Effects of Road Fencing on Population Persistence

JOCHEN A. G. JAEGER* AND LENORE FAHRIG

Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada

Abstract: *Roads affect animal populations in three adverse ways. They act as barriers to movement, enhance mortality due to collisions with vehicles, and reduce the amount and quality of habitat. Putting fences along roads removes the problem of road mortality but increases the barrier effect. We studied this trade-off through a stochastic, spatially explicit, individual-based model of population dynamics. We investigated the conditions under which fences reduce the impact of roads on population persistence. Our results showed that a fence may or may not reduce the effect of the road on population persistence, depending on the degree of road avoidance by the animal and the probability that an animal that enters the road is killed by a vehicle. Our model predicted a lower value of traffic mortality below which a fence was always harmful and an upper value of traffic mortality above which a fence was always beneficial. Between these two values the suitability of fences depended on the degree of road avoidance. Fences were more likely to be beneficial the lower the degree of road avoidance and the higher the probability of an animal being killed on the road. We recommend the use of fences when traffic is so high that animals almost never succeed in their attempts to cross the road or the population of the species of concern is declining and high traffic mortality is known to contribute to the decline. We discourage the use of fences when population size is stable or increasing or if the animals need access to resources on both sides of the road, unless fences are used in combination with wildlife crossing structures. In many cases, the use of fences may be beneficial as an interim measure until more permanent measures are implemented.*

Key Words: barrier effect, connectivity, fences, fragmentation, population viability analysis, roads, road avoidance, spatially explicit population model (SEPM), traffic mortality

Efectos del Cercado de Caminos sobre la Persistencia de la Población

Resumen: *Los caminos afectan a poblaciones animales de tres maneras adversas. Actúan como barreras al movimiento, incrementan la mortalidad debido a colisiones con vehículos y reducen la cantidad y calidad de hábitat. La colocación de cercas a lo largo de caminos remueve el problema de mortalidad por tráfico pero incrementa el efecto de barrera. Estudiamos esta compensación por medio de un modelo de dinámica poblacional basado en individuos, espacialmente explícito y estocástico. Investigamos las condiciones bajo las que las cercas reducen el impacto de caminos sobre la persistencia de la población. Nuestros resultados mostraron que una cerca puede o no puede reducir el efecto del camino sobre la persistencia de la población, dependiendo del grado de evasión de caminos del animal y de la probabilidad de que un animal que entra al camino sea matado por un vehículo. Nuestro modelo predijo un menor valor de mortalidad por tráfico bajo el cual una cerca siempre fue perjudicial y un valor superior de mortalidad por tráfico encima del cual una cerca siempre fue benéfica. Entre estos dos valores, la utilidad de las cercas dependió del grado de evasión de caminos. Las cercas tuvieron mayor probabilidad de ser benéficas a menor nivel inferior de evasión de cercas y mayor probabilidad de morir atropellado. Recomendamos el uso de cercas cuando el tráfico es tan intenso que los animales casi nunca tienen éxito en sus intentos por atravesar el camino o la población de la especie en cuestión esta declinando y se sabe que la mortalidad por tráfico contribuye a esa declinación. No recomendamos el uso de cercas cuando el tamaño de la población es estable o esta incrementando o si los animales necesitan recursos a ambos lados del camino, a menos que las cercas sean utilizadas en combinación*

**Current address: ETH Zürich, Department of Environmental Sciences, Nature and Landscape Conservation, ETH Zentrum, HG F 27.6, CH-8092, Zürich, Switzerland, email jochen.jaeger@env.ethz.ch*

Paper submitted July 7, 2003; revised manuscript accepted March 25, 2004.

Conservation Biology, Pages 1651–1657
Volume 18, No. 6, December 2004

con estructuras para que atraviese vida silvestre. En muchos casos, el uso de cercas puede ser benéfico como una medida provisional mientras se instrumentan medidas más permanentes.

