Title

Do highways fragment small mammal populations?

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Abstract: Small mammal populations separated by highways may be partially or completely isolated from one another due to low dispersal capabilities, low probability of surviving highway crossing attempts, and/or avoidance of areas adjacent to highways. Threats to small mammals are problematic at the ecosystem level because of their importance as seed dispersers and their role as prey for predators, such as marten, wolverine, and raptors. Our objective is to determine how movement and gene flow are affected by two- and four-lane highways for small mammals in forested areas of western Montana. We trapped small mammals at five highways sites for two summers using a mark-recapture protocol. We gave each animal an individual mark so that we could follow their movements through time and collected either hair or a small tissue sample for genetic analyses. We are assessing potential fragmentation of small mammals populations by comparing movement rates and gene flow adjacent to the highway versus across the highway. Our preliminary results suggest that highways inhibit movement of small mammals. Movement was hindered more by four-lane than by two-lane highways. We observed stronger effects on red-backed voles and chipmunks, and weaker effects on deer mice. Deer mice were responsible for the vast majority of highway crossings, while only one vole and no chipmunks crossed four-lane highways. Through ongoing genetic and mark-recapture analyses, we hope to determine whether or not this poses a biologically significant problem for forest small mammals.

Introduction

The Problem: Fragmentation

Highways can negatively affect wildlife by forming barriers that lead to fragmentation of populations. Small mammal populations separated by highways may be partially or completely isolated from one another due to low dispersal capabilities, low probability of surviving highway crossing attempts, and/or avoidance of areas adjacent to highways. Fragmentation of small mammal populations could prevent individuals from reaching critical habitat and break up populations into smaller groups, with demographic and genetic consequences, possibly affecting fitness. Threats to small mammals are problematic at the ecosystem level because of their importance as seed dispersers and their role as prey for predators such as marten, wolverine, and raptors.

Several authors have documented that roads hinder small mammal movement. For example, Mader (1984) found that none of the 121 marked small rodent individuals in his study crossed a 6 m two-lane paved highway in Germany, although numerous movements occurred parallel to the highway, and several species could theoretically have crossed within a few seconds. Even very small roads can function as barriers to wildlife. On a narrow (3 m) dirt road that received only 10-20 vehicles/day, Swihart and Slade (1984) observed inhibition of movement across the road in prairie voles *(Microtus ochrogaster)* and cotton rats *(Sigmodon hispidus),* although movement rates were likely high enough in this case to maintain gene flow across the road. Oxley et al. (1974) trapped small mammals adjacent to roads ranging from gravel to four-lane divided highways. They found that only three percent of white-footed mice *(Peromyscus leucopus)* crossed roads, and only one of these crossed a road as large as a two-lane highway. Only three percent of eastern chipmunks *(Tamias striatus)* crossed, and these crossed only gravel, not paved, roads. Notably, these species are among the most mobile (in speed, not necessarily distance) small mammals. Oxley et al. (1974) concluded that the clearance distance between habitats on either side of the road was more important than traffic volume or any other factor. In the first study to investigate the genetic effects of roads, Gerlach and Musolf (2000) demonstrated genetic subdivision in bank voles *(Clethrionomys glareolus)* separated by a four-lane highway in Germany that had been present for 25 years (although their estimates of F_{ST} and R_{ST} were small, less than 0.05 in all cases). Wilkins and Schmidly (1980) reported that highway mortality for mammals was highest on a highway with intermediate traffic volume, lowest on a highway with low volume, and intermediate at high volume, presumably because mammals did not attempt to cross high volume highways as often as those with low or intermediate traffic volume. Several authors have suggested that divided highways with clearances of 90 m may be barriers as effective in hindering the dispersal of small forest mammals as bodies of water twice as wide (Werner 1956; Sheppe 1965).

Fragmentation means decreased movement between populations; migration, and dispersal are restricted. A decrease in gene flow could follow, leading to genetic differentiation among populations. If populations are small, heterozygosity and allelic diversity could be lost, which in turn could lead to inbreeding depression and even local extinction.

