Under what conditions do fences reduce the effects of transportation infrastructure on population persistence?

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Abstract

Transportation infrastructure impedes the movement of animals, enhances their mortality due to collisions with vehicles, and decreases habitat size. We study the first two effects, using a spatially explicit individual-based model of population dynamics. We discuss the suitability of fences. Fences can either enhance or reduce survival probability, depending on the degree of road avoidance and the proportion of animals killed, of those that try to cross the road. There is a lower value of traffic mortality below which a fence is always harmful and an upper value of traffic mortality above which a fence is always beneficial. Between these two values the suitability of fences depends on the degree of road avoidance. The lower the degree of road avoidance and the higher the amount of traffic on the road, the more likely it will be that fences are beneficial. We recommend the use of fences when traffic is so high that animals never, or almost never, succeed in their attempts to cross the road, or the population of the species of concern is declining and 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 to access resources on both sides of the road, unless fences are used in combination with wildlife crossing structures.

Introduction

Continuous increase of landscape fragmentation

The dissection and fragmentation of landscapes by transport infrastructure is known as a major reason for the alarming loss of species in Central Europe. It also affects the water regime, the scenery, and the landscape's quality for recreation. Roads and railroads affect animal populations in three ways: (1) habitat loss (due to pavement and embankment and to emissions from the road such as noise and salt), (2) collisions of individuals with vehicles on the road, and (3) avoidance of venturing onto the road (resulting in diminished access to resources). As a consequence of (2) and (3), populations are subdivided resulting in a lack of immigrants in empty habitats and a lack of genetic exchange among sub-populations (Fig. 1).

Over the last 20 years, there has been a growing discrepancy between real development and the political objectives claimed by the federal government in Germany about a necessary "trend reversal in the landscape dissection and the widely dispersed urban sprawl" (Bundesminister des Innern 1985). For example, in Baden-Württemberg (Germany), the effective mesh size has decreased by 40% since 1930 (Fig. 2; Esswein et al. 2002). The definition of the effective mesh size is based on the probability that two randomly chosen points in a region will be located in the same non-fragmented land parcel after the region has been fragmented (Jaeger 2000, 2002). This probability is interpreted in the sense that two animals in a landscape can encounter each other. The possibility of two animals of the same species to find each other in the landscape is a prerequisite for the persistence of animal populations (e.g., because of the need for genetic exchange between populations and for the re-colonization of empty habitats). The encountering probability is converted into the size of an area which is called “effective mesh size”. If the region was fragmented evenly into parcels of this size then the probability of animal encounters would be the same. Thus, in the case that all remaining land parcels are of same size, the effective mesh size equals the average size of the land parcels. The more a landscape is fragmented the lower is the encountering probability, and the smaller is the effective mesh size.

Figure 1:
Impacts of transportation infrastructure on the persistence of wildlife populations. Both traffic mortality and inaccessibility contribute to population subdivision and isolation (modified after Fahrig 2002).

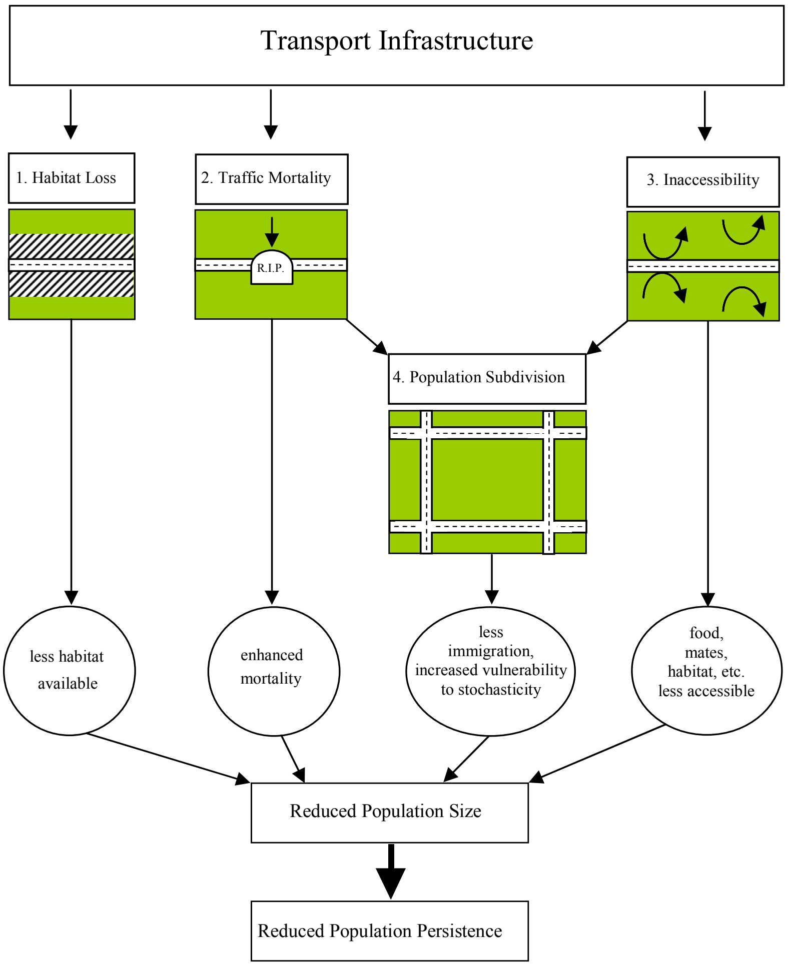


Fig. 2 shows a time series of the effective mesh size in Baden-Württemberg. When the noise bands of the roads are considered as well (according to the method suggested by Reijnen et al. 1995) then the effective mesh size decreases even more because of the continuous growth of traffic volume on the roads (Fig. 2). It is important to use a reliable measure for producing time series of landscape fragmentation. For example, the average size of the remaining non-fragmented land parcels has been suggested as a measure of fragmentation but, unfortunately, the measure is not suitable for this purpose. One reason is, for example, that it does not react consistently to different fragmentation phases, e.g., it decreases when habitat patches are dissected or when habitat size decreases, but it increases when small patches are lost, and decreases when large patches are lost (see Jaeger 2000, 2002 for details). Fig. 3 illustrates that the average patch size is not a suitable measure of landscape fragmentation.

