DISPERSAL AND COLONIZATION THROUGH OPEN FIELDS BY A TERRESTRIAL, WOODLAND SALAMANDER

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Abstract. The ability of animal species to disperse through matrix habitats is likely to have important implications for species' responses to habitat fragmentation. Within fragmented forests, open fields are among the most common matrix habitats. However, few empirical studies have measured the effects of open habitats on dispersal success of forest-dwelling species. We used two experiments to determine the effects of open habitats and distance on dispersal and colonization by red-backed salamanders, *Plethodon cinereus.* In the first experiment, salamanders were displaced from habitat edges 25 m and 55 m into an open field and farther into the forest. Return rates from salamanders crossing the field vs. the forest were then used to determine the barrier effects of open habitats. Although return rate declined with distance, salamanders returned successfully through open habitat as often as they returned successfully through forest. In the second experiment, we constructed "islands" of forest-like habitat within an open field. As in the previous experiment, colonization declined with distance. However, salamanders did colonize most of these field plots within one year. Initial colonists tended to be in the size range of young adults, suggesting that there may be a distinct dispersal phase for terrestrial salamanders. Collectively, these results suggest that even relatively sedentary species may be able to move through matrix habitats that are otherwise little used. Given that red-backed salamanders appear to be relatively abundant in fragmented forests, we suggest that movement through open habitats could help to offset some of the negative effects of habitat fragmentation.

Key words: amphibians; barrier effect; colonization; dispersal; habitat fragmentation; matrix; movement; Plethodon cinereus; *salamander.*

INTRODUCTION

Negative relationships between habitat fragmentation and species richness have been documented for a number of taxa (e.g., Leach and Givnish 1996, Boulinier et al. 2001, Laurence et al. 2002). However, the mechanisms by which fragmentation affects populations are generally not well understood (Harrison and Bruna 1999). This lack of understanding comes in part from the difficulty of conducting experiments at a landscape scale. As a result, most of our insights about the mechanistic effects of habitat fragmentation have come from spatial models. Models for individual species suggest that decline or extinction in fragmented habitats can occur through a combination of environmental stochasticity and reduced colonization rates (Lande 1988, Hanski et al. 1995, Sjogren-Gulve and Ray 1996). Stochastic effects can become increasingly important as patch sizes decrease, increasing extinction rates and the need for recolonization or rescue effects. Within communities, extinction can occur when balances between competitive ability and dispersal ability, predator–prey dynamics, or mutualisms are disrupted (Kareiva 1987, Tilman et al. 1994, Lennartsson 2002). Although these scenarios differ in a number of details,

reduced dispersal among habitat fragments ultimately contributes to extinction in each case.

Unfortunately, few data are available on dispersal rates in fragmented habitats (Harrison and Bruna 1999). In particular, little is known about the extent to which matrix habitats reduce dispersal, even though this may be a critical parameter in determining a species' risk of extinction from fragmentation. Generalizing about the effects of matrix habitats on dispersal is difficult because human-altered habitats can elicit a wide range of potential responses. Some species appear to be averse to crossing roads (deMaynadier and Hunter 2000, Develey and Stouffer 2001), open habitats (Stratford and Stouffer 1999, Rothermel and Semlitsch 2002), or forests (Haddad 1999, Ricketts 2001), even if they might be physiologically capable of doing so. Other species may enter matrix habitats, but alter the speed or trajectory of their movements as they move through the matrix (Hokit et al. 1999, Goodwin and Fahrig 2002). Finally, species might enter matrix habitats, but suffer high mortality while dispersing through these areas (Miller et al. 1997, Hels and Buchwald 2001). This variety of potential responses emphasizes the need for further empirical studies of the effects of fragmentation on dispersal of animal species.

In fragmented forests of the Eastern United States and Canada, open habitats such as old fields, residential areas, and natural grasslands are among the most com-

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mon matrix habitats. Even in heavily forested areas, small clearcuts and residential areas may be common features in the landscape (Gustafson et al. 2001). Terrestrial salamanders are important components of Eastern forest ecosystems, having biomass that may exceed that of larger vertebrate taxa and a concomitant importance for energy and nutrient cycling (Burton and Likens 1975a, b). Terrestrial salamanders are well suited to forest fragmentation studies because they are usually restricted to woodlands (Petranka et al. 1994, Welsh and Droege 2001). Because they do not require aquatic habitats for breeding, terrestrial salamanders are relatively sedentary, with home ranges on the order of tens of square meters and limited dispersal ability (Kleeberger and Werner 1982, Ovaska 1988, Gergits and Jaeger 1990, Gibbs 1998a, Marvin 1998). Terrestrial salamanders are also highly vulnerable to desiccation (Spotila 1972), which could make non-forest habitats particularly difficult to traverse.

