5$, $P = 0.004$; Fig. 3), and on more successive days (2.6 ± 0.5 vs. 1.2 ± 0.1; $F_{[1,4]} = 17.2$, $P = 0.01$; Fig. 4) in corridor pathways than in bare pathways. These patterns also existed in pathways that previous immigrants entered after they were returned to source patches, although with less statistical significance, in the number of *E. eschscholtzii* located (6.0 ± 0.9 vs. 3.6 ± 0.5; $F_{[1,4]} = 6.0$, $P = 0.07$; Fig. 2), distance moved (30.5 ± 2.7 vs. 37.9 ± 1.5 m; $F_{[1,4]} = 3.0$, $P = 0.15$; Fig. 3), and number of days spent in the first pathway entered (2.9 ± 0.2 vs. 1.1 ± 0.1; $F_{[1,4]} = 18.4$, $P = 0.01$; Fig. 4). We did not detect differences between treatments in the number of adult *E. eschscholtzii* located in target patches. There was no difference in either the initial target patch entered (6.8 ± 1.4 vs. 7.0 ± 1.5; $F_{[1,4]} = 1.6$, $P = 0.3$) or the target patch previously successful immigrants entered after they were returned to source patches (3.8 ± 0.7 vs. 3.2 ± 0.6; $F_{[1,4]} = 0.8$, $P = 0.4$; Fig. 5).