Figure 2:
Time series of the degree of landscape fragmentation in Baden-Württemberg (Germany) since 1930 using the effective mesh size of the remaining non-fragmented land parcels in km^2 (see text). Motorways, federal highways, state highways, political district roads, municipal roads, rivers > 6 m, lakes, settlements are considered as barriers. The lower line also includes noise bands the width of which depends on the traffic volume on the roads (from Esswein et al. 2002).

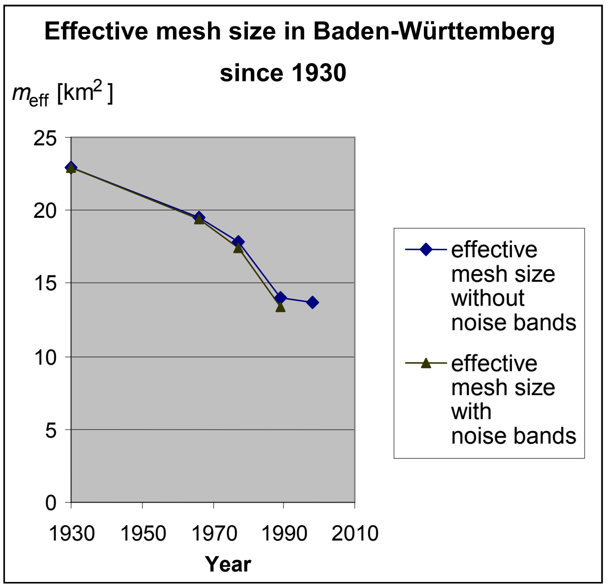


Figure 3:
Average size of the remaining non-fragmented land parcels in Baden-Württemberg since 1930 (considering the same barriers as in Fig. 2). The comparison with Fig. 2 illustrates that the average size of the remaining land parcels is not suitable as a measure of landscape fragmentation. For example, the loss of small habitat patches due to urban sprawl leads to an increase of the average size of patches. Data taken from Esswein et al. (2002).

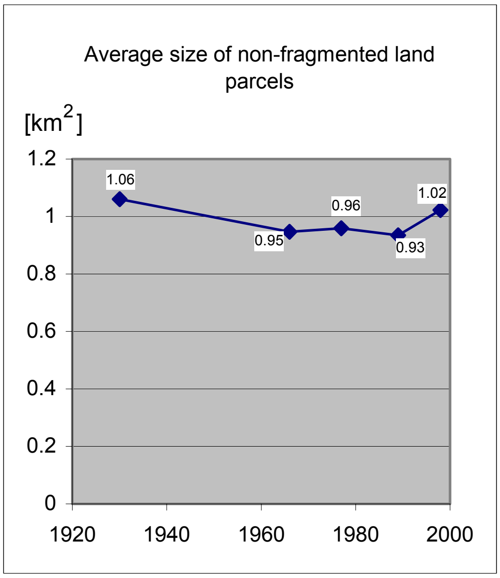
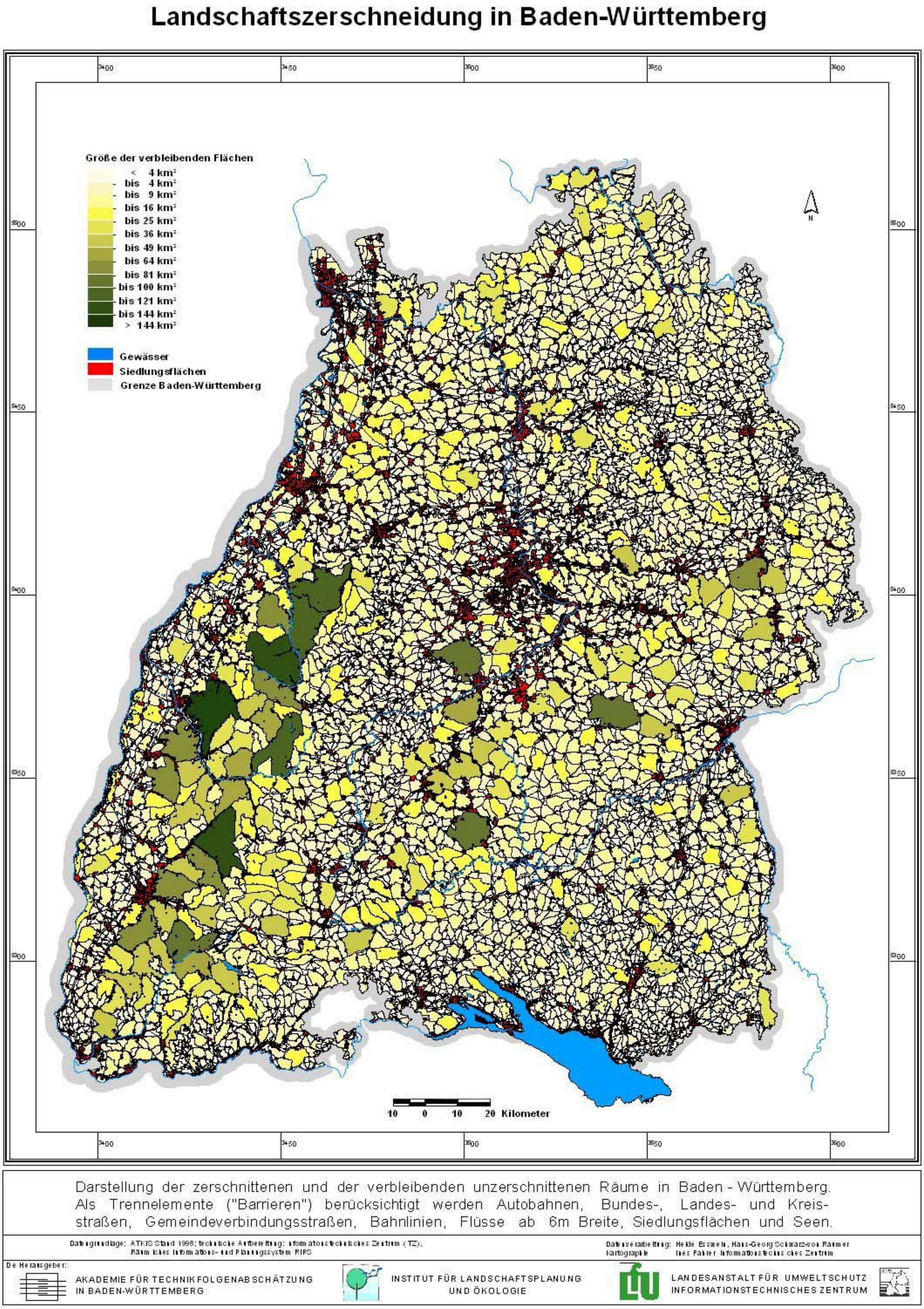


