Does the Configuration of Road Networks Influence the Degree to Which Roads Affect Wildlife Populations?

Jochen A.G. Jaeger (Phone: +41-1-632-08-26, Email: jochen.jaeger@env.ethz.ch), Postdoctoral Fellow, Swiss Federal Institute of Technology ETH Zurich, Department of Environmental Sciences, Nature and Landscape Conservation, ETH Zentrum, HG F 27.6, CH-8092 Zurich, Switzerland, Fax: +41-1-632-13-80

Lenore Fahrig (Phone: 613-520-2600, ext. 3856), Professor of Biology, Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada, Fax: 613-520-3539

Klaus C. Ewald, Professor of Nature and Landscape Protection, Swiss Federal Institute of Technology ETH Zurich, Department of Environmental Sciences, Nature and Landscape Conservation, ETH Zentrum, HG F 21.3, CH-8092 Zurich, Switzerland

Abstract: Roads act as barriers to animal movement, thereby reducing the accessibility of resources on the other side of the road. Roads also increase wildlife mortality due to collisions with vehicles, and reduce the amount and quality of habitat. The purpose of this study was (1) to determine whether or not the configuration of road networks has an influence on the degree to which roads detrimentally affect wildlife populations and (2) to identify characteristics of road network configurations that make road networks less detrimental to the persistence of animal populations. To explore these questions, we used a spatially explicit individual-based stochastic-simulation model of population dynamics.

A measure assumed to reduce the effects of the road network is the bundling of roads and traffic in order to keep as large areas as possible free from disturbances due to traffic. However, the suitability of this measure may be questionable because a group of several roads bundled together, or an upgraded road with more traffic on it, creates a stronger overall barrier effect that may be more detrimental to population persistence than the even distribution of roads across the landscape. Our modelling results clearly supported the bundling concept. Population persistence was generally better (and never lower) when all traffic was put on one road than when it was distributed on several roads across the landscape. If traffic cannot be combined on one road, the model results suggested it is better to bundle the roads close together than to distribute them evenly across the landscape.

We also were interested in the question of whether the effect of a road network was determined by the number and size of the pieces ("patches") that it fragments a landscape into or by the total length of roads in the landscape. We expected that the effect of a road network would be the more detrimental the more patches it creates. The results were surprising: The expectation that fragmenting the landscape into more patches would be more harmful to population persistence (while total road length is kept constant) was contradicted by the model results in the case where the degree of road avoidance by the animals was low. This implies that for animals that do not very strongly avoid roads, it is more important to preserve core habitats at a sufficient distance from roads than to keep the number of patches low.

Our results are an important step towards a network theory for road ecology and towards the design of less-detrimental road networks. Empirical studies comparing landscapes with differing road network configurations should be conducted in the future to validate the predictions and to provide a basis for developing more practical models for use in planning and designing of highway networks.

Keywords: barrier effect, bundling of roads, core habitat, landscape connectivity, landscape fragmentation, population viability analysis (PVA), road avoidance, road configuration, roads, spatially explicit population model (SEPM), traffic mortality.

Introduction

Road construction is a major driving force of landscape change almost everywhere in the world today. However, the increase of landscape fragmentation due to transportation infrastructure has a number of undesirable effects on wildlife (Forman et al. 2003). Noss (1993) alleges that roads may be the single most destructive element in the process of habitat fragmentation and pose a major threat to many species. The ecological effects of roads have been considered the "sleeping giant of conservation ecology" (Forman and Alexander 1998). Therefore, there is growing concern about these effects among traffic planners, landscape planners, wildlife biologists, and others involved in the decision-making process about the construction of new roads (Jaeger 2001, 2002; Forman et al. 2003).

The two main ways roads detrimentally affect wildlife populations are by increasing mortality due to collisions with vehicles and by acting as barriers to animal movement, thus effectively fragmenting habitat. They also reduce the amount of habitat and the quality of habitats adjacent to the roads (figure 1). The same amount of traffic can be accommodated by different road networks. Therefore, we asked whether the configuration of the roads, while total length of the roads is held constant, is likely to affect the degree to which roads detrimentally affect animal populations. As the amount of habitat lost due to road construction is relatively small, we focussed on the effects of traffic mortality and habitat subdivision on population persistence.

The effects of roads are expected to depend on animal behavior at the roads. Many studies have documented absolute numbers of animals killed by vehicles (e.g., Stoner 1925, Knutson 1987, Trombulak and Frissell 2000) and several have estimated the proportion of animals killed in relation to overall mortality (otters *Lutra lutra*, Hauer et al. 2002; European badger *Meles meles*, Clarke et al. 1998; hedgehogs *Erinaceus europaeus*, Huijser and 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) concluded that the black bear population in Banff National Park (Canada) has been declining since 1994; 36 percent of all mortality was highway mortality. Van der Zee et al. (1992) demonstrated that the increasing number of roads was most closely related to the decline of the badger in the Netherlands.

The number of animals killed by traffic depends not only on how often animals encounter roads, but also on their behavior at the roads. How often roads are encountered depends on the configuration of the landscape and on the movement behavior of the species. We characterize the behavior of animals at roads by 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 behavior “road avoidance” (figure 2). If the animals avoid the road entirely, there is no traffic mortality, but the population is entirely separated 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 road avoidance may be even more harmful than the mortality due to vehicle collisions. Therefore, if the animals strongly avoid the roads, traffic mortality is expected to be low and the effect of habitat fragmentation is expected to be more important (Jaeger and Fahrig 2004a, Jaeger et al. 2005).