Palabras Clave: análisis de viabilidad poblacional, caminos, cercas, conectividad, efecto de barrera, evasión de caminos, fragmentación, modelo poblacional espacialmente explícito (MPEE), mortalidad por tráfico

Introduction

Wildlife biologists, nature conservationists, traffic planners, and landscape planners are increasingly concerned about the effects of roads on animal populations (e.g., Ellenberg et al. 1981; Andrews 1990; Underhill & Angold 2000; Forman et al. 2003). Roads enhance mortality due to collisions with vehicles, act as semipermeable barriers to movement, and reduce the amount and quality of habitat. For some species, large roads are absolute barriers to gene flow (e.g., Gerlach & Musolf 2000; Keller & Largiadèr 2003). Noss (1993) maintains that roads may be the single most destructive element in the process of habitat fragmentation and pose a major threat to many species.

Fences have been suggested as a mitigation measure to reduce traffic-caused mortality of wildlife (e.g., Falk et al. 1978; Clevenger et al. 2001). However, the use of fences is a subject of controversy in traffic-planning institutions and among nature conservationists because fences also represent a barrier to animal movement. Fences along roads may separate a population into smaller subpopulations, each of which will have a higher extinction risk. Recolonization of local extinctions will not be possible, ultimately leading to extinction of the whole population. In some situations, this effect of fences might be even more harmful than the mortality due to vehicle collisions when there is no fence. Carr et al. (2002) posed the question as to which of these two effects is more severe. Our objective was to answer the following question: under what conditions do fences along roads reduce or increase population persistence?

What determines whether fences will reduce or enhance population persistence? An obvious factor is the magnitude of traffic mortality. If there is no traffic mortality then a fence is useless and may be detrimental. Many studies have documented the absolute numbers of animals killed by vehicles (e.g., Stoner 1925; Knutson 1987; Trombulak & Frissell 2000), and several have estimated the proportion of animals killed in relation to overall mortality (otters [*Lutra lutra*], Hauer et al. 2002; European badgers [*Meles meles*], Clarke et al. 1998; hedgehogs [*Erinaceus europaeus*], Huijser & Bergers 2000; gray wolves [*Canis lupus*], Paquet et al. 1996; Callaghan 2002). Gibbs and Shriver (2002) showed that road mortality may contribute significantly to widespread population declines in turtles in the United States. Hebblewhite et al. (2003) conclude that the black bear population in Banff National Park (Canada) has been declining since 1994; 36% of all mortality was highway related. A second factor is the degree to which an animal that encounters a road does not attempt to cross it (e.g., Oxley 1974; Wilkins 1982; Mader 1984; Clarke et al. 1998). We call this "road avoidance" (Fig. 1). If the animals avoid the road entirely, then no fence is needed (Falk et al. 1978). We used a simulation model to identify the ranges of traffic mortality and road avoidance within which the effect of an unfenced road is more detrimental to population persistence than the effect of a fence.

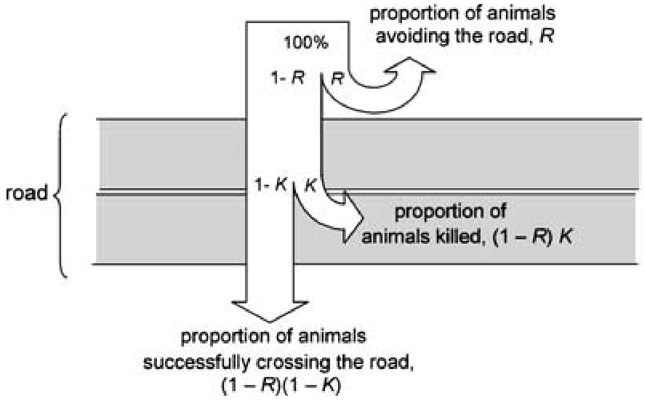

Figure 1. Illustration of road avoidance, R*, and the proportion of animals killed on the road,* K*. The two variables are specified independently of each other. Their ranges are from 0 to 1. Barrier strength,* B*, comprises both effects,* $B = 1 - (1 - R)(1 - K)$*.*