Fig. 4 shows the current patchwork of land parcels in Baden-Württemberg. Most of the remaining six large non-fragmented land parcels (> 100 km^2) are located in the Black Forest (Jaeger et al. 2001). Time series for the political districts (Landkreise) illustrate that there are significant differences in how much each of them has been fragmented (Fig. 5).

Figure 4.
Landscape fragmentation in Baden-Württemberg
(from Jaeger et al. 2001).



Time series of the effective mesh size (in km²) of seven political districts (Landkreise) in Baden-Württemberg (Germany); out of a total of 44 political districts (modified after Esswein et al. 2002).

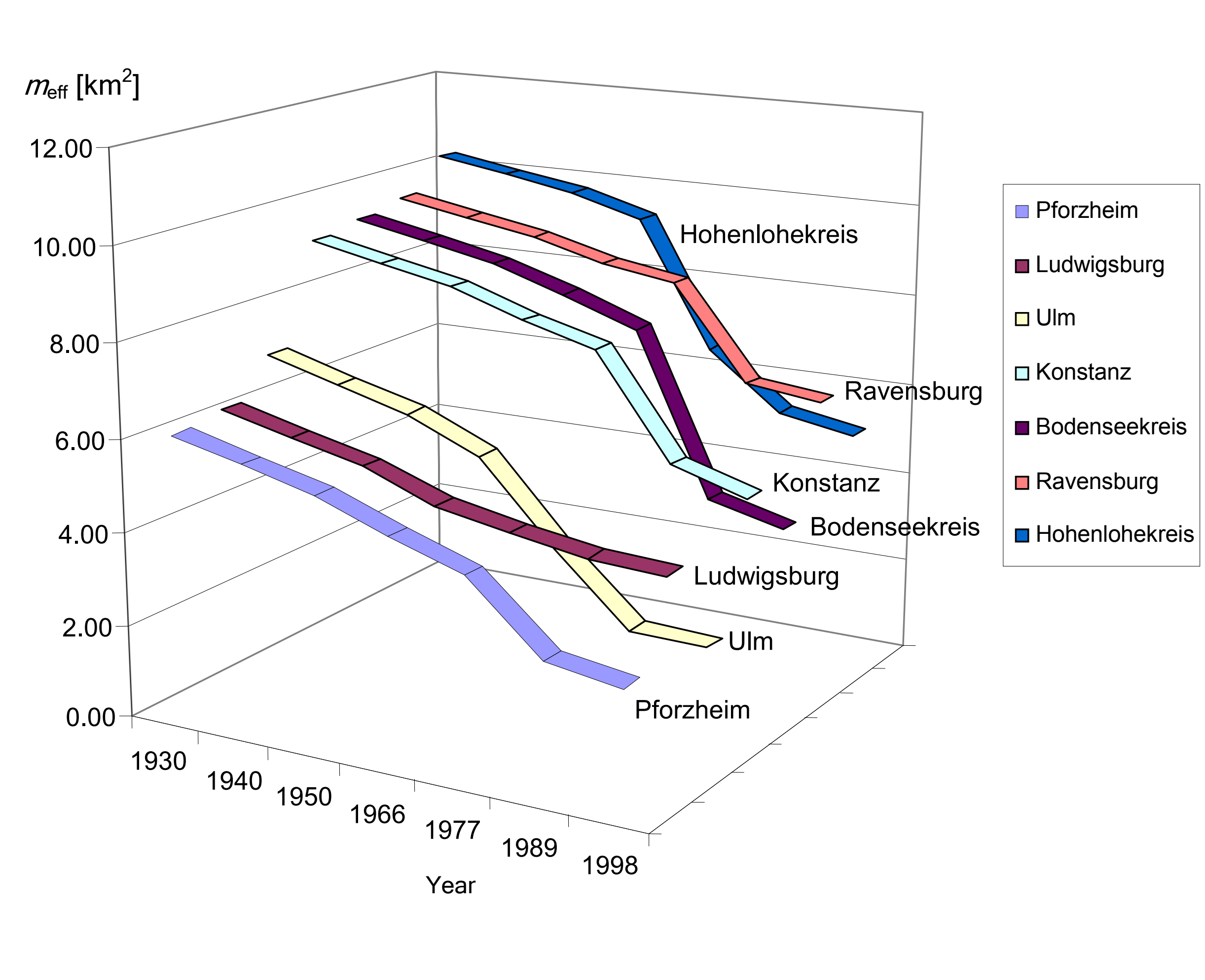


Figure 6:
A sign at the entrance of the Kootenay National Park in the Canadian Rocky Mountains warns drivers to be cautious (photo: J. Jaeger).