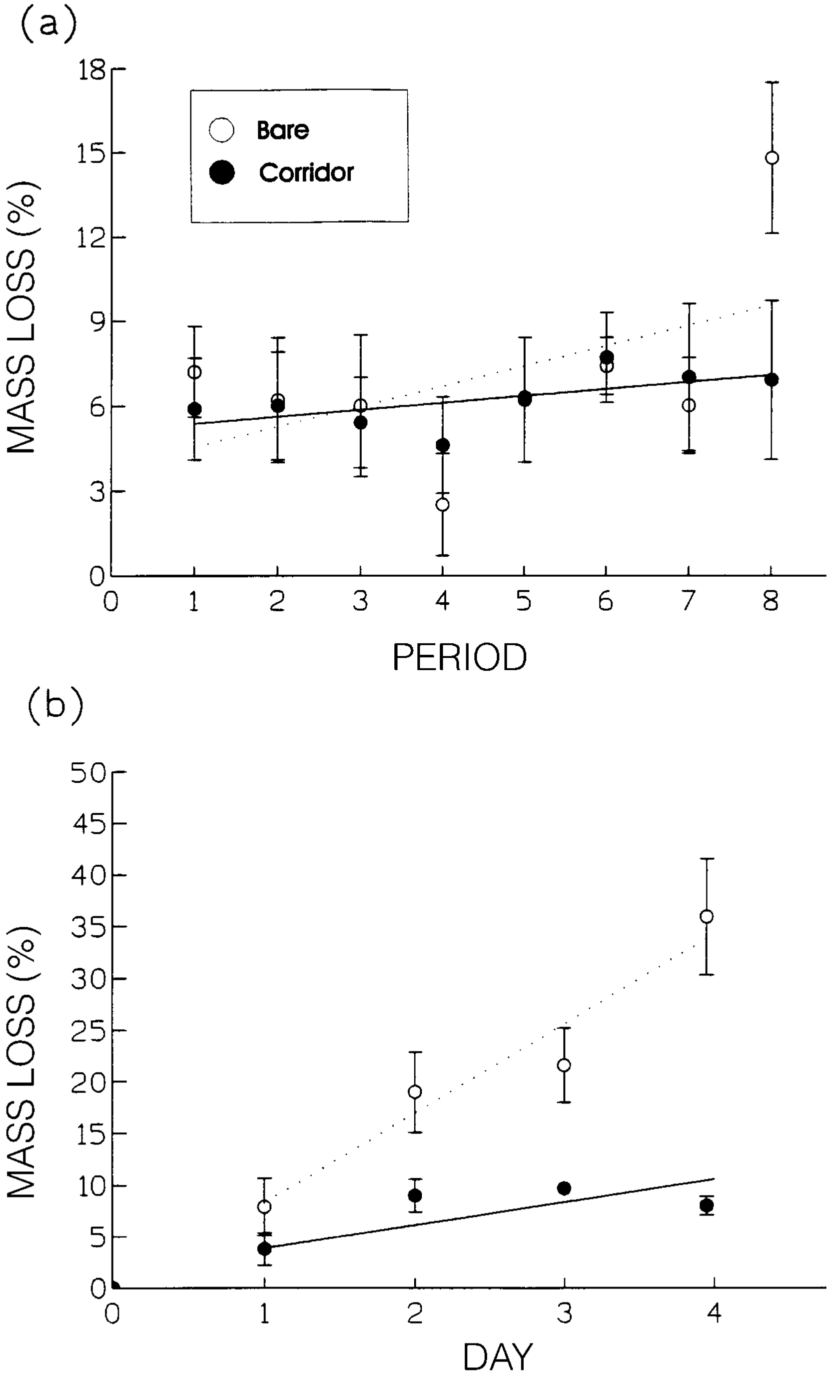
Assessment pens

Percent mass loss increased at a much faster rate in bare pens (slope = 8.5% g/day) than in corridor pens (slope = 2.8% g/day; Fig. 6). Percent mass loss was affected by the presence of a corridor ($F_{[1,32]} = 80.1$, $P = 0.0001$) and the interaction of day and presence of a corridor ($F_{[3,30]} = 25.7$, $P = 0.0001$), but not by day as a single factor ($F_{[3,30]} = 1.1$, $P = 0.37$). Day affected mass loss for *E. eschscholtzii* after the first day in bare pens but not for those in corridor pens (Fig. 6). A total of 16 of 25 (64%) *E. eschscholtzii* died in bare pens, whereas none died while in corridor pens. *Ensatina eschscholtzii* in bare pens in plots D and E showed the greatest percent mass loss (>42% by the last day of confinement); mass loss was strongly related to the probability of mortality ($\chi^2 = 21.1$, df = 1, $P < 0.001$). As in trial A, all *E. eschscholtzii* were observed (diurnally) in the 1 × 1 m area that contained moss; none were observed in the bare sections of the pens.

Discussion

Based on the assumption of increased immigration rates

Fig. 6. Relationship of percent mass loss in *Ensatina eschscholtzii* as a function of the number of days spent in bare and corridor assessment pens in trial A (*a*) and trial B (*b*) of expt. 2. The periods in trial A represent the number of days after initial release into the assessment pens; periods 1–5 represent days 1–5, period 6 represents days 6 and 7, period 7 represents days 8–11, and period 8 represents days 12, 13, and 15. Days are grouped into periods because not all plots were checked on the same day. The dotted and solid lines are the best linear representation of percent mass loss in the bare and corridor assessment pens, respectively. The bars represent the standard error of the mean of the plots. Mass loss was assessed just prior to expt. 2: May–June 1993 for trial A (juveniles) and June 1993 for trial B (adult males).



among habitat patches (reserves) embedded in less suitable matrix habitat, biological corridors are common components of conservation strategies designed to maintain biological diversity (Hobbs 1992; Rosenberg et al. 1997). The advantages of corridors are realized if such pathways are recognized and selected (i.e., animals are directed to corridors), and the animals achieve higher rates of movement in corridors and (or) higher survival rates within corridors than within the matrix environment (Fig. 7). The field experiments we conducted, which incorporated strong contrasts in habitat quality among possible movement pathways, affected the behavior of *E. eschscholtzii* that were placed in them. However,

Table 3. Variation ($\bar{x}$ ± SE) among plots of the number of marked adult male *Ensatina eschscholtzii* located outside of source patches, number located in target patches, initial day of movement, initial distance moved, and number of successive days animals were located in pathways entered during trial B of expt. 2, June–July 1993.

	Initial pathway					Second pathway[a]		
Plot	Outside[b]	Target[c]	Day[d]	Distance (m)	No.of days[e]	Outside[b]	Distance (m)	No. of days[e]
A	20	14	2.7±0.4	22.5±2.6	2.3±0.5	13	31.0±2.7	2.6±0.5
B	17	13	2.3±0.4	27.8±3.2	2.5±0.7	9	35.4±2.3	1.8 ± 0.6
C	22	15	3.4±0.5	26.5±2.6	2.2±0.5	11	28.3±4.2	2.3±0.6
D[f]	17	12	5.4±1.2	32.4±2.2	2.5±0.7	6	36.6±2.4	2.8±1.6
E[f]	16	15	4.5±0.9	36.9±2.2	1.0±0	9	34.2±3.8	1.9±0.8
All[g]	92	69	3.6±0.3	28.6±1.3	2.1±0.2	48	32.4±1.5	2.2±0.3

[a] Pathway entered after the animal was returned to a source patch following successful immigration.

[b] Number of *E. eschscholtzii* located at least once outside of source patches.