Methods

We used a stochastic, spatially explicit, individual-based model of population dynamics (Fahrig 1997), which we extended to include roads. The model included three subroutines—movement, reproduction, and mortality—applied in random order to each individual in each time step. Animals moved on a grid of habitat cells with a given probability: in a straight line to a distance between 0 and a maximum, and with an angle between 0 and 360°, chosen randomly. The number of offspring was selected from a Poisson distribution, and mortality was a simple probability. The model was density-independent, with the exception that there was a maximum number of individuals permitted per cell. When this maximum was

Table 1. Parameter values used in the simulation experiments of the effects of a road (fenced and unfenced) on population persistence.

Parameter	*Value*
Grid size	4 × 4 (16 cells)
Starting number of individuals	40
Time steps in simulation	500
Mean number of offspring	0.5/individual/time step (Poisson distribution)
Mortality probability in breeding habitat	0.34/individual/time step
Movement probability in breeding habitat	1.0/individual/time step
Maximum cell occupancy	5 individuals
Maximum movement distance	1 cell
Movement distance distribution	uniform
Movement direction distribution	uniform
Road avoidance, R	varied from 0.0 to 1.0 in steps of 0.1
Traffic mortality, K	varied from 0.0 to 1.0 in steps of 0.1

exceeded, the cell population size was reduced to the maximum by random killing of individuals. The model did not include environmental stochasticity or genetic effects.

We used two variables to describe road avoidance and traffic mortality: R for the degree of road avoidance—the probability of an animal avoiding the road when encountering it—and K for the probability of an animal being killed on the road, given that it attempted to cross (Fig. 1). Both variables ranged from 0 to 1. Barrier strength (i.e., the combination of these effects), B, also ranged from 0 to 1: $B = 1 - (1 - R)(1 - K)$. Putting up fences corresponded to 100% road avoidance ($R = 1$).

If, on encountering a road, an individual decided not to attempt to cross the road, it moved a second step away from the road for the remainder of its movement distance, with an angle corresponding to a reflection of its path at the road. Animals that encountered the edge of the grid were reflected back onto it.

The values of the other parameters used in the simulations are given in Table 1. The demographic parameters were chosen to represent a species with an extinction risk slightly higher than 0 when there was no road present because we were especially interested in the effects of roads on species that already have some risk of extinction (e.g., endangered species).

We varied both road avoidance, R, and traffic mortality, K, independently between 0 and 1 in steps of 0.1. We conducted 500 runs for each parameter combination, a total of 60,500 model simulation runs. For each model run, we recorded the number of individuals and the time to extinction. We calculated persistence probability as the proportion of the 500 populations that survived for 500 time steps.

To determine whether fences are preferable to no fences, we compared the persistence probability with fences to the persistence probability without fences and with the various levels of R and K. We also compared the average times to extinction for situations with and without fences for runs that did not persist for the 500 time steps.

Results

Effect of Traffic Mortality and Road Avoidance on Population Persistence

Extinctions and recolonizations of empty patches by individuals moving across the road did occur in the simulations (Fig. 2). Both traffic mortality and road avoidance had a strong effect on the probability of population persistence (Fig. 3). The situation $R = 0$ and $K = 0$ corresponds to a landscape with no road and led to the highest persistence probability. Traffic mortality alone had a much stronger effect on persistence probability than did road avoidance alone. For K between 0.1 and 0.7, there was an optimal level of road avoidance for population persistence. The higher the traffic mortality, the higher the predicted optimal level of road avoidance.

Average time to extinction (of the model runs in which the population went extinct within 500 time steps) was also strongly affected by traffic mortality and road avoidance (Fig. 4). Road mortality decreased persistence time, whereas road avoidance led to longer persistence times in most cases. A high level of road avoidance could compensate for high road mortality. This was true for extinction time only and not for persistence probability (Fig. 3).