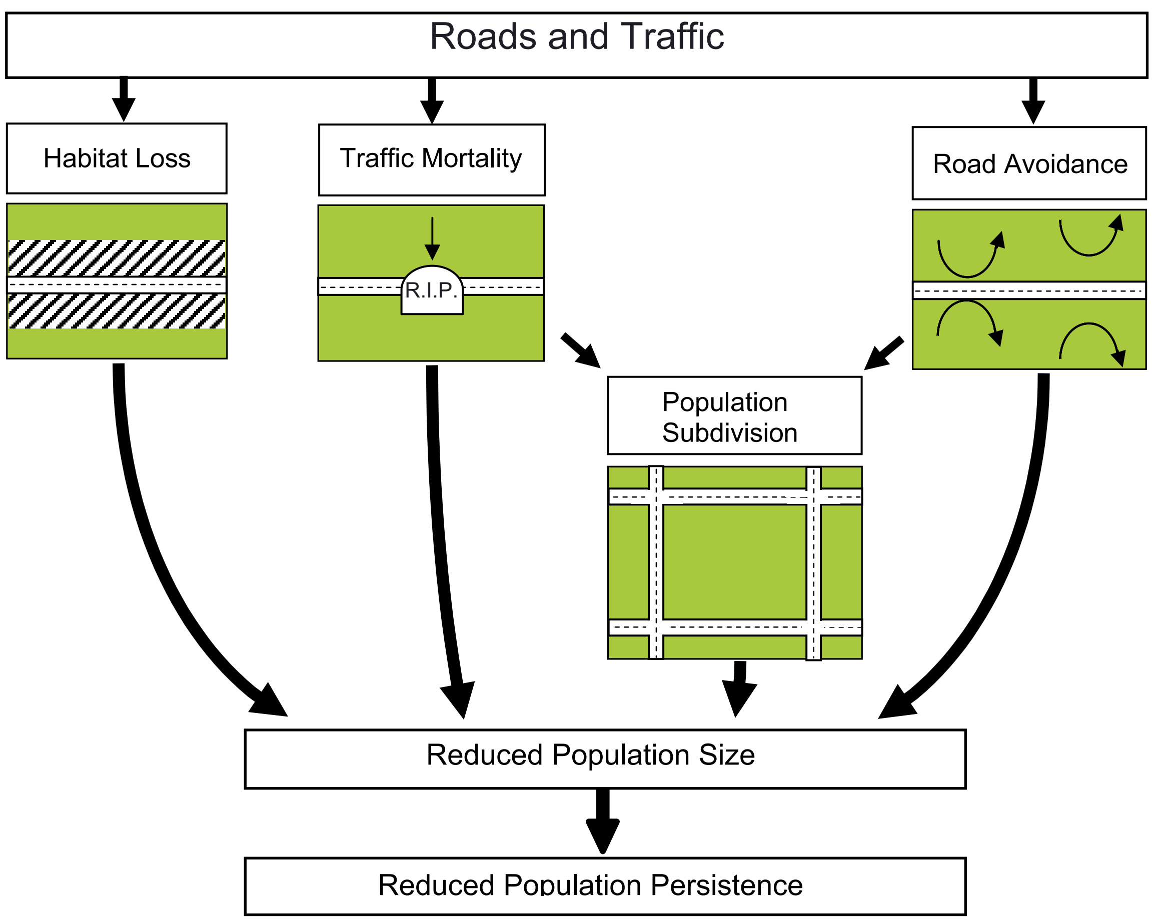

Figure 1. The four impacts of roads and traffic on the persistence of wildlife populations. Both traffic mortality and road avoidance contribute to population subdivision and isolation (modified after Jaeger et al. 2005).

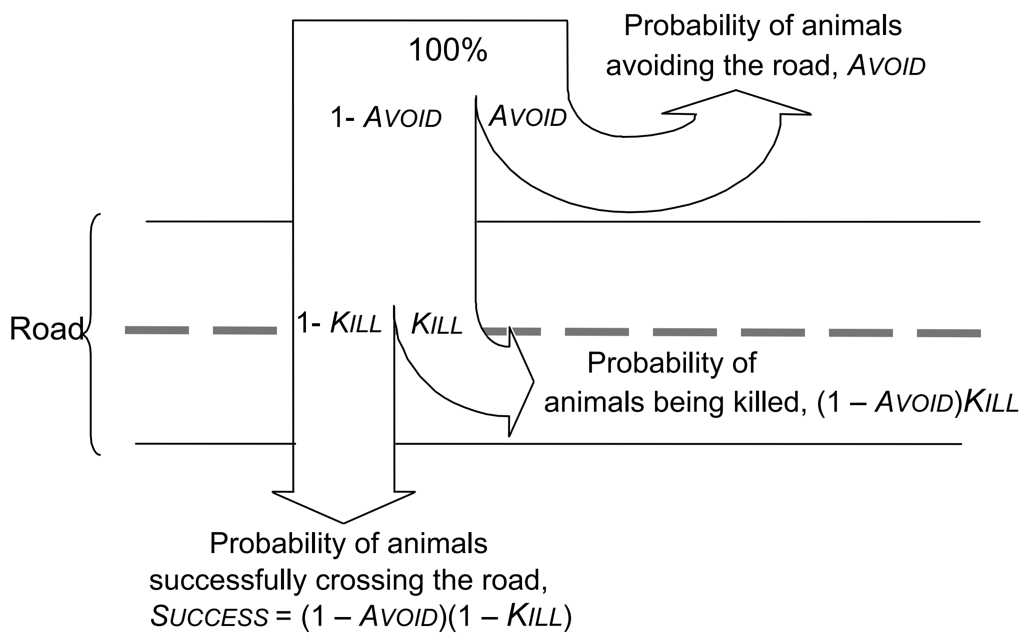

Figure 2. Illustration of road avoidance (*AVOID*) and the probability of animals killed on the road (*KILL*). The two variables are specified independently of each other; their ranges are from 0 to 1. Barrier strength, B, comprises both effects, B = 1 – *SUCCESS* = 1 – (1 – *AVOID*)(1 – *KILL*).

The purpose of this study was (1) to determine whether or not the configuration of road networks has an influence on the degree to which roads detrimentally affect wildlife populations and (2) to identify characteristics of road-network configurations that make road networks less detrimental to the persistence of animal populations. To investigate these questions, we used a spatially explicit individual-based simulation model of population dynamics.

One approach to reduce traffic impacts is to keep as large areas as possible free from disturbances due to traffic. The combination of traffic rather than spreading it out across the entire landscape can be done in two ways: (1) avoiding the construction of new roads by upgrading of existing roads (*"Ausbau vor Neubau"*) and (2) placing unavoidable new roads as close as possible to existing infrastructure, e.g., other roads, railways, canals (*"Verkehrsbündelung"*).

Accordingly, traffic planners and nature conservationists in Germany and Switzerland have proposed and used these two ideas as principles to guide road construction since the 1970s. However, the suitability of this approach may be questionable because a group of several roads bundled together or an upgraded road with more traffic on it creates a stronger overall barrier effect that may be even more harmful to population persistence than the even distribution of roads across the landscape. The effectiveness of the two principles for population persistence has never been tested and there is no direct empirical evidence so far that supports these principles or their criticism.

We also were interested in the question of whether the effect of a road network is determined rather by the number and size of the pieces ("patches") that it fragments a landscape into or by the total length of roads in the landscape. We expected that the effect of a road network generally is that the more patches it creates, the more detrimental the road network is (while total road length is kept constant).

We therefore compared two groups of networks: (1) roads that were evenly distributed across the landscape versus roads that were bundled together in one part of the landscape (close to each other or combining all traffic on one larger road) and (2) a parallel pattern of roads versus a gridded pattern (where the patches or "meshes" form a checkerboard). We recorded persistence probability, times to extinction, and critical road densities, i.e., the density of roads where the probability of population persistence is reduced to 0.5. We discuss our results in the context of road planning decisions and potential mitigation measures.