Movement (and connectivity) across highways is important for many reasons. First is the rescue effect, whereby empty areas of suitable habitat are recolonized. Second, animals must be able to move between different areas with distinct food resources and/or refugia. Third, at the community scale, small mammal movement is important because moving animals disperse seeds and spores. Finally, movement into a new area followed by reproduction results in gene flow and true connectivity.

Importance of Small Mammals

Small mammals are both interesting and tractable study organisms for investigating demographic and genetic effects of highways. Small mammals consume large amounts of seeds, fruits, insects, and fungal sporocarps and affect forest regeneration and seed dispersal. They are an important prey item for many predators. In addition, small mammals are relatively easy to capture and handle and live in fairly high densities, making them powerful model organisms for studying highway effects.

Small mammals are numerous in most areas, and consequently have large effects through consumption. Deer mice are the primary predator on seeds that reach the forest floor (Adams 1950; Schmidt and Shearer 1971), and chipmunks are also important predators on conifer seeds. Shrews and deer mice are important insect predators, and may control insect pest populations in some circumstances (Buckner 1958; Frank 1967). Platt and Blakley (1973) suggested that the masked shrew *(Sorex cinereus)* functioned as a keystone predator by suppressing populations of dominant insect competitors. Anderson and Folk (1993) showed that shrews and deer mice reduced survival in acorn weevils, an important forest pest.

Many plant species benefit from dispersal of their seeds by small mammals. Chipmunks cache seeds and forget the location of some caches, aiding in tree regeneration (Tevis 1953). Over 20 species of pines are dispersed by birds and rodents that improve germination by burying seeds (as opposed to wind dispersal, where seeds fall on the surface). They also carry seeds away from the parent tree, allowing colonization of new habitats (Vander Wall 1993).

Many higher plant species depend on a symbiotic relationship with mycorrhizal fungi to meet their nutritional requirements (Marks and Kozlowski 1973; Sanders et al. 1975). Most ectomycchorizal fungi produce fruiting bodies that develop underground, relying on mammals to dig up and eat the fruiting bodies, dispersing spores in their feces (Johnson 1996). The northern flying squirrel *(Glaucomys sabrinus)* and the southern red-backed vole *(Clethrionomys gapperi)* are important mycophagists (Maser et al. 1978; Ure and Maser 1982; Gunther et al. 1983; Maser et al. 1985; Hayes et al. 1986), while deer mice and chipmunks eat sporocarps opportunistically. However, they are more likely to deposit spore-containing feces in adjacent non-forested areas than are voles or flying squirrels (Maser et al. 1978; Li et al. 1986).

Many predators depend on a small mammal prey base for at least part of the year. For example, red-backed voles are the primary food source for American pine marten *(Martes americana)* (Weckwerth and Hawley 1962; Buskirk and Ruggiero 1994) and boreal owls *(Aegolius funereus)* (Hayward et al. 1993). Small mustelids such as least weasels *(Mustela rixosa)* also prey heavily on small mammals (Norrdahl and Korpimaki 1998).

Small mammal populations provide an ideal model system for studying the effects of highways on connectivity in wildlife. Due to relatively high densities and willingness to go into traps, small mammals can be captured in relatively high numbers, and handling is not difficult. Small mammals have short generation times, so they have the potential to show the signature of population subdivision long before it becomes detectable in longer-lived species. Using small mammals, we can measure and quantify fragmentation, whereas this would be fairly intractable for larger species.

Combining Demographic and Genetic Approaches

Although several studies have investigated abundance and movement of small mammals near roads (reviews by Andrews 1990; Bennett 1991; Spellerberg 1998; Trombulak and Frissell 2000), none has used a modeling framework to estimate both survival and movement, and only one has measured genetic effects of roads (Gerlach and Musolf 2000). My study does both, combining demographic and genetic approaches to gain insight into past and present movement and gene flow across highways. A demographic study may reveal how animals are moving in response to highways now, but movement rates alone cannot show how animals moved in the past, or whether individuals that cross highways are reproducing on the other side (providing genetic connectivity). In addition, there is the possibility of movement that is never detected. However, genetics alone would be an inadequate tool in this study because physical subdivision of a population occurs before any genetic subdivision becomes detectable. We maximized our chances of detecting fragmentation by highways by combining demographic and genetic approaches, ensuring two ways to judge whether or not highways cause a biologically significant problem for small mammal population connectivity.