Effect of Fences on Population Persistence

With fences (i.e., complete road avoidance, $R = 1$), persistence probability was independent of traffic mortality, K, because no animals went onto the road (Figs. 3 & 4). In our simulations, persistence probability for the situation with fences was 18.5% (Fig. 3). Therefore, adding a fence increased population persistence whenever the expected persistence level without a fence (for a given combination of R and K) was below 18.5%. The fence threshold line results from the intersection of the three-dimensional surface of persistence probability with the plane parallel to the diagram floor at persistence probability = 18.5%. This line determines the range of (R, K) values within which adding a fence would increase or decrease persistence (Fig. 5).

When road mortality (K) was higher than 0.8, adding a fence enhanced persistence probability for all values of R. If K was <0.2, adding a fence reduced population persistence for all values of R. If road mortality was between these values, the advisability of adding a fence depended on the level of road avoidance, R.

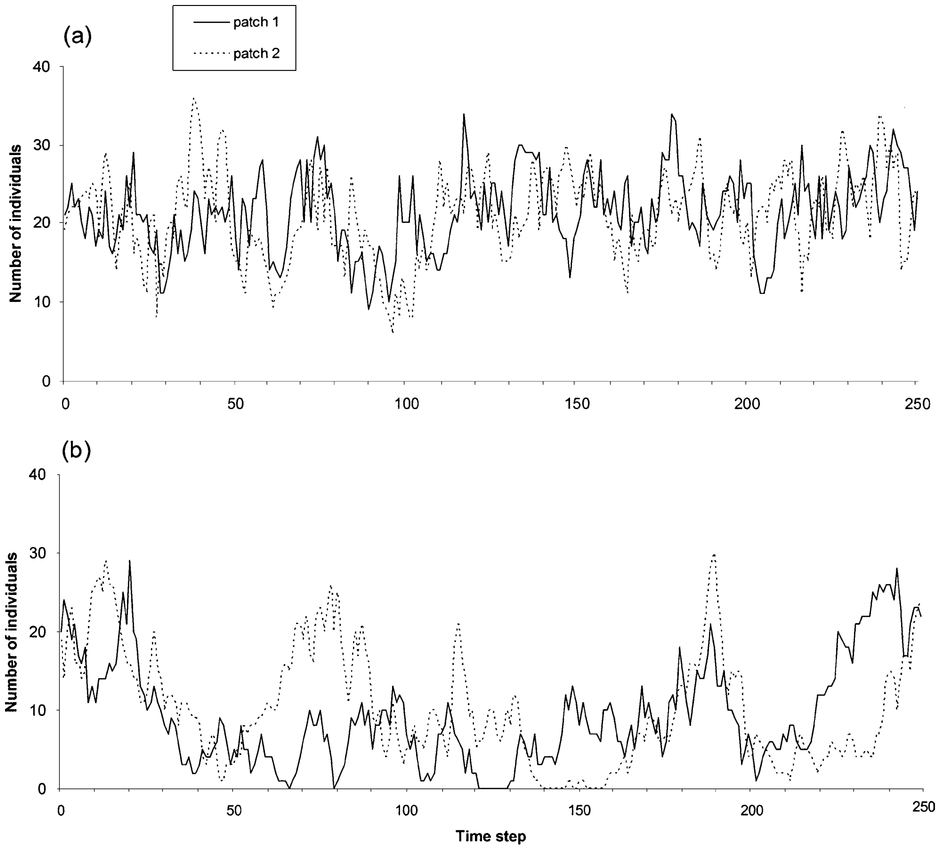

Figure 2. Examples of simulation runs (a) without a road and (b) with a road, where the degree of road avoidance (R) = *0.8 and there is no road mortality* (K = *0). In (b) there are three extinctions and recolonizations in each of the two patches. Only the first 250 of 500 time steps are shown.*