We used two experimental approaches to determine the effects of open habitats and distance on movement and colonization success of terrestrial red-backed salamanders, *Plethodon cinereus*. First, we experimentally displaced salamanders into an open habitat and compared rates of return of these salamanders to the rates of return of salamanders displaced equal distances into the forest. To study dispersal under more natural conditions, we also carried out a colonization experiment in which we constructed "islands" of forest-like habitat within an open field habitat. We then observed the extent to which islands at different distances were colonized over the course of one year. Finally, we used size data to ask whether colonizers of experimental plots were different from salamanders found in reference forest areas.

Methods

Study site and species

We conducted these experiments on Salt Pond Mountain in Giles County, Virginia, USA (see Plate 1). Elevation ranged across study sites from 1120 m to 1240 m. Forest areas consisted of mature mixed deciduous forest. Dominant trees at our study sites were white oak (*Quercus alba*), northern red oak (*Quercus rubra*), and red maple (*Acer rubrum*). Dominant understory plants were striped maple (*Acer pennsylvanicum*), New York fern (*Thelypteris noveboracensis*), and cinnamon fern (*Osmunda cinnamomea*).

The red-backed salamander is a terrestrial, woodland species that ranges from North Carolina north to central Quebec and west to Michigan (Petranka 1998). They are often abundant within this range, reaching average densities in excess of 2.0 individuals/m² near our study sites (Mathis 1991). They are most abundant in mature, deciduous forests, with relatively moist soil and large amounts of coarse woody debris (Grover 1998, Hyde and Simons 2001). Like other terrestrial salamanders,

PLATE 1. Study site for the colonization experiment. Photo credit: D. Marsh.

red-backed salamanders may disappear from clearcuts, or remain at very low densities where coarse woody debris or leaf litter is still found (Ash 1997, Knapp et al. 2003). Landscape-scale distribution patterns suggest that red-backed salamanders and other terrestrial salamanders may be relatively insensitive to landscape-scale habitat fragmentation (Gibbs 1998a). However, because of their preference for characteristics associated with mature forests, terrestrial salamanders have been suggested as good indicators of forest health (Welsh and Droege 2001).

Red-backed salamanders are most commonly found underneath rocks and logs, which they may defend against other salamanders (Mathis 1990). Seasonal activity of red-backed salamanders is quite variable. In Virginia, courtship and mating occurs primarily during the spring (March–May) and fall (October–November). Females store spermatophores and then nest in decaying logs and rock crevices in late summer (July–August). Females brood their young for several weeks, after which time hatchlings are commonly found on the forest floor (late August–October). Red-backed salamanders also spend a great deal of time underground (Test and Bingham 1948, Taub 1961). Most individuals are underground in the winter and during dry periods in the summer. However, even during periods of high activity, much of the population remains underground (Test and Bingham 1948).

Mark–recapture studies have found red-backed salamanders to have small home ranges on the order of 10–25 m² for juveniles and adults (Kleeberger and Werner 1982). These home ranges may persist from one year to the next (J. Gillette, *personal communication*), and most consider red-backed salamanders and related terrestrial species to be poor dispersers (Ovaska 1988, Gibbs 1998a, Marvin 1998). Although dispersal has never been assessed directly, red-backed salamanders are quite effective at homing to their territory after displacement to distances up to 90 m (Kleeberger and
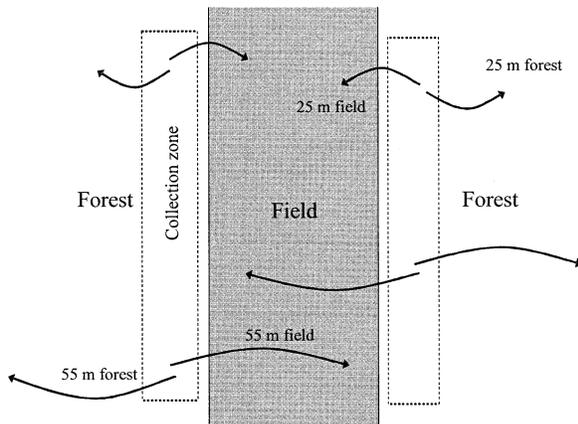
FIG. 1. Design for the homing experiment. Salamanders were caught in the collection zones and displaced either 25 m or 55 m into the field or farther into the forest. Arrows designate the displacement of salamanders from the collection zones for the four treatments. Replacement controls (not shown) were also used on both sides of the field.