Objectives

Our objective is to determine how movement and gene flow are affected by two- and four-lane highways for small mammals in forested areas of western Montana. We are using mark-recapture analyses to compare movement adjacent to highways to movement across highways, focusing especially on southern red-backed voles *(Clethrionomys gapperi)* and deer mice *(Peromyscus maniculatus).* Genetic techniques will provide further insight into current movement rates and gene flow (movement plus reproduction) for red-backed voles, deer mice, and vagrant shrews *(Sorex vagrans).* Our goal is to assess the barrier effect of highways of different widths on these species, so that these negative impacts can be identified and mitigated in the future.

We are testing the following hypotheses: 1) movement rates across highways are decreased relative to movement rates adjacent to highways; 2) fragmentation by highways has led populations to become genetically differentiated; 3) impacts on small mammals are greater for four-lane highways than for two-lane highways (due to road width and traffic volume); and 4) impacts of highways differ among small mammal species. Specifically, we predicted that red-backed voles would be more deterred by highways than deer mice, and that chipmunks would have an intermediate response. There is not enough information about the response of shrews to habitat edges to predict the direction of their response to highways.

Study Design

Study Area

We have established replicate trapping grids at three two-lane and two four-lane forested highway sites in western Montana. The vegetation at these sites is somewhat variable, but all sites are dominated by ponderosa pine and douglas-fir. We selected only undeveloped forested sites that were relatively flat and situated around a fairly straight stretch of road, avoiding steep, rocky terrain and curvy stretches of road that would have complicated the establishment of four square, equidistant trapping grids around the highway. The predominance of rivers, railroad tracks, and frontage roads near highways restricted the pool of sites, because they form potential barriers that would confound analyses of highway effects. The average annual daily traffic ranges from 1,300 to 2,400 cars/day for two-lane highways, and is about 7,000 cars/day on the four-lane interstate. There are no fences or concrete barriers at our sites. Small culverts exist at our four-lane sites, but they do not go all the way across the highway, instead connecting one side of the highway to the median.

Trapping Grid Design

At each site, there are four equidistant trapping grids (figure 1), two on one side of the highway and two on the other. This design allows for the comparison of movement rates adjacent to the highway versus across the highway. Each grid is square and contains seven traps by seven traps, for a total of 49 traps per grid and 196 traps per site. Traps are 15 m apart, and grids are 75 m apart. The distance of grids from the highway varies from site to site due to differences in highway width. We chose to maintain constant distance between grids, rather than constant distance from grids to the highway, so that we could remove distance as a nuisance variable that would have confounded the analysis of movement rates across two- and four-lane highways.