Discussion

Our objective was to characterize the combined levels of road avoidance and traffic mortality under which addition of fences along a road should increase persistence of animal populations. In our study, traffic mortality, K, was not the proportion of the population killed by traffic on the road. Rather, it was the proportion of those that attempted to cross the road that were killed (Fig. 1). Traffic mortality can be inferred from the number of animals killed within a certain time span by

$$K = \frac{D}{D + C},$$

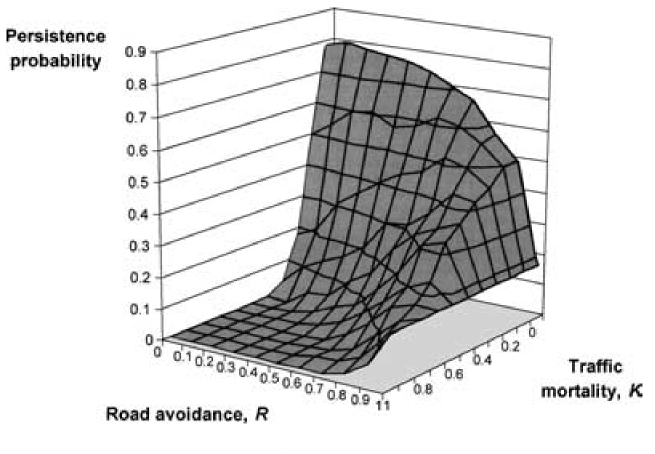

Figure 3. Probability of population persistence as a function of road avoidance, R, *and road mortality,* K, *based on 500 runs for each parameter combination. Parameter values are given in Table 1.*

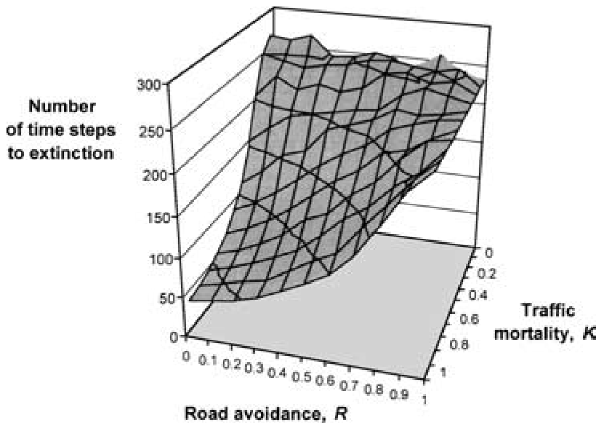

Figure 4. Average time to extinction as a function of road avoidance, R, *and traffic mortality,* K, *based on the subset of the simulation runs in which the population went extinct within 500 time steps. Parameter values are given in Table 1.*

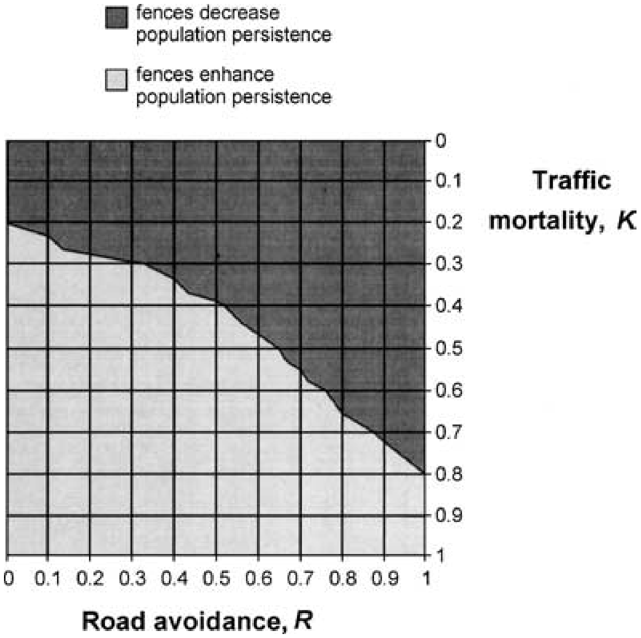

*Figure 5. Fence threshold line separating the ranges of (*R, K*) values within which fencing a road would increase or decrease population persistence.*

where D is the number of animals killed and C is the number of animals that successfully crossed the road. The latter would need to be obtained independently (e.g., from telemetry data).