As the meshes of this network become smaller and smaller, animals get in contact with these barriers more and more often (Fig. 6). As a consequence, nature conservationists, wildlife biologists, traffic planners, and landscape planners are increasingly concerned about the effects of transportation infrastructure on animal populations (e.g., Canters et al. 1997, Ellenberg et al. 1981, Forman et al. 2003, Glitzner et al. 1999, Holzgang et al. 2000, Institut für Naturschutz und Tierökologie 1977, Lodé 2000, Trombulak and Frissell 2000).

Should we put up fences along roads and railroads?

The discussion of mitigation measures includes the question of whether or not fences are a suitable measure to reduce mortality due to collisions with vehicles (Clevenger et al. 2001, Falk et al. 1978, Forman et al. 2003: 139-167). Much data have been collected about absolute numbers of animals killed on roads (e.g., Ashley and Robinson 1996, Fahrig et al. 1995, Glitzner et al. 1999, Knutson 1987, Reichholf and Esser 1981, Stoner 1925) and, to a lesser extent, on railroads (e.g., Grift 1999). However, data on the proportion of killed animals related to total mortality are scarce. They are needed to assess the impact of traffic mortality on population persistence, since higher absolute numbers of road kill can result from larger populations (Groot Bruinderink and Hazebroek 1996). Estimates on the proportion of killed animals related to total mortality have been made for otters in Eastern Germany (Hauer et al. 2002, Roth et al. 2000, Stubbe 1993), European badger in Great Britain (Clarke et al. 1998), hedgehogs in the Netherlands (Huijser and Bergers 2000), and gray wolves in the Canadian Rocky Mountains (Callaghan 2002, Paquet et al. 1996). Gibbs and Shriver (2002) recently showed that road mortality may have contributed significantly to widespread population declines in turtles in the United States. Serrouya (1999) reports an increasing trend of highway mortality for black bears in Banff National Park (Alberta, Canada). Hebblewhite et al. (2003) concluded that the black bear population in Banff National Park has been declining since 1994; 36% of all mortality was highway mortality.

Fences along roads prevent animals from venturing onto the road. However, fences make road crossings impossible and lead to a complete separation of the habitats on either side of the road, dividing a population into smaller sub-populations with higher extinction risk. Isolated habitats that have lost their inhabitants cannot be re-colonized. For some species, this effect might be even more adverse than the enhanced mortality due to vehicle collisions. The question as to which of these two effects is more severe has been asked by Carr et al. (2002). Currently, the use of fences is a subject of great controversy among traffic planners and nature conservationists.

The net effect of fences is not obvious because there are a number of different mechanisms involved (e.g., demographic stochasticity, dispersal of juveniles to find unoccupied habitat, searching for mates, re-colonization of empty habitats, traffic collisions, interaction with other species, interaction with other impacts on the population such as intensified land use). It is difficult to separate these mechanisms in an empirical field study. A simulation model is a useful tool to separate and compare different mechanisms that are responsible for the effects of roads on population density and to investigate their relative importance.
The purpose of this paper is to answer the following questions:

- When does road avoidance alone have an effect on population persistence?
- What is the relative importance of road avoidance and road mortality?
- Under what conditions is a fence expected to be beneficial for population persistence?

The larger project the results reported in this paper are a part of aims to compare different road network patterns with respect to their effects on population density and persistence and landscape connectivity.

What are relevant conditions for the use of fences?

What determines whether fences will reduce or enhance population persistence? An obvious factor is the magnitude of traffic mortality. If the animals are always successful when they try to cross the road and there is no traffic mortality then a fence is useless and may be detrimental.

A second factor is the degree to which an animal that encounters a road does not attempt to cross it; we call this behavior "road avoidance" (Fig. 7). If the animals avoid the road entirely then no fence is needed (Falk et al. 1978). Many animals have been shown to avoid roads to a certain degree (Bélisle and St. Clair 2001, Clarke et al. 1998, Falk et al. 1978, Korn and Pitzke 1988, Kozel and Fleharty 1979, Mader 1984, Mader et al. 1990, Merriam et al. 1989, Oxley et al. 1974, Richardson et al. 1997, Swihart and Slade 1984, Wilkins 1982, Yale Conrey and Mills 2002, Zande et al. 1980).

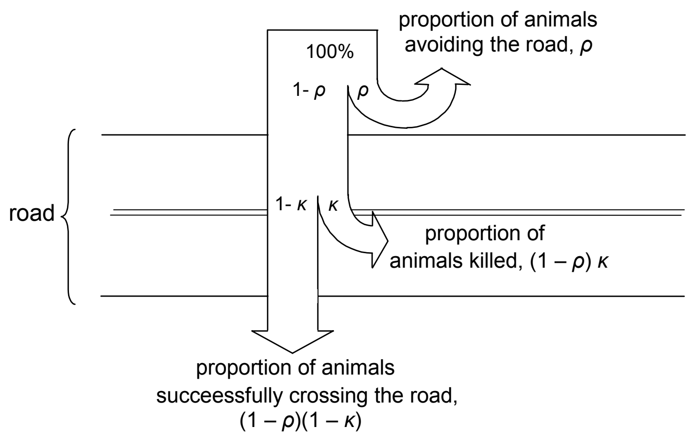


Figure 7:
Illustration of road avoidance, ρ, and the proportion of animals killed on the road, κ. The two variables are specified independently of each other. Their ranges are from 0 to 1. Barrier strength, β, comprises both effects, $\beta = 1 - (1 - \rho)(1 - \kappa)$; from Jaeger and Fahrig (subm.).