[c] Number of *E. eschscholtzii* located in target patches (i.e., “immigrants”).

[d] Initial day after release that *E. eschscholtzii* were first located outside of source patches.

[e] Number of successive days on which *E. eschscholtzii* were located in the first pathway within which an individual was found.

[f] *Ensatina eschscholtzii* that were found dead at first observation ($n = 2$ and 1 for plots D and E, respectively) were excluded from analysis of number of days and movement data.

[g] All individuals pooled.

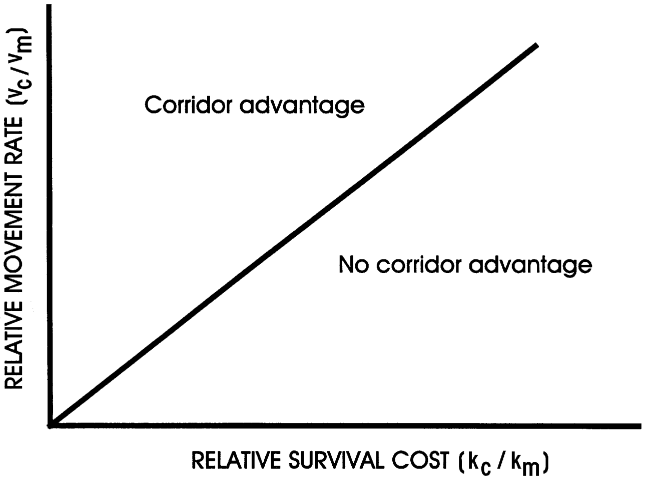
compensatory relationships between the likelihood of selection, movement velocity, and survival costs resulted in equal immigration rates to target patches connected by bare and corridor pathways.

Behavioral responses to pathway types were consistent among experimental plots. *Ensatina eschscholtzii* generally selected corridor pathways; this selection varied from weak to strong in the most severe matrix environments, suggesting that the difference in survival costs between the corridor and the matrix influences the likelihood of selecting corridor pathways (Rosenberg et al. 1997). Individuals moved more rapidly and had lower settling rates in bare pathways than in corridor pathways. *Ensatina eschscholtzii* that were returned to the source patch after successful immigration (expt. 2) typically responded as they did in their initial release. Differences in movement rates between bare and corridor pathways were less pronounced for previously successful immigrants than for those initially released in corridor pathways because of greater movement rates in corridor pathways. Successful immigrants that were returned to source patches may have represented a biased sample of *E. eschscholtzii* which were more likely to move away from source patches. Their behavior may have more closely approximated that of dispersers. In all experiments, mechanisms that contribute to successful immigration were consistently influenced by the presence of habitat in the pathway (the potential corridor), although the magnitude of the various behavioral parameters was not. This inconsistency of response rates resulted in immigration rates to target patches that varied spatially (plot) and temporally (timing of experiment) between patches connected by bare and corridor pathways.

The relatively low selection by *E. eschscholtzii* of corridor pathways to enter, despite the corridor’s proximity to the source patch (i.e., within a home-range diameter; Stebbins 1954), and the distinct difference in habitat between pathway types indicated a tendency towards random movement. Our experiments, however, were performed with displaced animals, and their movement patterns are likely different from those of individuals occupying established home ranges. Nevertheless, our results were consistent with those from previous studies of dispersal of various taxa. Long distance dispersal orientation is often relatively unaffected by habitat for a wide variety of organisms: butterflies (Fahrig and Paloheimo 1987; Harrison 1989), birds (Bump et al. 1947; Thomas et al. 1990), and mammals (Smith 1974; Storm et al. 1976). Indeed, several terrestrial species have been found to disperse through large bodies of water (Sheppe 1965; Peltonen and Hanski 1991), and in a laboratory experiment, stressed fish (*Lepomis macrochirus*) and crayfish (*Orconectes causeyi*) exited pens through inhospitable environments (Matter et al. 1989).

