Forest Roads as Partial Barriers to Terrestrial Salamander Movement

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Abstract: *Roads can fragment animal populations by disrupting movement among formerly continuous habitats. Although models have demonstrated that disrupted movement can contribute to long-term extinction, there are few empirical data on the effects of roads on animal movement. We used displacement and homing experiments to determine whether forest roads are barriers to the movement of terrestrial salamanders. We displaced 1471 red-backed salamanders (*Plethodon cinereus*) across five forest roads and compared return rates to those of salamanders displaced equal distances toward the forest interior. Roads significantly reduced the return rate of salamanders, with a mean reduction of 51%. Steep roadside verges further reduced return rates, particularly for salamanders moving downhill across verges. The permeability of roads to salamander movement did not appear to be related to road surface type. Gravel roads had both the highest and lowest observed permeability with the two paved roads intermediate between these. We conclude that narrow forest roads are partial barriers to salamander movement and that steep roadside verges may exacerbate these effects.*

Key Words: amphibians, dispersal, habitat fragmentation, landscape resistance, *Plethodon cinereus*

Carreteras en Bosques como Barreras Parciales para el Movimiento de Salamandras Terrestres

Resumen: *Las carreteras pueden fragmentar a las poblaciones animales al interrumpir el movimiento entre hábitats anteriormente continuos. Aunque los modelos han demostrado que la interrupción de movimiento puede contribuir a la extinción en el largo plazo, existen pocos datos empíricos sobre los efectos de carreteras sobre el movimiento de animales. Utilizamos experimentos de desplazamiento y de orientación para determinar si las carreteras en bosques son barreras para el movimiento de salamandras terrestres. Desplazamos a 1471 individuos de* Plethodon cinereus *a través de cinco carreteras y comparamos sus tasas de retorno con las de salamandras que fueron desplazadas a distancias equivalentes hacia el interior del bosque. Las carreteras aparentemente redujeron la tasa de retorno de salamandras, con una reducción media de 51%. Los bordes de carretera empinados redujeron aun más las tasas de retorno, particularmente para salamandras atravesando bordes cuesta abajo. La permeabilidad de las carreteras al movimiento de salamandras no pareció estar relacionado con el tipo de superficie de la carretera. Las carreteras cubiertas con grava tuvieron tanto la permeabilidad más alta como la más baja y las dos carreteras pavimentadas fueron intermedias entre las cubiertas con grava. Concluimos que las carreteras angostas son barreras parciales para el movimiento de salamandras y los bordes de carretera empinados pueden exacerbar estos efectos.*

Palabras Clave: anfibios, dispersión, fragmentación de hábitat, *Plethodon cinereus*, resistencia al paisaje

Introduction

Roads can have numerous detrimental effects on animal populations. First, collisions with vehicles (i.e., roadkill) can result in high mortality rates (Hels & Buchwald 2001; Erritzoe et al. 2003). Second, roads can reduce the quality of adjacent habitats by increasing light and wind penetration, exposure to pollutants, and the spread of invasive

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species. These edge effects have been noted for taxa as diverse as arthropods (Haskell 2000), birds (Reijnen et al. 1996), and salamanders (Marsh & Beckman 2004). Third, roads can fragment habitats by lowering rates of animal movement. Roads appear to be barriers to movement for some birds and mammals (Merriam et al. 1989; Develey & Stouffer 2001; Goosem 2001) but not for others (Goosem 2001; McDonald & St. Clair 2004). Taxa such as amphibians—with less dispersal capability and greater sensitivity to habitat alteration than birds and mammals—may be more sensitive to the barrier effects of roads (deMaynadier & Hunter 2000). This difference in sensitivity could be important because models of species in fragmented habitats suggest that reduced movement among fragments is a critical parameter in determining long-term persistence (With & Crist 1995). Reduced movement can also contribute to reduced gene flow, which may lead to inbreeding depression and local extinction (Saccheri et al. 1998). Terrestrial salamanders (Plethdontidae) are an important taxon for investigating the barrier effects of roads. Terrestrial salamanders are important components of forest ecosystems in eastern North America and have been proposed as indicators of forest health (Welsh & Droege 2001). We used displacement and homing experiments with marked red-backed salamanders (*Plethodon cinereus*) to investigate whether forest roads are barriers to salamander movement. We also examined the possible effects of road-surface type and the presence of steep roadside verges on salamander movement. Finally, we examined whether the potential barrier effects of roads differed among salamander size classes.