Our results indicate that, in general, for high traffic mortality, fences enhanced population persistence probability. For low traffic mortality, fences reduced population persistence. Between these two extremes, whether or not fences were beneficial depended on the combined effect of traffic mortality and road avoidance on the number of animals killed on the road. As traffic mortality increased, the fence was more likely to be beneficial. If road avoidance increased, however, adding a fence could be more detrimental for reasons outlined in the Introduction.

In 93% of the runs with fences (i.e., $R = 1$), when the population persisted, at the end of the simulation the population was present on only one side of the road. This means that even when they are beneficial, fences should be used only as an interim measure to slow down population decline and prolong persistence time. This provides time for implementation of a more permanent solution. For example, road fencing combined with wildlife-crossing structures has decreased vehicle collisions with ungulates by at least 80% (Ward 1982; Lavsund & Sandegren 1991; Child 1998; Clevenger et al. 2001).

Our study is a first step toward identifying the situations in which road fencing should increase or decrease population persistence. Our results (Fig. 5) are qualitative, not quantitative. Many factors would likely shift the fence threshold line downward or upward by affecting the relative susceptibility of the population to additional mortality and population fragmentation. For example, if the animals need access to resources on both sides of the road (e.g., breeding habitat is on one side, whereas foraging habitat is on the other), crossing the road is mandatory for survival and a fence will never be beneficial, unless accompanied by wildlife crossing structures. In fact, our model predicts that fences combined with crossing structures will always result in a higher probability of population persistence. This situation corresponds to a road with $R < 1$ and $K = 0$. The threshold line for the suitability of these combined measures results from the intersection in Fig. 3 of the surface with the plane parallel to the diagram floor at $R < 1$ and $K = 0$. This threshold line is above the fence threshold line (Fig. 5).

The effects of other factors, such as movement range of the organism, density dependence in movement rate or population growth rate, possible density dependence in R or K, environmental stochasticity, and reduced gene flow (possibly leading to loss of genetic variability) are not as straightforward. Further research is necessary to evaluate the direction and magnitude of the effects of these factors on our predictions. At this point we can only offer some preliminary hypotheses. For example, when the movement range of the animal is small, we predict that fences will be less useful because individuals will encounter the road less often. Conversely, for animals with larger movement ranges, fencing is more likely to be beneficial. If movement distance is density dependent (lower movement distances at lower densities), fences should be less useful because animals are less likely to encounter the road (and be killed by traffic) when their populations are most vulnerable (i.e., when they are small). Similarly, if population growth is density-dependent, mortality at low population sizes is compensated for to some extent by higher growth rates, so fences are less likely to be beneficial. Conversely, when small populations suffer from Allee effects due to factors such as inbreeding, difficulty in finding mates, or unbalanced sex ratios (e.g., Lande 1988; Hanski 1999), road mortality has a larger effect on population persistence and fences may be more useful. This may be counteracted by the fact that fences also reduce population sizes by confining populations into smaller areas.

To date there is no evidence that either road mortality or road avoidance is density-dependent. If K is lower and/or R is higher at lower population densities, the usefulness of fences would be reduced because mortality on the roads would be reduced when the population is vulnerable (i.e., when it is small). In contrast, if K is higher or R is lower at lower population densities, fences may be more useful.

Finally, the effects of environmental stochasticity on the fence threshold line are not obvious. Metapopulation theory suggests that population fragmentation reduces the negative effects of environmental stochasticity. However, spatially correlated environmental stochasticity has also been predicted to lead to higher detrimental effects of fragmentation (e.g., Wissel & Stöcker 1991).