A recent study conducted by Andreassen and co-workers (1996) on root voles (*Microtus oeconomus*) provides an interesting comparison with the study reported here. They tested behavioral mechanisms, similar to the ones we examined, that may be responsible for increasing immigration among patches connected by corridors. They found a strong effect of corridor width. Rates of immigration to the habitat patches were greatest in the midwidth (1 m) and lowest in the widest (3 m) corridor treatment. These results were attributed to differences in resistance to movement and in linear speed of movement. Resistance to movement was greatest in the narrowest corridor (0.4 m), as demonstrated by the high percentage (73%) of trials in which voles did not leave the habitat patch in which they were released. Movement rates were lowest in the wide corridor, which was attributed to frequent cross-directional use of the corridor. Andreassen et al. (1996) concluded that wider corridors are not necessarily more efficient as conduits for movement than narrower corridors, provided the latter are not so narrow that they are avoided as movement pathways. These authors correctly note that their conclusions are based on equal predation rates among corridor widths; if survival rates vary among corridor types, then immigration rates (a measure of corridor efficiency) will be a function of both time spent in each corridor and the corridor-specific survival rate. Their results are similar to ours in terms of the importance of pathway

Fig. 7. Hypothesized relationship between relative survival cost and movement rates that determines if a pathway functions as a corridor. Under the simple model of immigration rate, $(1 - k_i)^{d/v_i}$, where k_i is the survival cost per unit time in the ith pathway, v_i is the movement rate of an individual in the ith pathway, and d is the distance from the source to the target patch, increased immigration to a target patch via a potential corridor occurs only when the movement rate in a corridor relative to that in the matrix is greater than the relative survival cost. This illustrates the trade-off between these two parameters. The solid line, $v_c/v_m = k_c/k_m$, represents the equilibrium point at which immigration rates are equal for movement through the corridor or through the matrix. For a given relative rate of movement in the corridor (v_c) and the matrix (v_m), corridors increase immigration rates (corridor advantage) over those achieved through dispersal via the matrix as the survival cost per unit time decreases in the corridor (k_c) relative to that in the matrix (k_m), so that $v_c/v_m > k_c/k_m$. However, if movement rates increase in the matrix, owing to a response to perceived higher survival costs, then there is no corridor advantage; rather, when $v_c/v_m < k_c/k_m$, immigration rates are higher when organisms disperse through the matrix. This is true when it is assumed that $k_m \geq k_c$ and $v_m \geq v_c$. Both of these are reasonable assumptions (Rosenberg et al. 1997): survival cost in a "non-habitat" is likely higher than in the habitat with which it is normally associated, and velocity is likely lower in high-quality habitat, owing to a settling response. The results of our field experiments involving *Ensatina eschscholtzii* support these assumptions.



selection and movement rates and the compensatory nature of these mechanisms in determining the efficacy of corridors.

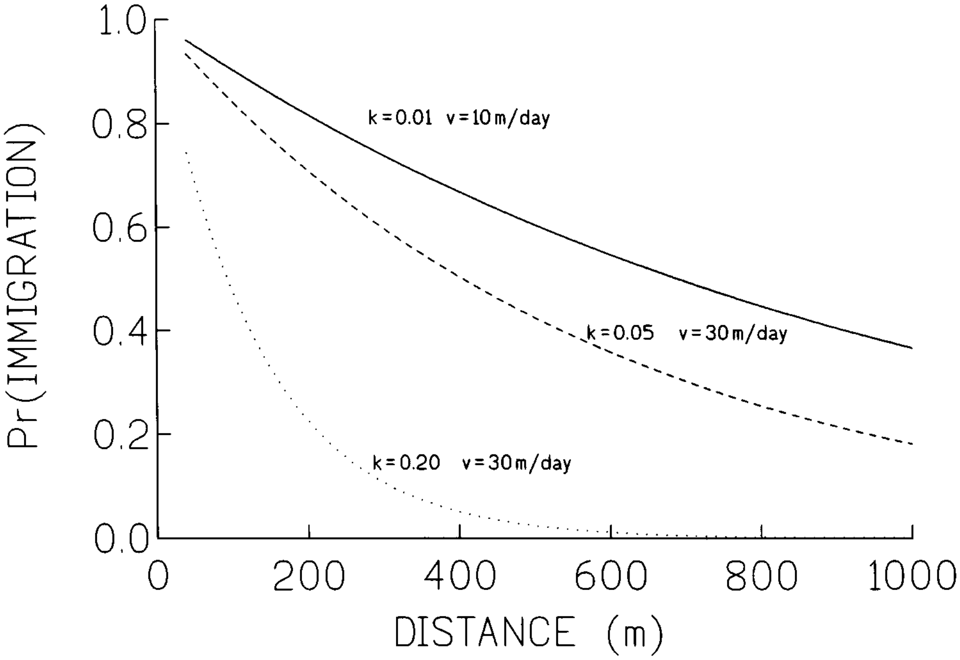
Our results and those of Andreassen et al. (1996) demonstrated that the rate of movement between patches is affected by the nature of the intervening habitat. Thus, simple distance-based metapopulation models (e.g., Levins 1970) that do not explicitly incorporate information on the context of patches may be too simple to adequately model the dynamics of populations in real landscapes. More recent models of movement among local populations have included variability in the costs of interpatch movements (Lamberson et al. 1994; With and Crist 1995). With and Crist (1995) identified habitat-specific rates of transit as a critical parameter affecting an individual's response to habitat fragmentation. Turchin (1991) emphasized the importance of including factors that affect the speed of movement when modelling population distribution. McKelvey et al. (1993) and Shumaker (1996) indirectly modelled habitat-specific movement rates by increasing the likelihood of linear movement out of poor-quality habitats. Habitat-induced variability in dispersal rates can have important effects on the colonization/extinction dynamics of a population (Goldwasser et al. 1994) and, therefore, on metapopulation persistence. When survival costs are high, but below a threshold value that may limit movement (Bernstein et al. 1991), animals may increase their velocity in order to decrease the time spent exposed and thus increase the overall probability of successful dispersal (Fig. 7; but see Johnson and Milne 1992). We documented higher movement velocity, as estimated by the initial unidirectional distance moved, and lower settling rates within habitats with high survival costs. When *E. eschscholtzii* entered bare pathways, they moved rapidly through them. Other taxa display similar responses to hostile habitat. For example, the results of field studies of fruit flies (Dobzhansky et al. 1979), voles (*Microtus* spp.; Stenseth and Lidicker 1992; Andreassen et al. 1996), and flea beetles (Kareiva 1982) support the notion that movement rates are positively related to the severity of the habitat.