Werner 1982). The mechanism involved in homing is unknown, though it may involve olfaction, as is common with other amphibians (Twitty 1966, Oldham 1967, Jaeger et al. 1993).

Homing experiment

We used the natural homing ability of red-backed salamanders to determine whether open habitats are barriers to red-backed salamander movement. We displaced salamanders into a field and compared return rates to those of salamanders displaced into the forest. For a field habitat, we used a 50 m wide powerline right-of-way. This right-of-way contained herbaceous vegetation dominated by invasive grasses and thistle (*Cirsium discolor*), most of which was 0.4–1.0 m high. It faced northwest, with a slope of ~30 degrees. There was no coarse woody debris and few rocks within the right-of-way, and no salamanders were ever detected there. The right-of-way was bordered by an abrupt forest edge, and red-backed salamanders were abundant in the forest within 5 m of the forest–field edge.

We established ''collection zones'' within the forest on both sides of the powerline right-of-way (Fig. 1). Collection zones were 20 m wide and went from 5 m inside the forest edge to 25 m inside the forest edge. Each collection zone was ~150 m long. In June 2002, we added 100 square, white oak cover boards (0.31 × 0.31 × 0.02 m) to each collection zone to facilitate the sampling of salamanders. From 27 July to 2 September 2002, and again from 28 June to 12 August 2003, red-backed salamanders were captured from underneath cover boards and rocks within the collection zones. We used numbered flags to label all cover objects where salamanders were initially captured.

Captured salamanders were individually marked ventrally with four fluorescent elastomer tags (Davis

and Ovaska 2001). Salamanders were then assigned to one of five treatments: 25-m displacement into the right-of-way, 55-m displacement into the right-of-way, 25-m displacement farther into the forest, 55-m displacement farther into the forest, and controls that were returned to the original site of capture (Fig. 1). To keep potential barrier effects of the field constant, we moved all salamanders in each field treatment the same distance into the right-of-way, regardless of where in the collection zone they were captured. Field salamanders displaced 25 m were always released in the field at a point 10 m from the forest edge and field salamanders displaced 55 m were always released at a point 40 m from the forest edge (Fig. 1). Thus, 25 m and 55 m represent the mean displacement distances for each treatment, while the actual distances varied by up to 10 m. Salamanders displaced into the forest were released at matched distances to ensure that there were no differences in mean distance traveled between the habitat treatments.

After marking salamanders, we released them underneath a moist cover board to reduce the stress of release. Displaced salamanders remained underneath these cover boards during the first day, but generally left during the first night after release. Displaced salamanders occasionally remained underneath these boards for two days, but almost all left by the second night.

We searched cover objects within the collection zone for recaptured salamanders periodically from July to October 2002 and from April to September 2003. We considered recaptured salamanders to have returned if they were found within 5 m of the site where they were originally captured. Almost all (91%) of these recaptured salamanders were found underneath the same cover object where they were first captured. On four occasions, salamanders were recaptured farther than 5 m from the original site. These salamanders were re-released and not included in the data set.

We used logistic regression to ask whether the probability of recapture depended on habitat of release (field vs. forest), release distance, or an interaction between the two. Models were fit by maximum likelihood and we used likelihood ratio tests based on Type III sums of squares to assess the significance of each parameter. We did not include terms for side of the right-of-way or year in the model because a preliminary analysis showed that neither of these variables approached significance ($P > 0.50$ in both cases). Additionally, we did not analyze dispersal rate because time to recapture was judged to be a poor correlate of the actual time for a salamander to return to its cover object of origin.

Colonization experiment

To study movement through open habitats under more natural conditions, we established 24 colonization plots in an abandoned golf course bordering forest habitat. The golf course had been abandoned in 1985, and
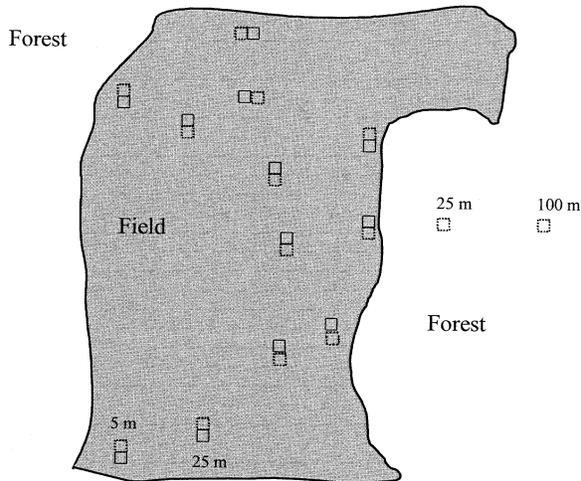
FIG. 2. Design for the colonization experiment. Paired plots were constructed in the field at 5 m and 25 m from the forest edge at six sites. Solid lines indicate fenced plots, and dashed lines represent unfenced plots. Forest plots were located 25 m and 100 m into the forest at all six sites but are only shown for one of the sites.