Methods

Study Site and Species

We established study sites along five roads in Giles County, Virginia (U.S.A.), where roads passed through mature, deciduous forest. Two of the study roads were paved roads and three others were surfaced with gravel. The roads had widths of 5–8 m, with 3–5 m verges between roads and forest edges. Elevations at study sites were between 820 and 1240 m.

Red-backed salamanders were the most common terrestrial salamanders at our study sites. Red-backed salamanders inhabit moist, deciduous forest and reach high densities in mature forests of eastern North America. They are commonly found under rocks and logs on the forest floor, although the majority of the population is usually underground (Test & Bingham 1948). Adults have home ranges of 10–25 m^2 (Kleeberger & Werner 1982) and are thought to be poor dispersers (Mathis 1991; but see Marsh et al. 2004). Displaced animals, however, may return to their territory (i.e., "home") from up to 90 m (Kleeberger & Werner 1982).

Experimental Design

We took advantage of salamanders' homing ability to test whether roads are barriers to movement. We captured and marked salamanders from areas near forest-road edges and moved them across the road or an equivalent distance into the forest interior. We used the recapture rates of homing salamanders to measure the relative permeability of roads to movement.

At each study site we selected a 100-m section of road and placed a strip of one hundred 25×25 cm cover boards 15 m into the forest on each side of the road. The two strips of cover boards (hereafter collection zones) were approximately 44 m apart. We also established release zones 44 m farther into the forest from each of the collection zones.

We captured and marked salamanders from 10 May to 15 August 2003. During this period, cover boards were checked approximately once per week. Captured salamanders were randomly assigned to one of three treatments: moved across the road, moved farther into the forest, or released at the collection site. We took captured salamanders back to our laboratory, recorded their snout-vent length (SVL), and batch-marked them with elastomer tags (Davis & Ovaska 2001) to indicate original capture location and treatment assignment. Salamanders in the road treatment were released under a new board across the road 44 m from the original board of capture. Salamanders in the forest treatment were released under a new cover board 44 m farther into the forest. Control salamanders were released under their board of capture and were used to estimate the expected recapture rate of returning animals. We recaptured returning animals from 16 May to 30 October 2003. Salamanders were recorded as recaptures if they returned to any board within their original collection zone.

Statistical Analysis

We analyzed recapture rates as a randomized block design in which each road was considered a block. Within each block, treatment (road vs. forest) was crossed with slope (uphill vs. downhill). Thus we used each group of salamanders crossing a specific area in a specific direction as the experiment unit. We used general linear models (Neter et al. 1996) on arc-sine transformed recapture rates to determine the significance of the effects for treatment, slope, treatment − direction interaction, and the block for site. Type III sums of squares were used for each variable.

We calculated the permeability of each road to salamander movement by dividing the recapture rate of salamanders moving across roads by the recapture rate of salamanders moving through forest (following Gibbs 1998). We bootstrapped confidence intervals to determine whether overall permeability differed significantly from one and used post hoc analyses to evaluate whether variation in permeability might be due to road surface type or the presence of steep roadside verges.

We tested for differences in size distributions between released and recaptured samples by dividing salamanders into seven size classes: SVL < 2.5; 2.5–3.0; 3.0–3.5; 3.5–4.0; 4.0–4.5; 4.5–5.0; and > 5.0 cm. We then used chi-square tests to determine whether the size distribution of recaptured salamanders differed from that of released salamanders for each of the habitat treatments. We also compared the size distribution of recaptures in the forest treatment to captures in the road treatment to determine whether roads inhibit movement of some size classes more than others. We used SAS 8.12 (SAS Institute 2001) for all analyses with $\alpha = 0.05$.

Results

We captured, marked, and displaced 1471 salamanders, and we recaptured 340 salamanders. Recapture rates were 49% (141 of 287) for replacement controls, 22% (131 of 593) for salamanders returning through forest, and 12% (71 of 594) for salamanders crossing roads.