Limitations of the study

The experimental model system we created was limited by our need to minimize the spatial and temporal scales that are normally conceived as important by landscape ecologists and conservation biologists. To minimize the temporal scale of the experiment, we used displaced animals as a surrogate for true dispersers, as did Andreassen et al. (1996). These displaced animals may exhibit homing tendencies. However, an earlier pilot study of displaced *E. eschscholtzii* showed no greater likelihood than chance that they would return in the direction from which they were collected (Rosenberg 1995). That the *E. eschscholtzii* were displaced could have resulted in hasty movements. However, the 4-day acclimation period resulted in initial detection of individuals outside of source patches throughout the study, whereas in pilot studies that did not include an acclimation period, individuals usually moved outside of source patches during the first few days following release (Rosenberg 1995). Another concern is that the high densities we used may have led to abnormal movement behavior. However, the results of an experiment using only 1 individual per plot corroborated the fact that the behaviors we observed were not specific to the high densities (Rosenberg 1995). Our study design also restricted movement in relatively small areas and limits our ability to extrapolate to the large landscapes that are of interest in conservation planning.

The fences that defined pathways likely affected immigration rates by limiting movement outside of the pathways. It is not known whether this potential fence effect was consistent between pathway types (bare, corridor). However, if *E. eschscholtzii* were more likely to move away from the direction of the pathway in poor-quality than in high-quality habitat, the increase in immigration rates caused by the fence could have been greater in the bare pathways, thus confounding the influence of the pathway type with that of the experimental method. The extent and direction of bias associated with the potential fence effect are unknown, but are likely to have influenced immigration rates through affecting the probability of directional

Fig. 8. Hypothetical representation of the probability of immigration to a target patch as a function of distance from a source patch. Each line represents a different combination of survival costs and movement velocities. These relationships were generated under the simple dispersal model Pr(immigration) = $(1 - k_i)^{d/v_i}$, where k_i is the survival cost per unit time in the ith pathway, v_i is the movement rate of an individual in the ith pathway, and d is the distance from the source to the target patch. Parameter estimates were derived from the field experiments. The solid line represents the conditions we generally found in corridor pathways during trial B of expt. 2, when *Ensatina eschscholtzii* were exposed to drought conditions. The dotted line represents the parameter estimates from the non-corridor pathways. The corridor "effect" (the difference in immigration probabilities) can be seen to increase with distance. However, if movement velocity remains constant and animals move during conditions in which daily survival costs are higher than in "corridor" pathways but are still reasonably low (e.g., 0.05; broken line), then the corridor effect remains relatively small even with increasing distance. These later conditions were observed in trial A of expt. 2, during relatively high levels of precipitation. These hypothetical patterns that result from increasing distance illustrate the sensitivity of the results from experiments on a small spatial scale, such as ours involving *E. eschscholtzii*. The probability of remaining in the corridor during transit becomes an increasingly important parameter determining immigration rates via corridors as distance increases. We expect the effect to be negative, since the assumption in these simple models is that the probability of remaining in the pathway is 1.0. We did not include this parameter, as it was not estimated in our study, nor are we aware of its estimation in any other studies.



movement rather than through the mechanisms of selection, velocity, or survival rate.