Methods

We used a stochastic, spatially explicit, individual-based model of population dynamics (Fahrig 1997), which we extended to include roads (Jaeger and Fahrig 2004a, 2004b). The model included three subroutines (for 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 360º, chosen randomly. The number of offspring was randomly selected from a Poisson distribution. 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 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: *AVOID* for the degree of road avoidance (i.e., the probability of an animal avoiding the road when encountering it) and *KILL* for the probability of an animal being killed on the road, given that it attempted to cross (figure 2). Both variables ranged from 0 to 1. Barrier strength (i.e., the combination of these effects), *BARRIER*, also ranged from 0 to 1: *BARRIER* = 1 – (1 – *AVOID*)(1 – *KILL*).

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 (figure 3). Animals that encountered the edge of the grid were reflected back onto it.

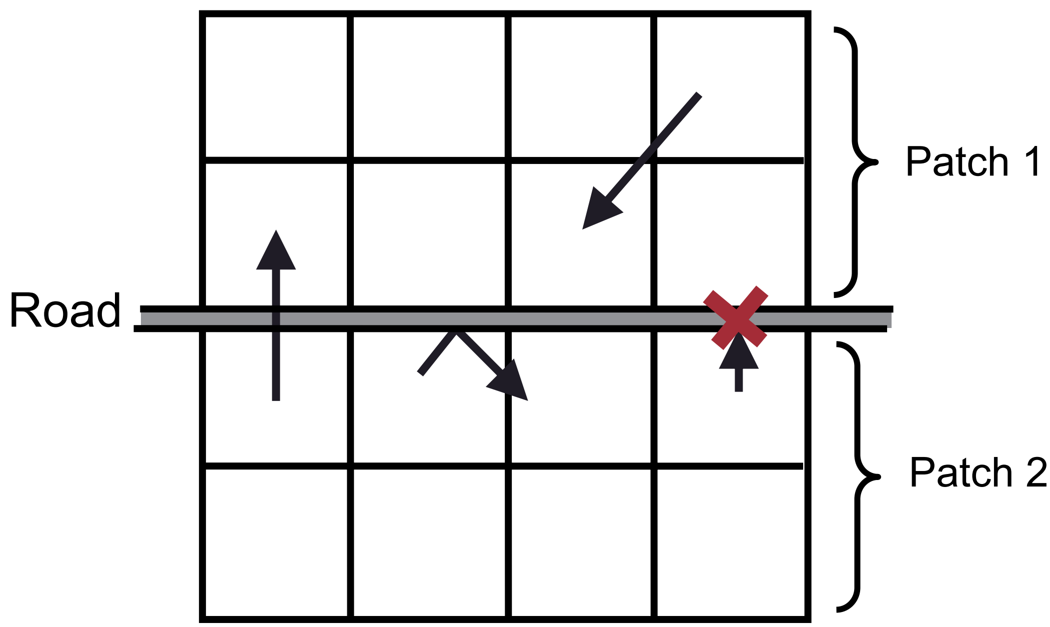

Figure 3. Illustration of the four types of movement of the individuals in the spatially explicit individual-based stochastic-simulation model (for a grid of 4 x 4 cells).

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 no extinction risk when there was only one road present regardless of the values of *AVOID* and *KILL*, because we were interested in the full range of road effects.

Table 1. Parameter values used in the simulation experiments.

Parameter	Values
Grid size	(1) 48 x 48 (2304 cells; figure 4) and (2) 24 x 24 (576 cells; figure 5)
Starting number of individuals	80
Time steps in simulation	1 000
Mean number of offspring	0.5/individual/time step (Poisson distribution)
Mortality probability	0.33/individual/timestep
Movement probability	1.0/individual/timestep
Maximum cell occupancy	2 individuals
Movement distance distribution	Exponential
Median movement distance	1.7 cells
Maximum movement distance (cut-off)	10 cells

Parameter	Values
Movement direction distribution	Uniform
Road avoidance, *R*	(1) Varied from 0.0 to 1.0 (in steps of 0.1). (2) Varied as a function of traffic volume.
Traffic mortality, *K*	(1) Varied from 0.0 to 1.0 (in steps of 0.1). (2) Varied as a function of traffic volume.
Number of roads	(1) Varied from 4 to 12 for two series of road configurations: (a) equidistant and parallel to each other versus (b) forming a rectangular grid (figure 4). (2) Varied from 1 to 2 in a bundled versus evenly distributed configuration (figure 5.)

We conducted 500 runs for each parameter combination. After each model run, we recorded the number of individuals remaining and the time to extinction if the population went extinct. We calculated persistence probability as the proportion of the 500 populations that survived for 1,000 time steps.

In the first set of simulations, we increased the number of roads and the number of patches using two different series of road patterns (figure 4). In the first series, all roads were equidistant and parallel to each other (patch number increased proportional to the number of roads); in the second, the roads formed a grid pattern and patch number increased as $n = (L/2 + 1)2$ where L is the number of roads. The roads were assumed to be between the cells of the grid and did not lead to habitat loss, i.e., all cells were habitat cells for all road patterns. We varied both road avoidance, *AVOID*, and traffic mortality, *KILL*, independently between 0 and 1. We recorded the probability of population persistence for these series. We then compared persistence probability of patterns with the same road length but different numbers of patches, and also of patterns with the same number of patches but different road length.