the topography was flat with vegetation consisting mostly of invasive grasses and with no coarse woody debris. The field did contain some rocks; these were all overturned and no salamanders were found beneath them. We established paired plots at two distances at each of six sites on the golf course (Fig. 2). Half of the plot pairs were 5 m from the forest edge, while the other half were at 25 m from the edge (Fig. 2). Each pair of plots consisted of one open plot and one plot that was fenced with aluminum flashing dug 0.3–0.6 m into the ground and rimmed with a 10 cm wide lip to prevent salamanders from entering or leaving. The fenced plots were designed as a control for any salamanders that might live underground and then come to the surface after establishment of the plots. Although there is little evidence to suggest that red-backed salamanders would live underground outside of forest habitat, we wanted to differentiate any such salamanders from salamanders that colonized the plots from the surrounding forest.

Each field plot was 3 × 3 m and contained sixteen 30 × 30 cm white oak cover boards. We added ~200 L of leaf litter to each plot. We collected leaf litter from a roadside area where we had never encountered red-backed salamanders. In addition, to be sure that no live red-backed salamanders were introduced to the plots, we froze leaf litter for a minimum of 24 h before placing it in the plots. We covered plots with a 70% shade cloth placed 1 m off the ground to simulate forest conditions. We also watered plots every three days with 300–400 L of water pumped from a truck-mounted water tank.

For comparative purposes, we also established two forest plots at each of the six sites where field plots

were located (Fig. 2). Forest plots were placed at 25 m from the forest edge and, when possible, at 100 m from the forest edge. At two of the sites, steep ledges prevented establishment of plots at exactly 100 m, so these sites were established at 55 m and 75 m. Forest plots, like the field plots, contained 16 wood cover boards. Unlike the field plots, forest plots were not fenced, watered, or covered with shade cloth.

We began censusing all plots on 2 July. We censused them every three days until 31 August, every seven days from 4 September through 30 October 2002 and from 18 April to 2 June 2003, and every three days from 5 June to 30 June 2003. Censuses consisted of turning over the cover boards, capturing all red-backed salamanders, and marking them with fluorescent elastomer tags. Salamanders were batch-marked so that previously captured animals could be recognized, but were not individually marked. We also measured the snout–vent length of all captured salamanders.

We analyzed the data separately for the summer/fall of 2002 and the spring of 2003 as these periods correspond with different components of red-backed salamanders' life histories (see *Methods: Study site and species*). For each period, we determined the total number of individual salamanders appearing on each plot. For the initial summer/fall period we also calculated the time to initial colonization of each plot. With the data from the field plots, we used generalized linear models to ask whether distance and the presence or absence of a fence affected the number of colonizing red-backed salamanders. Models were fit by maximum likelihood and we used likelihood ratio tests based on Type III sums of squares to test the significance of individual parameters. We modeled the number of salamanders in each plot as a Poisson-distributed variable, and frequency histograms were consistent with this assumption. We used a similar model to ask whether distance (25 m vs. 100 m) affected the number of salamanders captured within the forest plots. We analyzed time to colonization with a nonparametric log-rank test with time censored for plots where no salamanders colonized (Hosmer and Lemeshow 1999). We completed this analysis for the summer/fall data only since most plots had already been colonized by our spring 2003 surveys. For both time periods, we compared the size distributions of red-backed salamanders in the field to those in the forest to determine which individuals tended to be colonizers of new habitats. Size is thought to be closely related to age in most terrestrial salamanders (Hairston 1983). We divided salamanders into five size classes based on snout–vent length: 2.5–3.0 cm, 3.0–3.5 cm, 3.5–4.0 cm, 4.0–4.5 cm, and 4.5–5.0 cm. Salamanders 3.5 cm and larger were almost always reproductively mature as assessed by the presence of darkened testes or ova. Salamanders smaller than this size were mostly 1–2-year-old juveniles. We used a chi-square test to ask whether size distributions differed
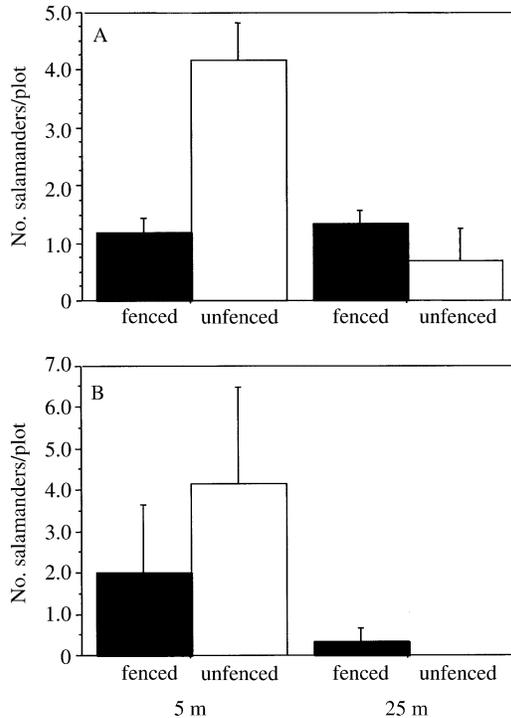
FIG. 3. Results from the colonization experiment for censuses of the total number of salamanders colonizing each plot in (A) summer/fall 2002 and (B) spring 2003. Error bars indicate one standard error.