There are other considerations that complicate the real-world decision of whether or not to fence a road. For example, the value of K is likely to vary over the year and through the day because traffic volume and animal activity levels vary. The effect of traffic therefore needs to be summarized over time in order to compare it to the effect of a fence. The possible effects of fencing on nontarget species also need to be evaluated. It may also be possible to influence R and K and thus change the conclusion that fencing is a useful measure. For example, clearing roadside vegetation or adding reflectors or wildlife detection systems alters animal and driver behavior, which changes R and K. Finally, it is important to remember that traffic mortality and degree of road avoidance can be affected by the amount and speed of traffic (e.g., Allen & McCullough 1976; Bertwistle 1999; Hubbard et al. 2000; Seiler 2004). Reducing traffic amount and speed may obviate the need for fencing and crossing structures.

Based on our results, we suggest the following guidelines for the use of fences in the situation of single-species management. For an existing road, if it is known that the population size of the species of concern is decreasing and there is evidence that high traffic mortality plays an important role in the population decline, then fences should be a useful measure. Even if the population is not declining, if the animals sometimes try to cross the road but never or almost never succeed due to high traffic mortality, then fences should be beneficial. On the other hand, if population size is stable or increasing, adding fences could be harmful. For a road that has not been built but is in the planning stages, if the species of concern does not show any road- or traffic-avoidance behavior, mortality due to traffic collisions is expected to be high. In this case, fencing should be included in the road construction plan. The lower the degree of road avoidance and the higher the anticipated amount of traffic on the road, the more likely it will be that fences will be beneficial. When none of the above-mentioned information is available for the species of concern, fences should be used in combination with wildlife crossing structures (Groot Bruinderink & Hazebroek 1996). Testing the model with empirical data on road avoidance and crossing behavior is a next logical step in evaluating these predictions and in developing more practical models for use in planning highway mitigation measures.

Acknowledgments

We are grateful to J. C. Nicolaides for programming assistance. We thank J. Bowman for inspiring discussions; B. Gruber, K. Tluk von Toschanowitz, and members of the Landscape Ecology Laboratory at Carleton University, Ottawa, for stimulating discussions about road effects; and J. Bouchard, N. Charbonneau, V. Keller, E. Main, A. Righetti, and three anonymous reviewers for helpful comments on the manuscript. This work was supported through a postdoctoral scholarship from the German Academy of Natural Scientists Leopoldina to J.J. (grant BMBF-LPD 9901/8-27) and through a Natural Sciences and Engineering Research Council of Canada grant to L.F.

Literature Cited

Andrews, A. 1990. Fragmentation of habitat by roads and utility corridors: a review. Australian Zoologist **26:**130–142.

Allen, R. E., and D. R. McCullough. 1976. Deer-car accidents in southern Michigan. Journal of Wildlife Management **40:**317–325.

Bertwistle, J. 1999. The effects of reduced speed zones on reducing bighorn sheep and elk collisions with vehicles on the Yellowhead highway in Jasper National Park. Pages 89–97 in G. L. Evink, P. Garrett, and D. Zeigler, editors. Proceedings of the third international conference on wildlife ecology and transportation. FL-ER-73-99. Florida Department of Transportation, Tallahassee.

Callaghan, C. J. 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the Central Rocky Mountains, Canada. Ph.D. thesis. Department of Zoology, University of Guelph, Guelph, Ontario, Canada.

Carr, L. W., L. Fahrig, and S. E. Pope. 2002. Impacts of landscape transformation by roads. Pages 225–243 in K. J. Gutzwiller, editor. Applying landscape ecology in biological conservation. Springer Verlag, New York.

Child, K. N. 1998. Incidental mortality. Pages 275–301 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution, Washington, D.C.

Clarke, G. P., P. C. L. White, and S. Harris. 1998. Effects of roads on badger *Meles meles* populations in south-west England. Biological Conservation **86:**117–124.