We describe traffic mortality and road avoidance by the two variables κ for the proportion of animals killed on the road, of those that try to cross it, and ρ for the degree of road avoidance (Fig. 7). Both range between 0 and 1. Barrier strength, β, denotes the sum of both effects and ranges from 0 to 1 as well. It describes the reduction of successful movements across the road; $\beta = \kappa + \rho - \kappa \cdot \rho$. Putting up fences reduces the proportion of animals killed ($\kappa = 0$) but enhances road avoidance to is maximum ($\rho = 1$).

Research questions

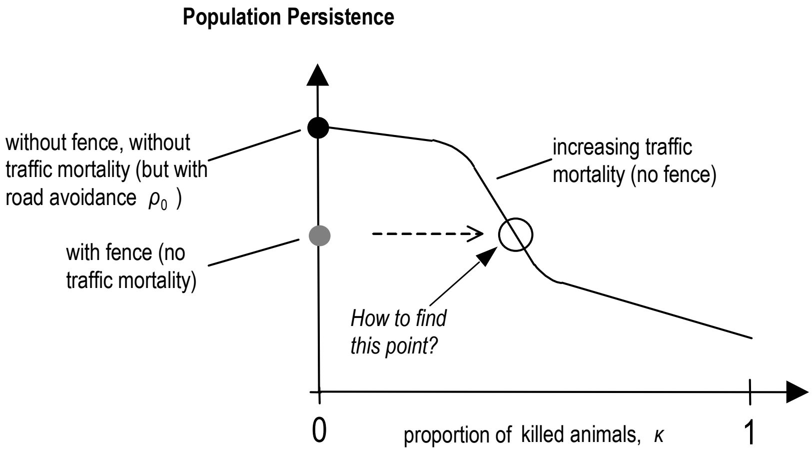
We investigate the following research questions:

- At what values of road avoidance do we predict an effect of road avoidance alone on population persistence?
- At what values of traffic mortality do we predict an effect of traffic mortality alone on population persistence?
- Which one is more important?
- Under what conditions do we predict a mitigation of traffic mortality by putting up a fence?
- How do the results change if the road separates different required types of habitat?

Expectations about the effect of road avoidance and traffic mortality

In principle, both mitigation or intensification due to a fence are possible, depending on the magnitude of traffic mortality. Putting up a fence means that ρ is set to 1 (unless there are underpasses or overpasses or leaks in the fence) and κ is set to 0. Without the fence, κ may have any value between 0 and 1. We denote the value of ρ in the situation before putting up the fence as ρ_0. When κ increases (e.g., due to increasing traffic density on the road) and if ρ is constant, we expect a curve like the one in Figure 8 due to higher overall mortality.

Figure 8:
Expectation for the effect of increasing road mortality, κ, as compared with the effect of a fence. The situation that all animals cross the road and are never killed is always better than a fence. The situation that all animals crossing the road are killed is always more harmful than the effect of a fence (because the animals return but are not killed). Therefore, at some value of κ between these two situations, the curve for population persistence (as a function of traffic mortality) assumes the value of population persistence for putting up a fence. This point is the threshold separating the range of traffic mortality where a fence is beneficial (right side of the diagram) from the range of traffic mortality where a fence is disadvantageous (left side of the diagram).



At what values of κ is population persistence higher when there is a fence than without the fence? A given probability of traffic mortality is always more detrimental than the same probability of road avoidance alone because when an animal is killed is also does not cross the road. Therefore, the curve for population persistence as a function of traffic mortality at some point has to go below the value of population persistence for the fence (Fig. 8). The fence either reduces population persistence to a value > 0, or the fence reduces the population persistence to 0 (then the curve goes down to the *x*-axis).

It follows that there is always a critical value of the proportion of animals killed on the road, κ_c, so that for all $\kappa > \kappa_c$, the population would be better off with a fence. However, there is also a range at lower values of κ where the influence of the fence on the population is more adverse than the traffic mortality. At what magnitude of road mortality is a fence expected to be advantageous?

This line of thought argues that for every degree of road avoidance, ρ, there is a critical value of κ in the sense that a fence is harmful at lower and beneficial at higher values of κ. When both road avoidance and traffic mortality are varied at the same time, κ_c depends on the degree of road avoidance. To study the combined effect, a model is needed.