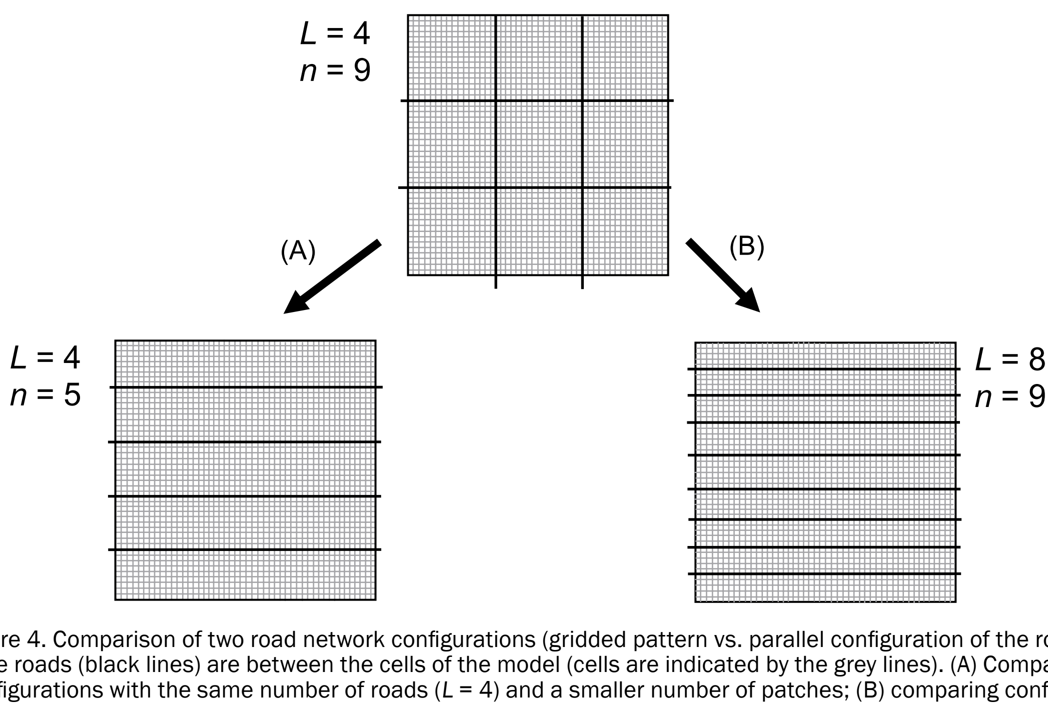

Figure 4. Comparison of two road network configurations (gridded pattern vs. parallel configuration of the roads). The roads (black lines) are between the cells of the model (cells are indicated by the grey lines). (A) Comparing configurations with the same number of roads (L = 4) and a smaller number of patches; (B) comparing configurations with the same number of patches (n = 9) and an increased number of roads.

In the second set of simulation runs, we used three different road configurations where total traffic volume was the same (figure 5): evenly distributed versus close together versus all traffic combined on one road. Consequently, the number and size of the habitat patches differed among the three configurations.

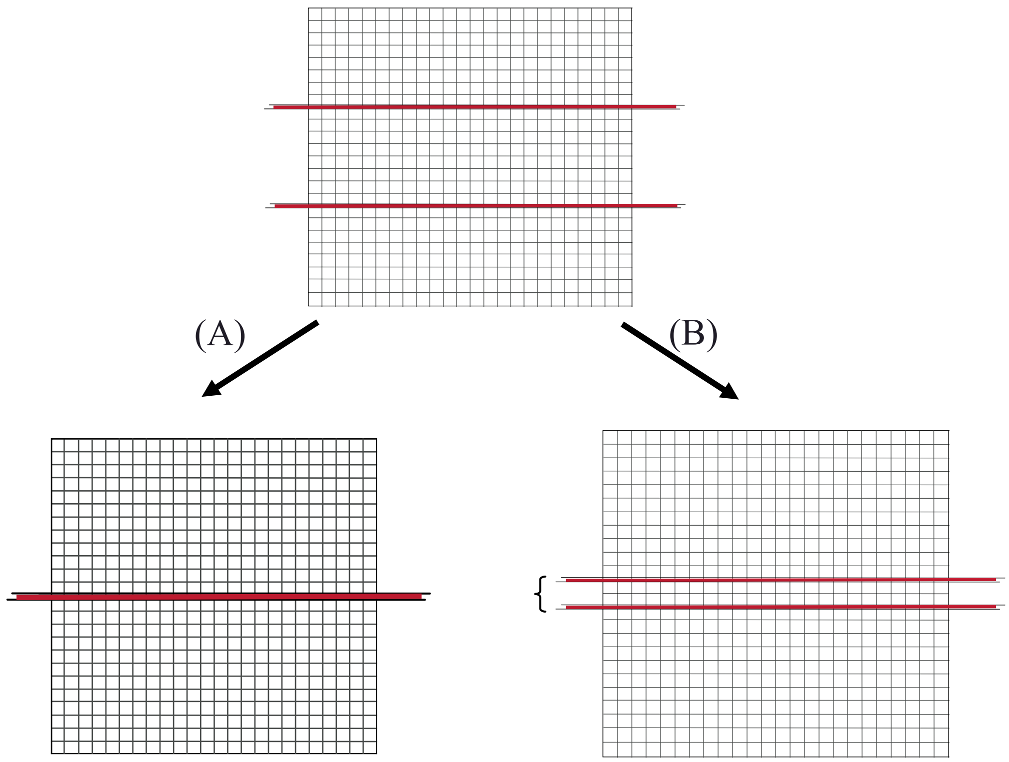

Figure 5: Comparison of three road network configurations (bundled versus evenly distributed). The roads (black lines) are between the cells of the model (cells are indicated by the grey lines). Total traffic amount is the same in all three situations shown. (A) Comparing configurations with two evenly distributed roads and all traffic on one large road and (B) comparing configurations with two evenly distributed roads and two roads located close to each other.

Results

Both extinctions and recolonizations of empty patches by individuals moving across a road occurred in the simulations when *AVOID* < 1. Road configuration clearly had an influence on population persistence.

Comparison of parallel pattern with gridded pattern
For constant degree of road avoidance, the probability of population persistence decreased as a function of increasing traffic mortality (figure 6). For constant traffic mortality, the probability of population persistence increased as a function of increasing road avoidance, *AVOID,* at least as long as road avoidance was below 0.9 (figure 7). For very high values of *AVOID* (i.e., > 0.9), population persistence decreased (figure 7).

In contradiction to our expectation that increasing the number of patches would always reduce population persistence, the effect of the crossed road patterns was in most cases less detrimental than the effect of the parallel road patterns (figures 6 and 7) when *AVOID* was less than 0.7, even though the number of patches in the crossed road pattern was higher than in the parallel road pattern. However, the two lines intersected at some degree of road avoidance which implied that, for higher values of *AVOID*, the impact of the crossed road pattern was more severe than the impact of the parallel road pattern (figure 7), which was in correspondence with out expectation.

A parallel road pattern with higher number of roads, while patch number was constant, always resulted in a more detrimental impact on population persistence than the gridded road pattern (figures 6 and 7).