among the two habitat types. A *G* test could not be used because several of the cells contained zeros.

Because red-backed salamanders prefer moist soils (Sugalski and Claussen 1997), we measured soil moisture in the field plots and the forest plots during mid-August 2002. We determined soil moisture by taking four 25–30 mL samples of soil from random sites on the surface of each plot. We weighed and dried these samples in a drying oven, and used the difference between wet mass and dry mass to determine the percent water by weight for each sample. We then used ANOVA and pre-specified contrasts to ask whether the mean soil moisture per plot differed between the 5-m plots and the 25-m plots and between field plots and forest plots. We used SAS 8.2 for all analyses (SAS Institute 2001).

RESULTS

Homing experiment

Three hundred sixty-four salamanders were marked and released and 54 of these (15%) were recaptured. Twelve of the 34 control salamanders were recaptured (35%), so we expected to see only this percentage of salamanders that returned to the original site of capture. Recapture rates for salamanders moving across the field were virtually identical to recapture rates for salamanders moving across the forest ($\chi^2 = 0.02$, $P = 0.89$). For the 25 m treatments, 17% of salamanders moving

through the field were recaptured, while 18% of salamanders moving through the forest were recaptured. For the 55 m treatments, 9% of salamanders moving through the field were recaptured, while 8% of salamanders moving through the forest were recaptured. Recapture rates for salamanders moving 25 m were significantly higher than return rates for salamanders moving 55 m ($\chi^2 = 6.56$, $P = 0.01$). There was no significant interaction between habitat (forest vs. field) and release distance on recapture rate ($\chi^2 = 0.11$, $P = 0.74$).

Colonization experiment

In the summer of 2002, no salamanders were found from the start of the census on 3 July until 11 September, when the first colonists were recorded. For the period from 11 September through 31 October, significantly more salamanders colonized the plots at 5 m from the forest edge than the plots at 25 m from the edge ($\chi^2 = 46.13$, $P < 0.001$; Fig. 3A). Although salamanders did colonize some of the fenced plots, the number of salamanders in fenced plots was significantly lower than the number in unfenced plots ($\chi^2 = 32.82$, $P < 0.001$; Fig. 3A). Results for time to first colonization were similar. Salamanders colonized the 5-m plots marginally more quickly than they colonized the 25-m plots ($\chi^2 = 3.57$, $P = 0.058$; Fig. 4). Furthermore, salamanders colonized the unfenced plots more quickly than they colonized the fenced plots ($\chi^2 = 4.25$, $P = 0.039$; Fig. 4), and salamanders did not appear in the fenced plots until almost three months after these plots were established. This suggests that the salamanders in the fenced plots were not originally underground in these areas, but were eventually able to breach the fences.