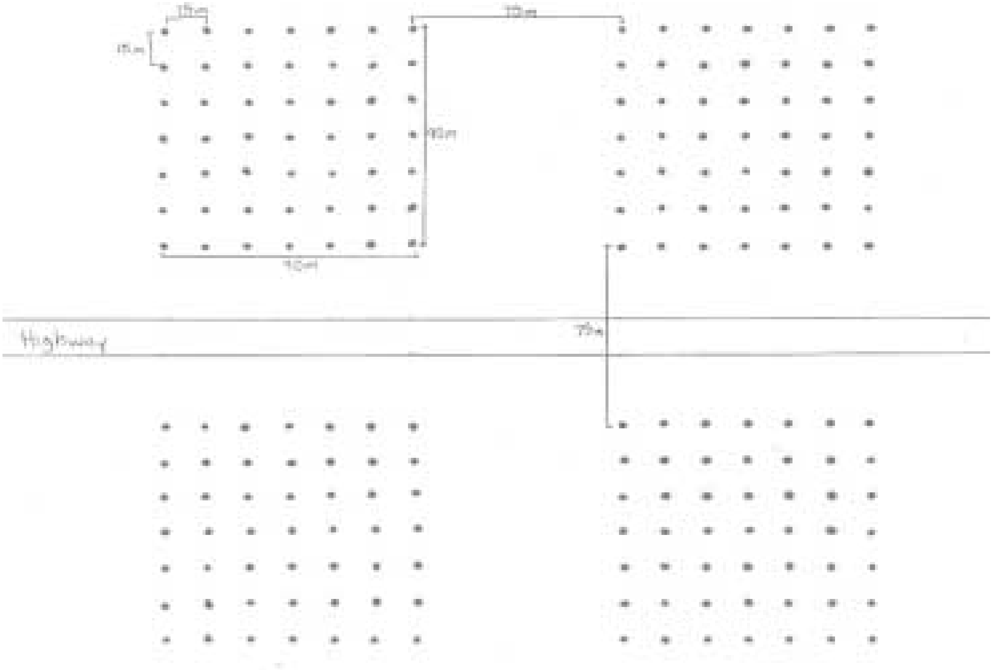

Fig. 1. Layout of trapping grids around the highway

At three sites in 2001, this grid setup was expanded from four highway trapping grids to six grids total. As a part of Jeremy Moran's undergraduate honors thesis, we added two new forest interior grids on one side of the highway only (due to logistical constraints). Each forest interior grid is the same size as the original grids, separated by 75 m from the original highway grids. Jeremy is comparing abundance (or relative abundance), survival, and species richness for small mammals captured near the highway versus the forest interior. If differences are found, we hope to determine whether these are due to differences in vegetation between edge and interior, or to a fence-effect caused by the highway acting as a barrier.

Trapping: Mark-Recapture

We used large baited Sherman traps to live-trap small mammals. Trapping sessions consisted of three consecutive nights of trapping. We trapped each site three times during summer 2000 and again in summer 2001. We gave each animal an individual mark and collected either hair or a small tissue sample for genetic analyses. Since each animal has a unique mark, we were able to follow their movements through time, trapping our sites at 25-day intervals.

Genetic Analysis

Genotyping Individuals

We are in the process of genotyping red-backed voles, deer mice, and vagrant shrews, with the goal of estimating gene flow across highways. In summary, the procedure is as follows: 1) extract DNA from tissue, 2) genotype all individuals at microsatellite loci, and 3) estimate movement (or gene flow) using several genetic measures. Microsatellites are highly variable non-coding regions of nuclear DNA (Ashley and Dow 1994; Bowcock et al. 1994; Jarne and Lagoda 1996). We are using microsatellites because their high mutation rates and high variation give relatively high power to detect genetic subdivision (low gene flow) between fragmented populations. Currently, we have five working loci for red-backed voles, ten for deer mice, and four for vagrant shrews. We hope to increase our number of vole loci to six or seven, but we will be unable to increase the number of shrew loci unless more primers are developed by other researchers in the next year, before this study is completed.

Measuring Gene Flow

Ideally, we would like to use three types of approaches to analyze gene flow across highways- F_{ST}-type measures, the assignment test, and parentage analysis- but we will use the assignment test only, if necessary, due to time constraints. Each of these approaches has advantages and disadvantages. F_{ST} is the proportion of total genetic variation due to divergence among subpopulations (trapping grids), which is inversely related to the number of migrants per generation between subpopulations (Wright 1969). F_{ST}-type measures have been used for many years to examine genetic divergence and gene flow, and the theory behind them is well-developed (see Mills and Allendorf 1996). However, F_{ST}-type measures cannot reveal current levels of gene flow, and they assume genetic equilibrium, an assumption that is probably often violated. In addition, F_{ST}-type measures assume that there are a large number of subpopulations, between which migration is equally likely to occur.

Unlike equilibrial measures, which estimate past gene flow, the assignment test and parentage analyses can provide insights into current gene flow. The assignment test assigns individuals to their populations of origin according to the likelihood of their genotypes occurring in each population (Waser and Strobeck 1998). Misassignments identify immigrants. The assignment test does not require genetic equilibrium, and it more accurately portrays current gene flow than do equilibrial measures like F_{ST}. However, this method has not yet been tested extensively, and it assumes that researchers are adequately sampling the whole metapopulation, so that the test can assign individuals to their populations of origin. In addition, assignment tests tend to fail when populations are not distinct, although power is improved by testing more individuals at more loci (Rannala and Mountain 1997). Parentage analysis is potentially a very strong method for inferring whether or not animals move between populations to breed (in our case, between grids around the highway), but a lot of data is required to decisively determine parentage. It is also possible that one or both parents may have moved off our grids.