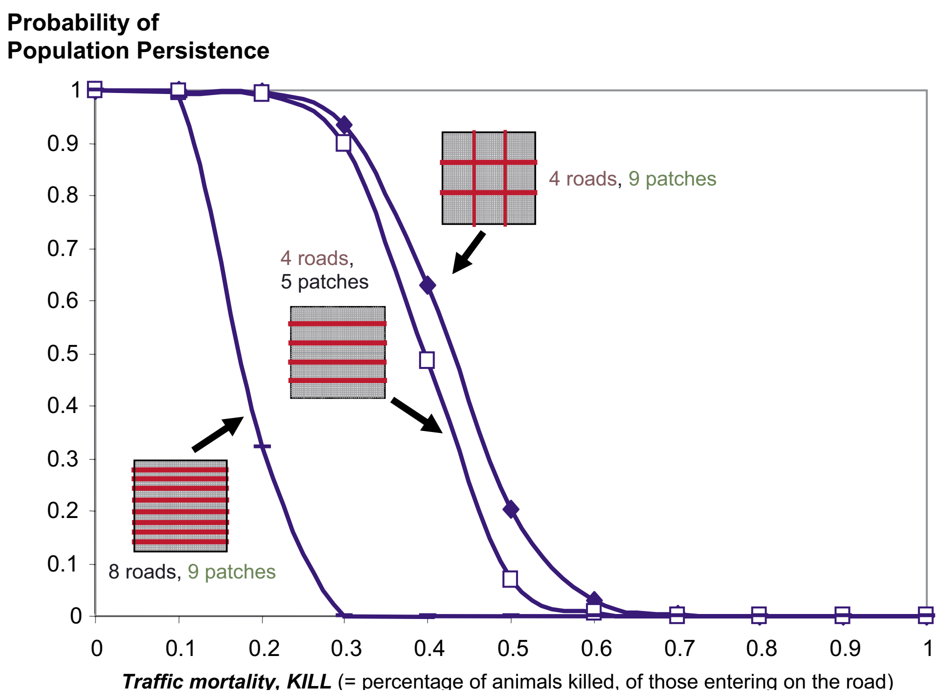

Figure 6: Results of the simulations for comparison of a gridded road configuration (with four roads and nine patches) with a parallel road configuration that has the same number of roads (but fewer patches) and with a parallel configuration that has the same number of patches (but more roads). All patches are of same size within each configuration. Road avoidance, *AVOID*, was kept constant in all simulation runs (= 0.5) while traffic mortality, *KILL*, was varied from 0 to 1.

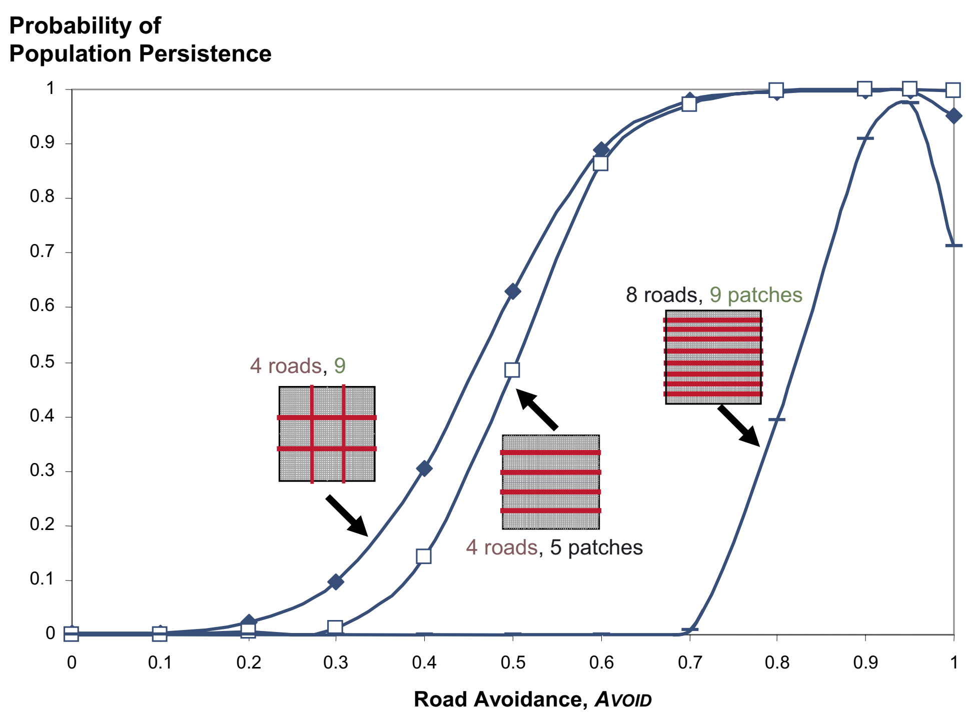

Figure 7: Results of the simulations for comparison of a gridded road configuration (with four roads and nine patches) with a parallel road configuration that had the same number of roads (but fewer patches) and with a parallel configuration that had the same number of patches (but more roads). All patches were of same size within each configuration. Traffic mortality, *KILL*, was kept constant in all simulation runs (= 0.4) while road avoidance, *AVOID*, was varied from 0 to 1.

The comparison of the critical road densities, where population persistence is reduced by 50 percent as a function of increasing road density while traffic mortality, *KILL*, and road avoidance, *AVOID*, are kept constant, also demonstrates that the degree to which roads affect wildlife populations depends on the configuration of the road network (figure 8). For low values of road avoidance, the parallel road pattern was more detrimental. For high values of road avoidance, the gridded road pattern was more detrimental. For intermediate values of road avoidance, both road patterns were equally detrimental to population persistence (figure 8). For more details, see Jaeger et al. (in prep.).