Within the forest, salamanders had colonized many of the plots by the 3 July census and were significantly more common at 100 m than at 25 m from the forest
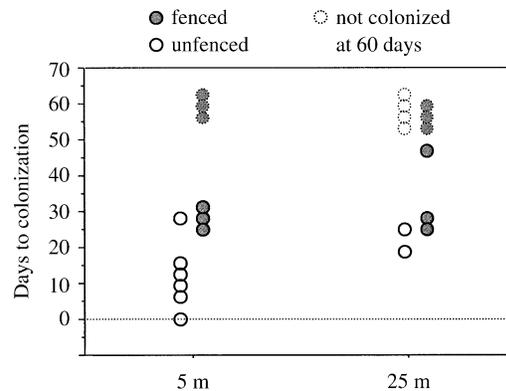

FIG. 4. Results of the colonization experiment for time from first census to first colonization during the summer/fall 2002 census period. Dashed circles at the top of the graph indicate both fenced and unfenced plots that were not colonized during this census period.
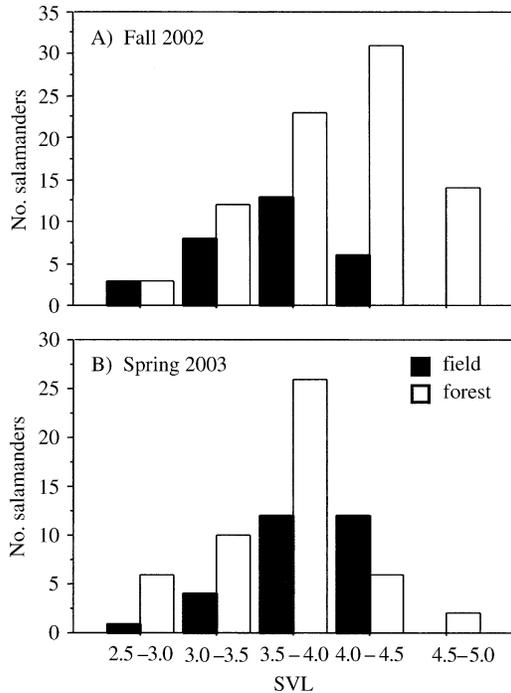
Fig. 5. Size distributions (snout–vent length, SVL) of salamanders caught in field and forest plots (A) during the summer/fall 2002 census period and (B) during the spring 2003 census period.

within the field did not differ significantly in soil moisture by volume ($F_{1,10} = 0.00$, $P = 0.98$).

Discussion

Open fields should be harsh matrix habitats for desiccation-prone, poorly dispersing, woodland species like red-backed salamanders. Nevertheless, we found that open habitats were not resistant to the dispersal of red-backed salamanders. In displacement experiments, return rates of salamanders moving through fields were virtually identical to return rates of salamanders moving through forest. In the colonization experiment, naturally dispersing salamanders were able to colonize newly created habitats that were isolated within an open field. Initial colonists of these new habitats were primarily young adults, rather than the older adults that were more common in the forest. In both of these experiments, distance reduced successful dispersal over scales of tens of meters, implying that dispersal ability may indeed be limited in red-backed salamanders, even if forest cover is not a factor.

The absence of barrier effects of open habitats on these terrestrial salamanders is somewhat surprising. Terrestrial salamander population densities track forest characteristics such as age, soil moisture, and the density of coarse woody debris (Grover 1998, Hyde and Simons 2001, Knapp et al. 2003). Much of the literature about habitat fragmentation has focused on the harshness of the matrix, and the interior-edge contrast as important determinants of edge effects and population persistence (e.g., Ricketts 2001, Collinge and Palmer 2002). Our study suggests that habitat-specific dispersal abilities may not always correspond to edge contrast and patterns of habitat use, and that even relatively sedentary species may be surprisingly good at moving though harsh habitats.

Our results can be compared with those of other studies that have addressed related questions. For example, Gibbs (1998b) found evidence that residential areas are readily entered by red-backed salamanders. Our study shows that red-backed salamanders not only enter open habitats, but can also disperse successfully through them, at least up to distances of 55 m. In contrast, other studies have demonstrated partial avoidance of open habitats by juveniles of some pond-breeding amphibian species (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002). These latter studies did not determine the ultimate success or failure of movements into open habitats. It would be useful to know if a tendency to enter open habitats generally corresponds with the ability to successfully disperse through these habitats. Alternatively, it is possible that open habitats cause high rates of mortality in species that lack adaptations to avoid them, as occurs with many species that attempt to cross roads (Forman and Alexander 1998). Which of these alternatives is the case likely has important consequences for dispersal

edge (mean $\pm$ 1 SE = 15.0 $\pm$ 6.63 for 100-m plots vs. 7.83 $\pm$ 2.60 for 25-m plots, $\chi^2 = 15.01$, $P = 0.001$). Salamanders colonizing the field plots had size distributions that differed from those of salamanders in the forest plots ($\chi^2 = 12.32$, df = 4, $P = 0.015$; Fig. 5A). Field plots contained high proportions of smaller adults and relatively low proportions of larger, older adults as compared to the forest plots. Most of the smaller adults were likely breeding for the first time.