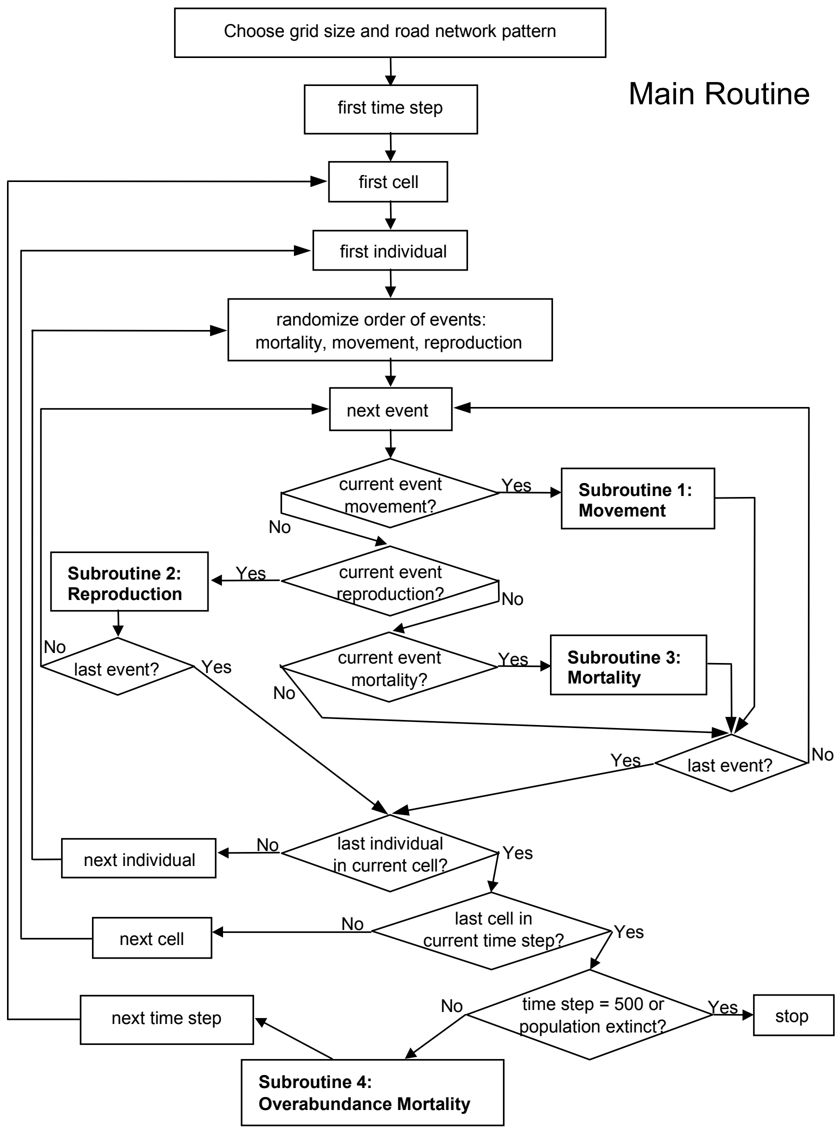
Methods

We used a spatially explicit individual-based stochastic model of population dynamics. The model was developed earlier to investigate the effects of habitat fragmentation on population persistence (Fahrig 1997, 1998). We extended the model to include roads (compare Schippers et al. 1996). Fig. 9 and 10 show the structure of the model. For subroutines 2, 3, and 4, see Fahrig (1998).
Accordingly, our model has two more parameters than the original model:

- proportion of animals that avoid the road, of those encountering it, ρ;
- proportion of animals that are killed on the road, of those trying to cross it, κ.

During the movement phase, the animals move in a straight line with a dispersal distance between 0 and maximum dispersal distance and with an angle between 0 and 360° chosen randomly (Tab. 1). On its way to the new habitat cell, an animal may encounter a road and has to decide whether or not it wants to cross the road or not. This is done randomly (with probability 1-ρ). When the individual encounters a road and does *not* want to cross it, it moves to the road and then moves a second step away from the road for the remaining part of the dispersal distance (movement direction chosen randomly). On the road, the animals are killed with probability κ.

Figure 9:
Flow diagram of the main routine in the simulation model.



Parameters used in the simulation are given in Tab. 1. All cells were breeding habitat. Throughout the simulations we used reflecting boundaries. We chose parameter combinations where we observed an extinction risk slightly greater than 0 when there was no road present because we are especially interested in the effects of roads on species that already have some extinction risk, e.g., endangered species. We conducted 500 runs for each parameter combination, a total of 60500 model simulation runs (and the same for the situation of landscape complementation, see below). We varied both proportion of animals avoiding the road, ρ, and traffic mortality, κ, independently between 0 and 1 in steps of 0.1. The road configuration is shown in Fig. 11.

Figure 10:
Flow diagram of the model subroutine for individual movement.

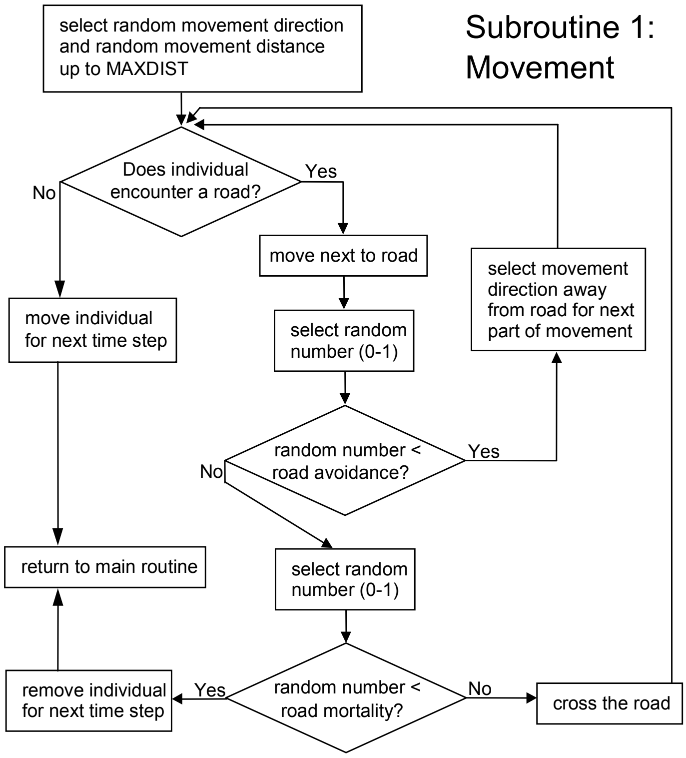
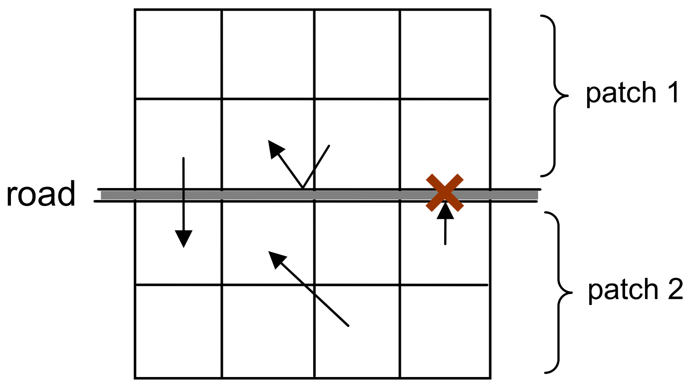


Table 1:
Parameter values in the simulation experiments.