Roads significantly reduced return rate compared with continuous forest ($F_{1,12} = 14.39$, $p = 0.0026$). The permeability of roads compared with forest was 0.485 with 95% confidence intervals of 0.368 to 0.598. Slope (uphill vs. downhill) did not significantly affect return rate, and there was no significant direction by habitat-treatment interaction (Table 1). The slope of sites, however, varied from 9 to 15 degrees at the two flattest sites to 35 to 50 degrees at the three sites with steep roadside verges. When we analyzed only the three sites with steep verges, both slope and the direction-by-treatment interaction were significant ($F_{1,6} = 21.56$, $p = 0.004$ and $F_{1,6} = 7.08$, $p = 0.038$, Fig. 1a). Surprisingly, return rates were lower when salamanders had to move downhill and were even lower when salamanders had to move downhill and across a road (Fig. 1a). At the two sites without steep verges, there was no significant effect of slope ($F_{1,3} = 0.96$, $p = 0.40$, Fig. 1b) and no direction-by-treatment interaction ($F_{1,3} = 0.41$, $p = 0.57$, Fig. 1b). There was no qualitative evidence that road surface affected return rate. Gravel roads had low (0.25), medium (0.49), and high permeabilities (0.76), with both paved roads intermediate in value (0.42 and 0.50).

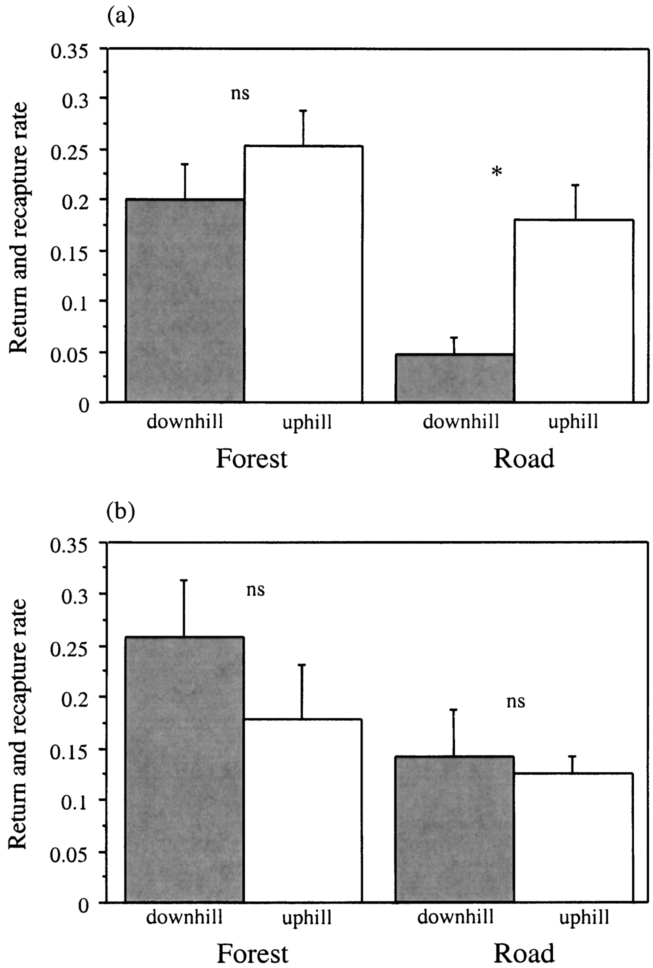

Figure 1. Salamander return rates relative to habitat treatment (forest vs. road) and movement direction (uphill vs. downhill): (a) three sites with steep roadside verges and (b) two sites without steep roadside verges (error bars, 1 SE; asterisk [*], significance at $\alpha = 0.05$; and ns, nonsignificant difference).

Returning salamanders were depauperate in smaller size classes compared with released salamanders for both habitat treatments (Table 2). When only recaptured salamanders were considered, size distributions between salamanders returning through forest and salamanders returning across roads did not differ ($\chi^2 = 2.94$, df = 4, $p = 0.57$). This suggests that roads reduced movement similarly across all salamander size classes.

Table 1. Effects of treatment (road vs. forest), slope (uphill vs. downhill), and site on return rate of displaced salamanders.

Variable	*df*	*SS**	*MS*	F	p
Site	4	0.123	0.031	4.08	0.026
Treatment	1	0.108	0.108	14.39	0.0026
Movement direction	1	0.017	0.017	2.19	0.164
Treatment * direction	1	0.019	0.019	2.57	0.135

**SS, sum of squares for each variable; MS, mean square (SS/df) for each variable.*

Discussion

Forest roads reduced red-backed salamander movement by approximately 51%, and steep roadside verges also

Table 2. Size classes of released and recaptured salamanders in the forest and the road treatments.