From 16 April to 30 June 2003, smaller numbers of salamanders were encountered in field plots. There were again significantly more salamanders in the 5-m plots as compared to the 25-m plots ($\chi^2 = 38.29$, $P < 0.001$; Fig. 3B). There were no significant effects of fences during this period ($\chi^2 = 3.15$, $P = 0.076$; Fig. 3B). Within the forest, differences in captures between 25-m and 100-m plots were also less apparent in the spring of 2003 ($\chi^2 = 1.99$, $P = 0.16$). Size distributions of salamanders again differed between forest and field plots ($\chi^2 = 10.46$, df = 4, $P = 0.03$). These size differences were due largely to an absence of young juveniles from the field plots, not due to a paucity of older adults as in the previous fall (Fig. 5B).

On 7 August 2003, after approximately one month of watering, there were significant differences in soil moisture between field and forest plots ($F_{1,22} = 5.01$, $P = 0.041$) with forest plots having ~26% more water per unit volume. However, 5-m plots and 25-m plots

mortality and population persistence in fragmented landscapes (Fahrig 2002, Schlaepfer et al. 2002).

One issue with the results of the homing experiment is that homing after displacement is probably not a common scenario for red-backed salamanders in nature. It is possible that individuals that home are somehow "hard-wired" to return, and that natural dispersers might nevertheless avoid open habitats. There are two lines of evidence against this. First, analogous experiments using similar techniques with forest roads have shown that displacement across roads does reduce return rates of red-backed salamanders (D. M. Marsh, *unpublished data*). Thus, red-backed salamanders will not always home, and other types of matrix habitat may be less permeable to salamanders than open fields. Second, dispersal through open habitats was also seen in the colonization experiment, and this experiment involved only natural dispersers. The homing experiment therefore appears to produce results that are consistent with results from experiments with natural dispersers.

In the colonization experiment, red-backed salamanders colonized plots that were designed to mimic forest conditions, but that required crossing a field habitat. Even though numbers in this experiment were fairly low and salamanders did not colonize plots during the warm summer period, we feel any colonization is perhaps a surprise, given that dispersal to new habitats has not previously been documented as an important feature of terrestrial salamander life histories. The observation that early colonizers were largely composed of young, sexually mature salamanders (as opposed to older adults) is also interesting. It suggests that terrestrial salamanders may have life histories similar to those of some territorial forest birds, in which newly mature individuals often disperse to find a new breeding territory (e.g., Plissner and Gowaty 1996, Forsman et al. 2002, Pasinelli and Walters 2002). This kind of life history would make sense for red-backed salamanders, since individuals may be highly territorial and larger individuals generally have a territorial advantage (Mathis 1990). Additionally, high-density populations such as the one we studied may tend to be near carrying capacity (Jaeger 1980), putting a premium on new breeding territories.

Finding salamanders within the fenced plots to some extent complicates our interpretation of the results from the colonization experiment. Although we cannot rule out the possibility that some of these animals were underground before the plots were established, we believe that the majority of animals captured within fenced plots were in fact dispersers from forest habitats. This is supported by the three-month delay between establishment of the plots and the capture of the first salamanders. It is also supported by reduced salamander captures within the fenced plots during the first season and increased time to colonization for fenced plots as compared to the unfenced plots. Given that red-backed salamanders are skilled at burrowing underground (Taub 1961), we expect that some salamanders were likely able to burrow underneath the fences.

While open habitats did not appear to impede salamander dispersal, dispersal did decrease with distance in both experiments. In the colonization experiment, we recorded a mean of 2.67 salamanders in 5-m plots as compared to 1.1 salamanders in 25-m plots. Because soil moisture in the 25-m plots was similar to that of the 5-m plots, and because red-backed salamander abundance generally tracks soil moisture (Sugalski and Claussen 1997, Grover 1998), it is likely that these were truly effects of distance and not effects of other habitat gradients. It should also be noted that most colonizing salamanders likely came from beyond 5 and 25 m away. The forest edge along the abandoned golf course was not an abrupt edge. Within 20 m of the forest edge, the forest understory was composed largely of grasses, and there was little leaf litter or coarse woody debris (as there was at the site used in the homing experiment). At 25 m into the forest, salamander abundance was reduced as compared to 100 m, at least during the initial colonization period. Thus, the dispersal scale for salamanders in this experiment was likely in the tens of meters. These results are generally consistent with other suggestions that terrestrial salamanders are not good long-distance dispersers.