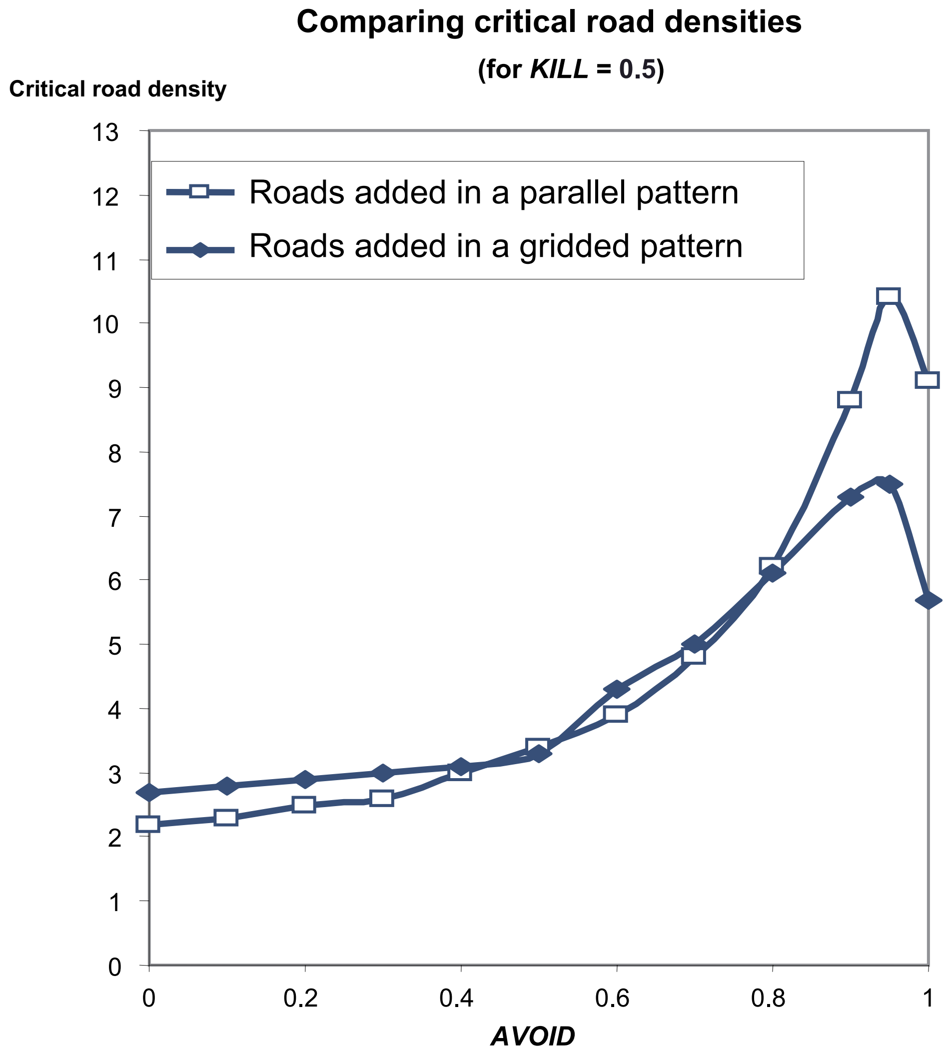

Figure 8. Results of the simulations for comparison of a gridded road configuration with a parallel road configuration. Traffic mortality, *KILL*, was kept constant in all simulation runs (= 0.5) while road avoidance, *AVOID*, was varied from 0 to 1. The critical road density is the density of roads where population persistence probability is reduced to 50 percent. For *AVOID* < 0.4, population persistence was reduced to 50% at lower road densities in the parallel road pattern than in the gridded road pattern, i.e., the parallel road pattern was more detrimental. For 0.4 < *AVOID* < 0.8, both patterns were equally detrimental. For *AVOID* > 0.8, the gridded road pattern was more detrimental, i.e., population persistence was reduced to 50 percent at lower road densities in the gridded road pattern than in the parallel road pattern.

Bundling of roads

We tried several functions for the dependency of *KILL* and *AVOID* on traffic volume (for details see Jaeger and Fahrig, in prep.), starting with data from Seiler (2003) for ungulates. In most cases, putting all traffic on one road was less detrimental (and never more detrimental) than the other two configurations. Two roads bundled in the center were almost always less detrimental (and never more detrimental) than the two roads distributed evenly (figure 9).

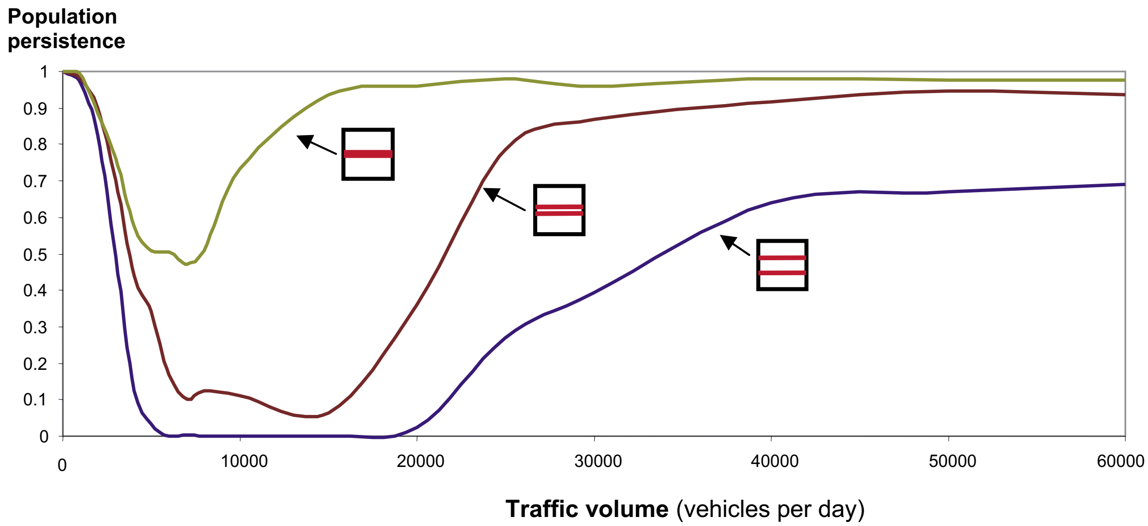

Figure 9: Results of the simulations for comparison of three road configurations (figure 5). The same traffic volume was distributed over two roads distributed evenly or bundled in the center or placed on one large road leaving larger areas undissected, using Seiler's (2003) data on *AVOID* and *KILL*. Natural mortality was 0.32 (per individual and time step). (These curves are based on only 200 model runs per data point.) For details, see Jaeger and Fahrig (in prep.).

Discussion

Our objective was to examine whether the degree to which road networks affect population persistence depends on the configuration of the road networks and on the interaction of the target species with the roads. This dependency has important implications for the management of landscapes. For example, our results suggest that even though a population may show no negative response to a certain number or density of roads, a different configuration of the road network (with the same total length of roads) may cause the extinction of the population.

One example of an animal population that crossed the extinction threshold is the European badger in the Netherlands (Van der Zee et al. 1992). Others that are suspected to be across or close to the threshold are turtles in the U.S. (Gibbs and Shriver 2002), otters in Eastern Germany (Hauer 2002), and badgers in Great Britain (Clarke et al. 1998).

The model results clearly supported the bundling concept. Population persistence was generally higher (and never lower) when all traffic was put on one road than when it was distributed on several roads across the landscape. If traffic cannot be combined on one road, the model results suggested it is better to bundle the roads close together than to distribute them evenly across the landscape.

The results for the gridded versus parallel road pattern were surprising: The expectation that fragmenting the landscape into more patches would always be more harmful to population persistence (while total road length is kept constant) was contradicted by the model results when the degree of road avoidance by the animals was low (figures 7 and 8).

One explanation is that the amount of core habitat is larger in the gridded road pattern (figure 10). Individuals located in the cells close to a road ('road effect zone,' Forman and Deblinger 2000) were more likely to encounter a road during their next movement and be killed if they exhibited low road avoidance (e.g., amphibians). Individuals located in the cells far away from any road (i.e., located in core habitat) would survive during their next movement because they cannot encounter a road. Therefore, there were more cells where individuals were not affected by traffic mortality in the gridded road pattern. However, when road avoidance was high, then the 'road effect zone' became less harmful and the isolation of the patches became relatively more important. In this case, the gridded pattern was more harmful because the number of patches was higher.