	Size class (cm)						
	<2.5	*2.5–3.0*	*3.0–3.5*	*3.5–4.0*	*4.0–4.5*	*4.5–5.0*	*>5.0*
Forest							
released	11	78	77	152	186	83	3
recaptured	0	0	5	24	63	35	1
Road							
released	13	70	93	158	183	70	7
recaptured	0	0	1	16	30	24	0

appeared to reduce movement. This latter effect resulted from reduced movement downhill across roadside verges. Additionally, the effects of roads and roadside verges were generally similar across salamander size classes. Smaller salamanders were less likely to return home in all treatments, which may reflect a lack of territoriality in younger individuals (Jaeger et al. 1995).

Our results are consistent with previous work showing that terrestrial salamanders less commonly enter roadside habitats compared with forest habitats (Gibbs 1998). Our results also suggest that the barrier effects previously inferred from capture data at a major (12 m wide) logging road (deMaynadier & Hunter 2000) hold for gravel recreation roads and small, paved roads (5–8 m wide). Thus we believe there is now substantial evidence that most forest roads are partial barriers to terrestrial salamander movement. In contrast, narrow bands of open field habitat do not appear to impede movement of terrestrial salamanders (Marsh et al. 2004). Although we cannot be certain how much roadkill may have contributed to our results, we believe the observed barrier effects mainly reflect behavioral avoidance of roads by salamanders. Salamanders experimentally moved across roads were often seen there months after release, whereas salamanders moved into the forest were almost never found at the release site.

Road surface type did not appear to have substantial effects on permeability to salamander movement. The two paved roads had permeabilities intermediate between the lowest and highest permeabilities of the three gravel roads. Given the small number of roads ($n = 5$), however, these results should be interpreted with caution. The presence of steep verges appeared to affect permeability. In particular, return rates across roads were reduced when salamanders also had to cross steep downhill verges. This unexpected result underscores the need for empirical studies of landscape barriers in place of general assumptions about resistance. From an applied perspective, the barrier effect of steep verges suggests that roads built through flat areas may be less detrimental to amphibians than roads built on steeper hillsides. This is also consistent with recommendations for stream-dwelling species because roads built on steep hillsides lead to increased stream sedimentation (Gucinski et al. 2001).

What are the conservation implications of reduced movements across roads for terrestrial salamander populations? For red-backed salamanders the consequences may be minor given their wide distribution and high abundance. Many other terrestrial salamanders, however, are similar in size and life history to red-backed salamanders but have extremely small geographic ranges. For example, both the Peaks of Otter salamander (*P. hubrictii*) and the federally endangered Shenandoah salamander (*P. shenandoah*) have extremely small ranges within the southern Appalachian Mountains (Petranka 1998). Because these ranges are already fragmented by roads, logging, and competing species (Jaeger 1970; Kramer et al. 1993), additional fragmentation by roads could push these species closer to extinction. In terms of gene flow, a 50% reduction in dispersal from a single road is unlikely to substantially reduce genetic diversity. Multiple roads in the landscape, however, could have stronger effects. For example, based on our results, three roads would reduce movement by about 88% and five roads would reduce movement by 97%. Correlations between road density and genetic distance in other amphibians have been found (Reh & Seitz 1990; Hitchings & Beebee 1996). Additionally, larger roads are likely to be greater barriers to gene flow than the smaller roads we studied. A 12-m-wide road had an estimated permeability to salamander movement of 0.27 (deMaynadier and Hunter 2000), lower than any observed for the narrow roads in our study. Ongoing studies of genetic differentiation across highways will clarify the barrier effects of even larger roads.

Because of the many negative impacts of roads on species and ecosystems (Trombulak & Frissell 2000), protection of roadless areas has been proposed as a key element for conservation within the United States (Gucinski et al. 2001). Yet the costs and benefits of roadless areas, both economic and environmental, have inspired substantial political controversy. Although our results are relevant specifically to terrestrial salamanders, they provide added evidence that roads decrease connectivity for many species. In landscapes where fragmentation is a concern, our results support the potential utility of roadless areas for conservation.

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