Clevenger, A. P., B. Chruszcz, and K. E. Gunson. 2001. Highway mitigation fencing reduces wildlife-vehicle collisions. Wildlife Society Bulletin **29:**646–653.

Ellenberg, H., K. Müller, and T. Stottele. 1981. Straßen-Ökologie: Auswirkungen von Autobahnen und Straßen auf Ökosysteme deutscher Landschaften. Pages 19–122 in Ökologie und Straße. Broschürenreihe der Deutschen Straßenliga, Ausgabe 3, Bonn, Germany.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management **61:** 603–610.

Falk, N. W., H. B. Graves, and E. D. Bellis. 1978. Highway right-of-way fences as deer deterrents. Journal of Wildlife Management **42:**646–650.

Forman, R. T. T., et al. 2003. Road ecology: science and solutions. Island Press, Washington, D.C.

Gerlach, G., and K. Musolf. 2000. Fragmentation of landscape as a cause for genetic subdivision in bank voles. Conservation Biology **14:**1066–1074.

Gibbs, J. P., and W. G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology **16:**1647–1652.

Groot Bruinderink, G. W. T. A., and E. Hazebroek. 1996. Ungulate traffic collisions in Europe. Conservation Biology **10:**1059–1067.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, United Kingdom.

Hauer, S., H. Ansorge, and O. Zinke. 2002. Mortality patterns of otters (*Lutra lutra*) from eastern Germany. Journal of Zoology **256:**361–368.

Hebblewhite, M., M. Percy, and R. Serrouya. 2003. Black bear (*Ursus* *americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. Biological Conservation **112:**415–425.

Hubbard, M. W., B. J. Danielson, and R. A. Schmitz. 2000. Factors influencing the location of deer-vehicle accidents in Iowa. Journal of Wildlife Management **64:**707–712.

Huijser, M. P., and P. J. M. Bergers. 2000. The effect of roads and traffic on hedgehog (*Erinaceus europaeus*) populations. Biological Conservation **95:**111–116.

Keller, I., and C. R. Largiadèr. 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London Series B **270:**417–423.

Knutson, R. M. 1987. Flattened fauna. Ten Speed Press, Berkeley, California.

Lande, R. 1988. Genetics and demography in biological conservation. Science **241:**1455–1460.

Lavsund, S., and F. Sandegren. 1991. Moose-vehicle relations in Sweden: a review. Alces **27:**118–126.

Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation **29:**81–96.

Noss, R. F. 1993. Wildlife corridors. Pages 43–68 in D. S. Smith and P. C. Hellmund, editors. Ecology of greenways. University of Minnesota Press, Minneapolis.

Oxley, D. J., M. B. Fenton, and G. R. Carmody. 1974. The effects of roads on populations of small mammals. Journal of Applied Ecology **11:**51–59.

Paquet, P. C., J. Wierzchowski, and C. Callaghan. 1996. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in J. Green, C. Pacas, S. Bayley, and L. Cornwell, editors. Ecological outlooks project: a cumulative effects assessment and futures outlook of the Banff Bow Valley. Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, Ontario, Canada.

Seiler, A. 2004. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. Wildlife Biology **10:**11–23.

Stoner, D. 1925. The toll of the automobile. Science **61:**56–57.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14:**18–30.

Underhill, J. E., and P. G. Angold. 2000. Effects of roads on wildlife in an intensively modified landscape. Environmental Reviews **8:**21–39.

Ward, A. L. 1982. Mule deer behavior in relation to fencing and underpasses on Interstate 80 in Wyoming. Transportation Research Record **859:**8–13.

Wilkins, K. T. 1982. Highways as barriers to rodent dispersal. Southwestern Naturalist **37:**459–460.

Wissel, C., and S. Stöcker. 1991. Extinction of populations by random influences. Theoretical Population Biology **39:**315–328.