The outcome of the experiment might have been different if the distance between source and target patches had been substantially increased. For example, given the data from trial B in expt. 2, the following parameter estimates were obtained: survival costs per day were 0.01 for corridor pathways and 0.2 for bare pathways, and average velocity was estimated at 10 and 30 m/day for corridor and bare pathways, respectively. Given these parameter estimates, and assuming that the corridor pathway is chosen, individuals dispersing from the source patch via a given pathway would be expected, under a simple dispersal model,

$$\mathrm{Pr(dispersal\ success)} = (1 - k_i)^{d/v_i}$$

where k_i is the survival cost in the ith pathway, d is the distance between source and target patches, and v_i is the average velocity in the ith pathway (Rosenberg et al. 1995), to have a probability of 0.96 of dispersing to a target patch (40 m from the source patch); dispersal to a target patch connected by the bare linear pathway would be expected to have a probability of 0.74. The difference between corridor and bare pathways in the probability of successful dispersal increases dramatically as the distance between source and target patches increases (Fig. 8). Note, however, that when survival costs are similar between pathway types, as demonstrated in trial A in expt. 2, the differences in successful immigration diminish (Fig. 8), and immigration rates can actually increase in non-corridor pathways relative to corridor pathways as the distance increases. As the distance increases, however, the likelihood of an animal remaining in the pathway and surviving becomes a critical parameter in determining the probability of successful immigration to a target patch.

Conclusions

Despite a large literature advocating the incorporation of corridors into conservation strategies, there is little evidence of their efficacy (Simberloff et al. 1992, Rosenberg et al. 1997). In extremely degraded landscapes, linear patches of habitat may function as corridors (e.g., Beier 1993, 1995) and may be a useful "band-aid" to apply to a damaged environment. However, in such cases it is not clear if corridors are effective in reducing local and regional extinction rates. Real landscapes that contain dispersal habitat (i.e., habitat of a quality high enough to allow movement but not necessarily reproduction) distributed throughout significant portions of the landscape matrix or arranged as "stepping stones" (Gilpin 1980) may serve the function of connectivity as well as or better than corridors (Rosenberg et al. 1997). Although corridors may at times increase movement between patches (e.g., Haas 1995; Andreassen et al. 1996; Coffman 1997; Haddad 1997), the increase in connectivity must be evaluated in terms of a reduction in the likelihood of extinction. To develop optimal conservation strategies in the context of area constraints, the trade-off between habitat intended to provide connectivity among populations and that intended to function as a reserve must be considered (Simberloff et al. 1992; Rosenberg et al. 1997); corridors may not mitigate additional habital loss.

Our inability to examine the movement behavior of animals on large spatial and temporal scales led to our exploration of a "model" experimental system (Wiens et al. 1993; Barrett et al. 1995). The generality of our findings is limited by our single-species approach and by the reduction in spatial and temporal scales normally perceived as important in the process of animal dispersal and conservation-reserve design. Although corridors as narrow as 4 m have been proposed (e.g., Saunders and De Rebeira 1991), usually widths in the order of hundreds of metres are considered (Hudson 1991). Further, habitat patches (i.e., source or target patches) managed in real landscapes usually range in size from hundreds to thousands of hectares. Despite these limitations, we believe that our findings offer a useful framework for landscape-scale tests of the efficacy of corridors, and provide alternative hypotheses concerning how animals move in fragmented and heterogeneous landscapes. Experimental model systems offer an opportunity to test mechanisms that may be responsible for ecological patterns at the landscape scale, patterns that would otherwise be extremely difficult to test. Comparisons among studies, using a variety of scales, approaches, and species, may facilitate generalizations concerning pattern and process that could be useful in guiding conservation strategies in specific cases.

The process of designing reserves for spatially structured animal populations requires that the conservation planner be able to discriminate suitable from unsuitable habitat and to differentiate habitat that facilitates dispersal from that which impedes it. Our study demonstrates that identifying candidate corridor habitats on reserve design maps may be difficult because animals may show compensatory behavioral responses to different landscape features. Justifying corridors as essential reserve-design elements will require that we know considerably more about how a given species behaves in and moves through heterogeneous landscapes.

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