Parameter	Value
Model / landscape size	4 x 4 grid (16 cells)
Starting number of individuals	40
Time steps in simulation	500
Reproduction: mean number of offspring	0.5/individual/time step (Poisson distribution) in breeding habitat cell
Mortality probability in breeding habitat	0.34/individual/timestep
Movement probability in breeding habitat	1.0/individual/timestep
Maximum cell occupancy	5 individuals
Maximum movement distance	1 cell
Movement distance distribution	uniform
Movement direction distribution	uniform
Road avoidance, ρ	varied from 0.0 to 1.0 in steps of 0.1
Traffic mortality, κ	varied from 0.0 to 1.0 in steps of 0.1

Figure 11:
Position of the road in the model runs using a 4x4 grid model. Four examples of movement are indicated by the arrows: movement across the road, avoidance of the road, movement without encountering the road, movement onto the road terminated by traffic mortality.



Results

We recorded both number of individuals in each habitat patch and the time to extinction (in each habitat patch and in total). We also recorded the number of re-colonizations in each patch; and we calculated extinction probability.

Figure 12 shows the effect of traffic mortality and road avoidance on persistence probability when both variables are varied. The situation of $\rho = 0$ and $\kappa = 0$ corresponds to a landscape with no road and leads to the highest persistence probability. Traffic mortality alone has a much stronger effect on persistence probability than road avoidance alone.

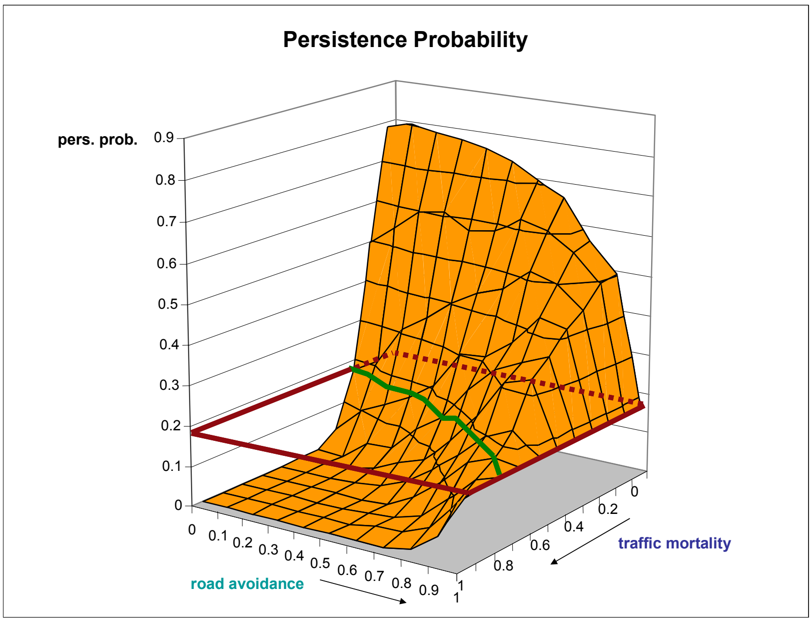


Figure 12:
Persistence probability as a function of road avoidance, ρ, and road mortality, κ, based on 500 runs for each parameter combination (500 time steps). The red frame corresponds to the effect of fences. The green line is the resulting fence threshold line; see Fig. 13. Parameter values are given in Table 1.

In the range of κ between 0.1 and 0.7 there is an optimal level of road avoidance for persistence. The higher traffic mortality is the higher is the predicted optimal degree of road avoidance.

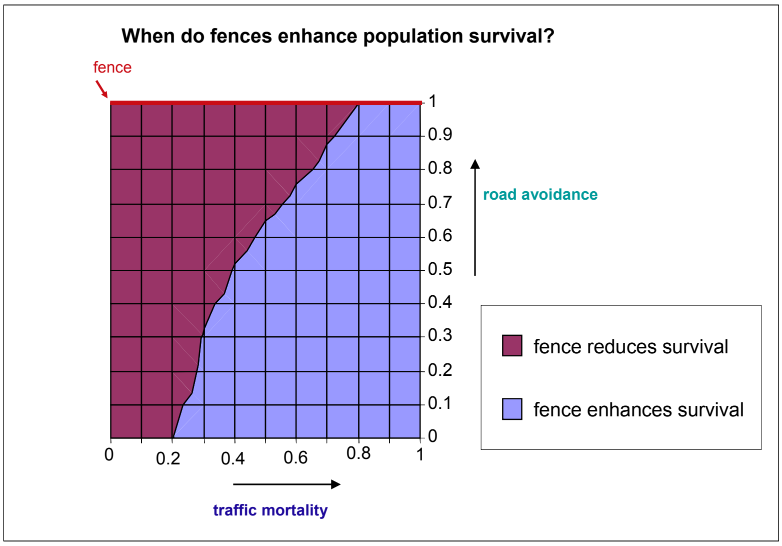
Road mortality always decreases persistence time, but higher road avoidance leads to longer extinction times in most cases (not shown in Fig. 12; see Jaeger and Fahrig, subm.). A high degree of road avoidance can compensate for a high magnitude of road mortality. This is true for extinction time only but not for persistence probability.