We believe that the results of the two experiments support the conclusion that red-backed salamander dispersal is limited primarily by distance, but not by the presence of forest cover. This suggests that small, intervening, open habitats such as powerline right-of-ways, mountaintop balds, and small residential areas will not contribute strongly to fragmentation effects for terrestrial salamanders. Small intervening fields may be quite common in many regions; Gustafson et al. (2001) found that mean distances of unfavorable habitat for red-backed salamanders under several forest management scenarios were on the order of tens of meters. Indeed, other work has found that terrestrial salamanders are relatively resistant to landscape-scale fragmentation effects (Gibbs 1998*a*). Gibbs (1998*a*) hypothesized that this may be due to the small home ranges and sedentary nature of these animals. Although we do find red-backed salamanders to be poor long-distance dispersers, we suggest that the ability of red-backed salamanders to move through open habitats may play a role in reducing the effects of forests fragmentation. This ability may also be associated with the unusually large range and microhabitat distribution of these animals in comparison to other terrestrial salamanders (Petranka 1998).

Our experiments were restricted to narrow bands of open habitat, and the fragmentation effects of larger areas of open habitat may well be more severe. Since dispersal is limited over scales of tens of meters and red-backed salamanders do not appear to live in open field habitats, salamanders may be unable to cross large clearings that would require long-distance movement.

In contrast, salamanders moving through forest areas would have years or even generations to cross into new habitats, and limited dispersal distances would be much less of a problem. This possibility is consistent with Gibbs (1998*c*) finding that genetic differentiation of red-backed salamanders was increased among forest patches without historical connections between them. It is also consistent with the observation of Kolozsvary and Swihart (1999) that small forest patches were occupied by red-backed salamanders only when these patches were close to a larger area of continuous forest. Finally, this suggestion is similar to Rosenberg et al.'s (1998) finding that *Ensatina eschscholtzi*, a related terrestrial salamander, moved successfully through bare-ground corridors by increasing their rate of movement relative to their movement rate through leaf litter. However, as the body condition of *Ensatina* in these bare habitats also declined, at some spatial scale *Ensatina* would presumably not be able to compensate for harsh habitats by dispersing more quickly. We suggest a similar scenario could occur with red-backed salamanders, although more data on the actual costs of dispersal through open and forest habitats of various sizes would be helpful in this regard.

In terms of our general understanding of species' responses to fragmentation, our results add some complexity to an ongoing debate about the relationship between dispersal ability and sensitivity to habitat fragmentation. Traditionally, species with greater dispersal ability have been thought to be more resistant to the effects of habitat fragmentation, since these species may be able to recolonize more isolated fragments even in heavily fragmented landscapes (Tilman et al. 1994, Kareiva and Wennergren 1995). However, species that are better dispersers may also be more dependent on successful dispersal for long-term population persistence. These species may also be more likely to attempt to disperse through harsh matrix habitats where mortality will be increased. Thus, it is possible that more sedentary species could actually be more resistant to the negative effects of habitat fragmentation (Gibbs 1998*a*, Thomas 2000). Our results show that species that are largely sedentary and that have fairly limited dispersal distances may nevertheless be relatively good at moving through harsh matrix habitats. Indeed, other studies suggest that the corollary may also be true; that is, some species that are excellent dispersers in continuous habitat may show substantially reduced dispersal in matrix habitats (Stratford and Stouffer 1999, Develey and Stouffer 2001). Thus, dispersal distances in continuous habitats and ability to disperse through matrix habitats may not always be closely related, and collapsing these into a single measure of dispersal ability may lead to misleading conclusions. As a result, more caution is needed when comparing the negative effects of habitat fragmentation across species that vary in a single measure of overall dispersal ability (e.g., Gibbs 1998*a*, Carr and Fahrig 2001, Davies et al. 2001).

Additionally, our results suggest that ecologists need to be careful in predicting dispersal behavior from data collected in landscapes that differ substantially in the degree of fragmentation (see also Diffendorfer et al. 1995). On the positive side, the realization that dispersal in fragmented habitats contains several distinct components should help focus future efforts to model the effects of habitat fragmentation and to study patterns of animal dispersal in fragmented habitats.

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