Our gene flow analyses are incomplete at this point, as we are still in the process of genotyping individuals.

Demographic Analysis

Estimates

We are estimating survival and movement rates for red-backed voles and deer mice near highways in a mark-recapture framework, using multi-state models. Multi-state models (Hestbeck et al. 1991; Brownie et al. 1993) are open population models, meaning that births, deaths, immigration, and emigration that occurred during trapping are considered in the modeling process. Multi-state models use mark-recapture data to obtain maximum likelihood estimates of encounter probabilities, survival, and movement between states. In our case, the states are trapping grids, so we are estimating probabilities of moving across the highway versus adjacent to the highway. The most parsimonious model that fits the data, as determined by AIC (Akaike's Information Criterion: Akaike 1973), will include only variables (such as sex, year, and presence of the highway) that are necessary to explain variation in encounter probability, survival, and movement. In addition to capture survival and movement probabilities, we will estimate abundance or relative abundance, mainly for the purpose of comparing between highway and forest interior grids.

Counts

In addition to modeling, we can quantify potential fragmentation of small mammal populations by simply counting the number of movements adjacent to and across highways, as well as the number of individuals that moved. Examining the differences between species at two- and four-lane highways provides further insight. Although genetic and mark-recapture analyses are incomplete, we have analyzed these counts of animals moving around highways.

Preliminary Results

Over two summers we recorded 3,812 captures of 1,556 individuals of 15 different small mammal species (table 1). Deer mice were the species most often captured, followed by vagrant shrews, red-backed voles, and red-tailed chipmunks. For those individuals that were marked and released, we averaged 2.6 captures per individual, ranging from 1 to 15 captures. For red-backed voles, deer mice, and chipmunks, preliminary results indicate that more movement occurred between grids on the same side of the highway than between grids separated by the highway: 104 movements adjacent to the highway versus 35 movements across the highway. These 139 movements were completed by 85 individuals, 75 percent of which were male. Deer mice were responsible for the vast majority of highway crossings. Figure 1 shows that more individuals moved adjacent to the highway than moved across the highway: 67 versus 27.

Table 1
Number of individuals captured per species

Species	Individuals
Deer mice	501
Vagrant shrews	324
Southern red-backed voles	296
Red-tailed chipmunks	138
Yellow pine chipmunks	95
Masked shrews	64
Western jumping mice	44
Meadow voles	23
Shrews spp.	19
Chipmunks spp.	14
Bushy-tailed woodrats	13
Short-tailed weasels	8
Montane shrews	7
Northern flying squirrels	6
Pygmy shrews	2
Golden-mantled ground squirrels	1
Northern pocket gophers	1
Total Individuals	**1556**

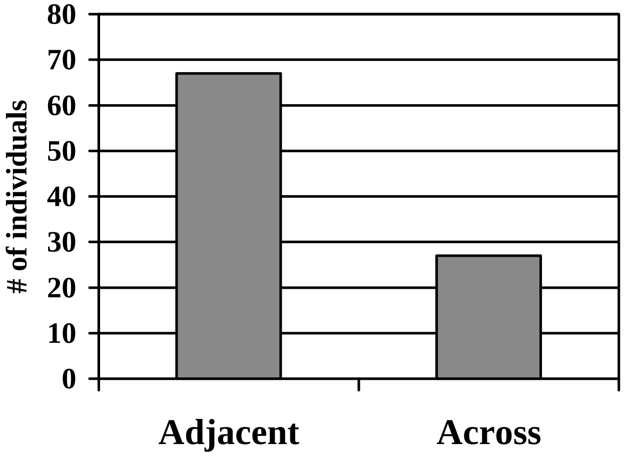

Fig. 2. Number of individuals that moved between highway trapping grids. More individuals moved adjacent to the highway than moved across it.

As expected, there were fewer crossings of four-lane highways than of two-lane highways (figure 2). We observed that one vole crossed a two-lane highway (he crossed twice), and that one crossed a four-lane highway (permanent dispersal). At four-lane highways, even the deer mice were hindered: 10 percent crossed two-lane highways, while only 3 percent crossed four-lane highways. Although 4 percent of chipmunks crossed two-lane highways, none crossed four-lane highways.