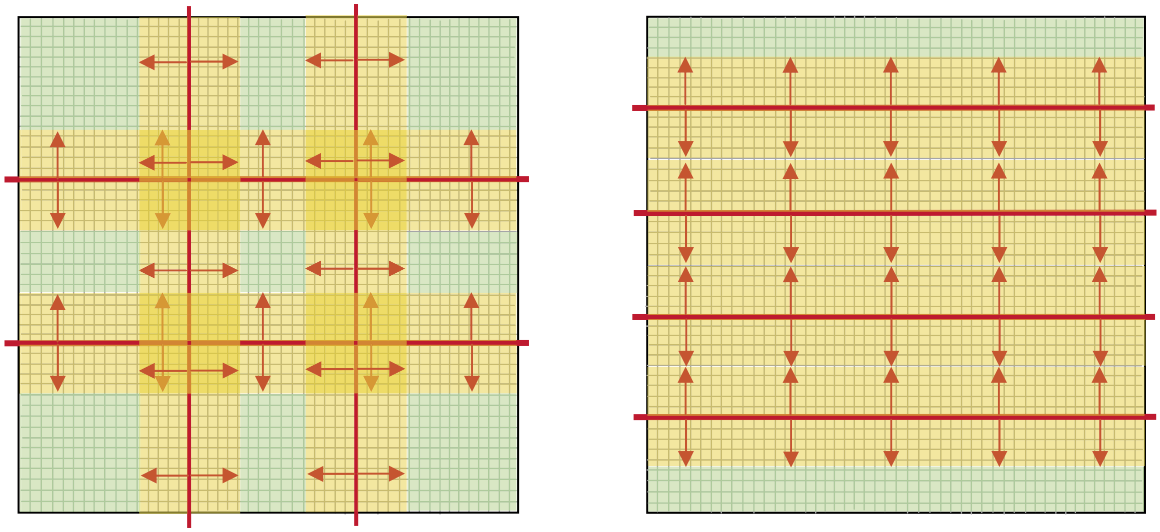

Figure 10: Explanation of why the parallel road pattern was observed to be more detrimental to population persistence than the gridded road pattern when road avoidance is low. Individuals located in the cells close to a road ('road effect zone' indicated by the arrows assumed as extending over five cells) are more likely to encounter a road during their next movement. Individuals located in the cells far away from any road (i.e., located in core habitat) will survive during their next movement because they cannot encounter a road. The gridded pattern (left) has more core habitat (784 cells) than the parallel road pattern (right, 384 cells). Therefore, there are more cells where individuals are not affected by traffic mortality. If road avoidance is high, then the 'road effect zone' is less dangerous for the individuals but the isolation of the patches becomes relatively more important.

Our results indicate that, for animals exhibiting low road avoidance, the effect of the roads is determined by the density of roads and the shape of the patches rather than by the number of patches. Increasing the number of patches (while road configuration changed from parallel to crossed) in many cases increased, or did not decrease, population persistence when road density was kept constant. This was counter to our expectation that increasing the number of patches would always reduce population persistence.

The reason was that the animals encountered the roads less often in the crossed road pattern series because, on average, the locations of the animals were farther away from the nearest road (figure 10). However, for animals strongly avoiding roads, the crossed road pattern often became more detrimental. For animals entirely avoiding roads, the effect of the road network on population persistence is determined by the number (and shape) of the patches rather than the density of roads.

This implies that for animals that do not strongly avoid roads, it is generally more important to preserve core habitats at a sufficient distance from roads than to keep the number of patches low (figure 10).

Our results are qualitative, not quantitative. Several factors will influence the degree to which the road network affects population persistence by affecting the relative susceptibility of the population to additional mortality and population fragmentation. The most important of these factors are habitat loss and reduction of habitat quality. If the animals need access to resources on both sides of the road (landscape complementation, e.g., breeding habitat is on one side, whereas foraging habitat is on the other), crossing the road is mandatory for survival. The effects of both traffic mortality and fragmentation will then be more detrimental.

Conclusion

Most current studies of population viability do not include the effects of roads; if they have been included then only incorporated into the overall mortality rate (e.g., Kramer-Schadt et al. 2004) which does not account for the effects of road avoidance and road configuration. However, the spatial configuration of the road network is potentially an important factor and should be included in viability analyses of animals that are affected by roads.

The degree to which a road network affects wildlife populations depends on the configuration of the road network. Which configurations are less detrimental than others? Our results indicate that this may depend on the behavior of the animals at roads. However, some general statements can be made:

1. It is always beneficial (or never harmful) to bundle the traffic.
2. If road avoidance is low, a gridded pattern is less harmful than a parallel pattern of same total road length because of the amount of core habitat is higher.
3. Core habitat should be maximized if animals are affected by road mortality: Large un-dissected areas should be protected from road construction.

4. If road avoidance is high, then the parallel road pattern is less harmful because the number of patches is lower (i.e., the patches are larger) and traffic mortality is not an issue: The number of patches should be low if road avoidance is high because the animals are strongly affected by isolation.

If animals avoid roads entirely, it is wise to minimize the number of patches (fragmentation) rather than the number of roads. If animals do not avoid roads but are often killed by traffic (e.g., amphibians), it is more useful to minimize the number of roads. When the target species exhibits both road avoidance and traffic mortality (or if their behavior at roads is unknown) then both the number of roads and the number of patches should be minimized.

Putting up fences along both sides of the roads corresponds to 100-percent road avoidance (*AVOID* = 1). Fences 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 is even more harmful than some mortality due to vehicle collisions when there is no fence (Carr et al. 2002; Jaeger and Fahrig 2004a). When the number of roads increases (while *K* and *AVOID* are constant), fencing may become a more useful measure.

Road fencing combined with wildlife-crossing structures has decreased vehicle collisions with ungulates by at least 80 percent (Ward 1982; Lavsund and Sandegren 1991; Child 1998; Clevenger et al. 2001). Fenced roads in combination with crossing structures correspond to roads with *AVOID* < 1 and *KILL* = 0. However, it is unlikely that all roads in any large region will be fenced in combination with crossing structures because of the high costs. Therefore, other measures need to be considered, including the removal of roads. In the case that the animals need access to resources on both sides of the roads, fencing will never be beneficial, unless accompanied by wildlife-crossing structures.

It may also be possible to influence the interaction of the target species with the roads. For example, clearing roadside vegetation or adding reflectors or wildlife detection systems will alter animal and driver behavior, which may change *AVOID* and *KILL*. Finally, it is important to remember that traffic mortality and the degree of road avoidance are affected by traffic volume and speed (e.g., Allen and McCullough 1976; Bertwistle 1999; Hubbard et al. 2000; Seiler 2004, Seiler 2005).

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 *AVOID* or *KILL*, environmental stochasticity, and reduced gene flow (possibly leading to loss of genetic variability) are not straightforward. Further research will be necessary to evaluate the direction and magnitude of the effects of these factors on our predictions.

Important topics for future research are:

- Road avoidance behavior (empirical data and modeling)
- Relative importance of total road length and road configuration
- Effect of different habitat types (landscape complementation)
- Effect of different matrix types
- Landscape connectivity, e.g., the effects of overpasses and underpasses and the question of where to place them

The results from this model are an important step towards a network theory for road ecology and towards the design of less-detrimental road networks. Future research should investigate the behavior of animals at roads in empirical studies and focus on how traffic mortality and road avoidance depend on traffic volume. Such data will greatly improve the model predictions.