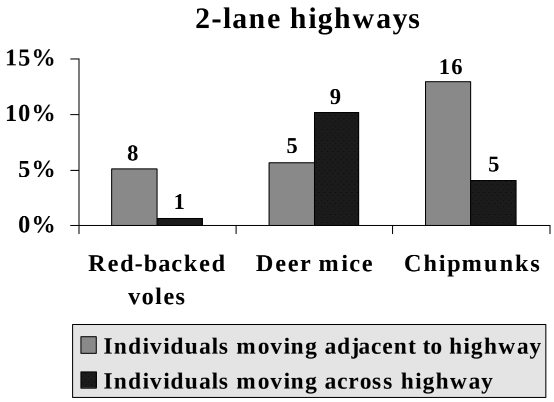

Fig. 2a. Percentage of individuals that moved between grids at two-lane highway sites. The numbers above the bars are the actual numbers of individuals that moved. For example, 5% of the voles at two-lane sites moved adjacent to the highway, 8 of 157 captured.

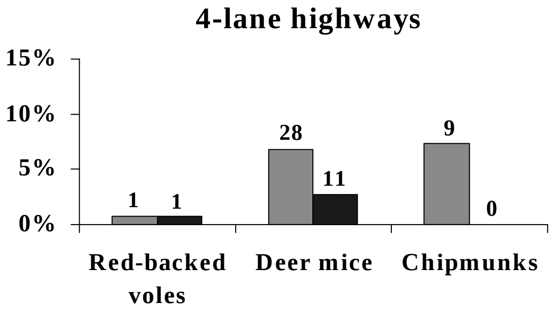

Fig. 2b. Percentage of individuals that moved between grids at four-lane highway sites. The numbers above the bars are the actual numbers of individuals that moved. For example, 7 percent of the deer mice at four-lane sites moved adjacent to the highway, 28 of 414 captured.

Different species responded differently to highways (figure 2). Deer mice crossed two- and four-lane highways more often than either of the other two species. Deer mice at two-lane highways were the exception to the rule, in that more crossed the highway than moved adjacent to it. We have not yet formed an explanation for this oddity in the data. It may in fact be due to sampling variance; the multi-state analysis will help us interpret this by providing estimates of sampling error. Chipmunks did quite a bit of moving adjacent to highways, and it seemed that some individuals had home ranges that included more than one grid. We are not sure why more chipmunks moved adjacent to two-lane highways than to four-lane highways. Vegetation analyses may reveal an explanation. Voles moved around less than either deer mice or chipmunks, except that one vole crossed a four-lane highway, while we never detected a chipmunk crossing a 4-lane highway. In addition to the species shown in figure 2, we detected two western jumping mouse crossings of a two-lane highway (only one jumping mouse was ever captured at a four-lane highway site), and one bushy-tailed woodrat crossing of a four-lane highway (only two woodrats were ever captured at a two-lane highway site).

Habitat preferences may explain these species differences. Red-backed voles prefer high-cover areas with abundant coarse woody debris. Chipmunks, too, are truly forest species, although they may inhabit more open forests than will voles. In contrast, deer mice are habitat generalists and will live in and move through more open areas.

Conclusions

Our preliminary results suggest that highways inhibit movement of small mammals. Movement is hindered more by four-lane than by two-lane highways. We observed stronger effects on red-backed voles and chipmunks, and weaker effects on deer mice. Our goal is to formally quantify these preliminary findings with mark-recapture and genetic measures.

Biographical Sketch: Reesa Yale is a graduate student in wildlife biology at the University of Montana. She is working with Dr. L. Scott Mills on the effects of highways on small mammal population connectivity. As an undergraduate in environmental biology at Dartmouth College, Reesa worked on ecological studies and conservation-related projects in New Hampshire, Massachusetts, Minnesota, Costa Rica, Jamaica, and Kenya. Before starting graduate school, Reesa worked for the Wildlife Conservation Society as a wild animal keeper at the Prospect Park Wildlife Center in Brooklyn, NY.

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