In addition, empirical studies comparing landscapes with differing road network configurations (while total road length is constant) should be conducted to validate our model results and provide a basis for developing more practical models for use in planning and designing of highway networks.

Acknowledgements: We are grateful to J. C. Nicolaides for programming assistance. We thank Felix Eigenbrod, Kringen Henein, Rachelle McGregor, and the members of the Geomatics and Landscape Ecology Laboratory (GLEL) at Carleton University for helpful comments on an earlier version of this manuscript. This work was supported through a postdoctoral scholarship from the German Research Foundation, DFG, to Jochen A.G. Jaeger (grant number JA 1105/1-1) and through a Natural Sciences and Engineering Research Council of Canada grant to Lenore Fahrig.

Biographical Sketches: Jochen A. G. Jaeger is a postdoctoral fellow in the Department of Environmental Sciences at the Swiss Federal Institute of Technology Zurich (ETH Zurich), Switzerland, with Prof. Dr. Klaus Ewald. He studied physics at the Christian-Albrecht University in Kiel, Germany and at the ETH Zurich. He received his Ph.D. from the Department of Environmental Sciences at the ETH Zurich. He has held a position at the Center of Technology Assessment in Baden-Württemberg in Stuttgart, Germany and has lectured at the University of Stuttgart, Germany. In 2001, he won a two-year research grant from the German Academy of Natural Scientists Leopoldina and went to Carleton University in Ottawa, Ontario, Canada as a postdoctoral fellow with Dr. Lenore Fahrig in her Landscape Ecology Laboratory (Department of Biology). Dr. Jaeger is currently working on his habilitation thesis, funded by a research fellowship from the German Research Foundation (DFG). His research interests are in landscape ecology, quantification and assessment of landscape change, assessment of the suitability of landscape metrics, environmental indicators, road ecology, modelling, urban sprawl, and novel concepts of problem-oriented transdisciplinary research.

Lenore Fahrig is professor of biology at Carleton University, Ottawa, Canada. Dr. Fahrig studies the effects of landscape structure on wildlife populations. She uses spatial-simulation modeling to formulate predictions and tests those predictions using a wide range of organisms, including plants, insects, amphibians, mammals, and birds. Her current work on road-system ecology includes empirical studies of road impacts on small mammal and amphibian populations and movements, as well as generalized simulation modelling of population responses to road networks. Dr. Fahrig has published over 50 papers in landscape ecology. Many of her recent papers focus on ecological impacts of roads. She is currently a member of the U.S. National Academy of Sciences Committee on Ecological Impacts of Road Density.

Klaus C. Ewald has been full professor of nature and landscape protection in the Department of Forest and Wood Sciences since 1993 and since 1998 in the Department of Environmental Sciences of the ETH Zurich, Switzerland. Dr. Ewald studied geography and biology at the University of Basle and graduated in geography in 1969. Afterwards he spent five years as a scientific employee of the Swiss League of Nature Protection. During this period, he continued his education at the Institute of Landscape Management and Nature Conservation at the University of Hanover. A grant form the Swiss National Science Foundation enabled him to carry out one of the first examinations of historical and ongoing landscape changes in Switzerland. From 1977-1986 he established and directed the Section of Landscape Research at the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) in Birmensdorf. He completed his habilitation thesis in geography in 1980 at the University of Basle and lectured on nature and landscape protection. In 1986, Dr. Ewald received a professorship in the Faculty of Forestry Science at the Albert-Ludwigs University in Freiburg im Breisgau, Germany. From 1987 until 1993, he was professor of landscape management and director of the Institute.

References

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. G. L. Evink, P. Garrett, and D. Zeigler (eds.). Proceedings of the third international conference on wildlife ecology and transportation. FL-ER-73-99. Florida Department of Transportation, Tallahassee, Florida.

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.

Carr, L.W., L. Fahrig, and S.E. Pope. 2002. Impacts of landscape transformation by roads. K.J. Gutzwiller (ed.). *Applying landscape ecology in biological conservation*. Springer Verlag, New York.

Child, K.N. 1998. Incidental mortality. 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.

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

Forman, R.T.T., and L.E. Alexander. 1998. Roads and their major ecological effects. *Annual review of ecology and systematics* 29: 207-231.

Forman, R.T.T., and R.D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conservation biology* 14: 36-46.

Forman, R.T.T., D. Sperling; J.A. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Heanue, J.A. Jones, F.J. Swanson, T. Turrentine, and T.C. Winter. 2003. *Road Ecology. Science and Solutions*. Island Press, Washington, D.C.

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

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.

Jaeger, J. 2001. Curtailing landscape fragmentation due to transportation infrastructure by the introduction of quantitative limits (in German: *Beschränkung der Landschaftszerschneidung durch die Einführung von Grenz- oder Richtwerten*). *Natur und Landschaft* 76 (1): 26-34.

Jaeger, J. 2002. *Landschaftszerschneidung. Eine transdisziplinäre Studie gemäß dem Konzept der Umweltgefährdung*. Ulmer-Verlag, Stuttgart, Germany.

Jaeger, J.A.G., and L. Fahrig. 2004a. Effects of road fencing on population persistence. – *Conservation Biology* 18 (6): 1651-1657.

Jaeger, J.A.G., and L. Fahrig. 2004b. Under what conditions do fences reduce the effects of transportation infrastructure on population persistence? IENE Conference 2003 Proceedings.

Jaeger, J.A.G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. Tluk von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* 185: 329-348.

Jaeger, J.A.G., L. Fahrig, and K.C. Ewald. Thresholds in species' responses to landscape fragmentation by roads. (In prep.).

Jaeger, J.A.G., and L. Fahrig Effects of traffic bundling on population persistence. (In prep.).

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

Kramer-Schadt, S., E. Revilla, T. Wiegand, and U. Breitenmoser. 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology* 41: 711-723.

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. D. S. Smith and P. C. Hellmund (eds). *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. J. Green, C. Pacas, S. Bayley, and L. Cornwell (eds.). 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.

Seiler, A. 2003. The toll of the automobile: wildlife and roads in Sweden. *Acta Universitatis Agriculturae Sueciae Silvestria* 295. Swedish University of Agricultural Sciences, Uppsala.

Seiler, A. 2004. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology* 10 (4): 11-23.

Seiler, A. 2005. Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology* 42 (2): 371-382.

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.

Van der Zee, F.F., C.J.F. Ter Braak, and R.C. van Apeldoorn. 1992. Landscape change as a possible cause of the badger *Meles meles L*. decline in The Netherlands. *Biological Conservation* 61: 17-22.

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.