Effect of fences

For road avoidance = 100%, the probability of persistence is independent of κ because no animals venture onto the road any more. This is the persistence probability that corresponds with a fence; shown in red in Fig. 12.

In our model simulations, survival probability for the situation with fences was 18.5% (Fig. 12). Therefore, adding a fence will increase population persistence whenever the expected persistence level without a fence (for a given combination of ρ and κ) is below 18.5%. This corresponds to the intersection of the 3D-surface of persistence probability in Fig. 12 with the plane parallel to the diagram floor at persistence probability = 18.5% (red frame in Fig. 12). Figure 13 shows the resulting fence threshold line, which determines the range of (ρ, κ)-values within which adding a fence would increase or decrease persistence.

Figure 13:
Illustration of the fence threshold line. The threshold separates situations where fences on both sides of the road are predicted to reduce vs. enhance population persistence. The dark red areas (at low values of κ) indicate that a fence would reduce persistence probability. The light lilac area (high values of κ) are situations in which a fence would improve population persistence.



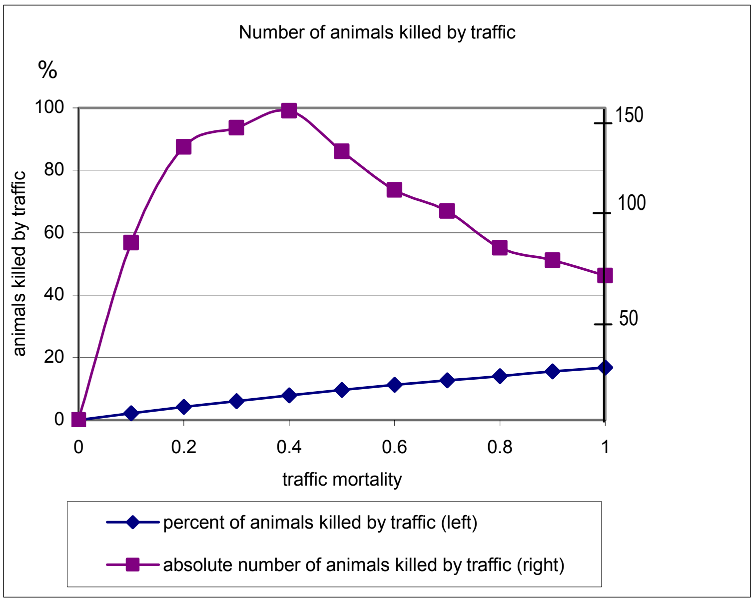
The average extinction time in case of a fence, for those runs where the population went extinct, is 235 time steps as opposed to 38 time steps in the situation with $\kappa = 1$ and no road avoidance. Note that when road mortality is higher than 0.8 we do not need to know what the degree of road avoidance is for the decision about fencing because a fence enhances persistence probability in any case, i.e., a fence can be a useful measure for a couple of years until a more effective mitigation measure will have been realized. However, in the model runs when there was a fence and the population survived, a sub-population of one side of the road went extinct quite often. This occurred in 93% of these runs. Such events are equivalent to a 50% loss of habitat because the habitat patches are isolated and cannot be re-colonized. Since the amount of habitat is reduced to 50% of its potential amount, the population has a high probability of extinction in the near future.

If road mortality is lower than 0.2 we do not need to know the degree of road avoidance because a fence would always reduce population persistence. If road mortality is between these values the suitability of fences depends on the degree of road avoidance.

We define the critical value of road mortality, κ_c, by the condition that persistence probability is the same as if there was a fence (Fig. 13). The value of κ_c depends on the degree of road avoidance. If road avoidance is low then the critical value of road mortality is lower than for high degrees of road avoidance. For low degrees of road avoidance, an increase of road avoidance does change the critical value of road mortality only slightly, but at higher values, an increase of road avoidance has a strong influence on the critical value of road mortality.

Road mortality doesn't have to contribute a large proportion to overall mortality to be detrimental for population persistence. In our model runs with $\rho = 0.4$, population persistence was reduced by more than 50% when road mortality had a share of only 5% of overall mortality and by more than 90% when road mortality had a share of 10% of overall mortality (Fig. 14).

Figure 14:
Number of animals killed by traffic in percent of overall mortality (traffic fatalities and natural deaths) when the degree of road avoidance was 0.4 and traffic mortality, κ, was varied from 0 to 1. When the population had zero probability of persistence (i.e., for $\kappa > 0.65$, see Fig. 12) the proportion of animals killed by vehicles was between 12% and 17%.



Landscape complementation

When the animals need access to resources on both sides of the road (Fig. 15) the effects of both road avoidance and traffic mortality are more severe. The results are shown in Fig. 16. When the other side of the road is inaccessible the population always goes extinct. A fence is no mitigation.

Figure 15:
Position of the road in the case of landscape complementation. The animals need access to both breeding habitat and feeding habitat.

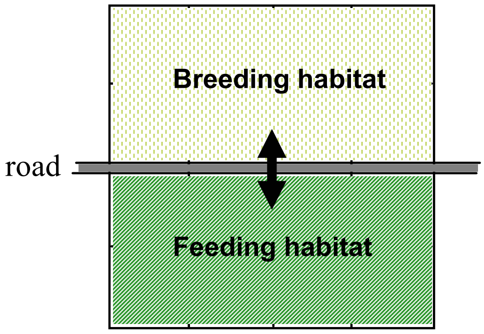
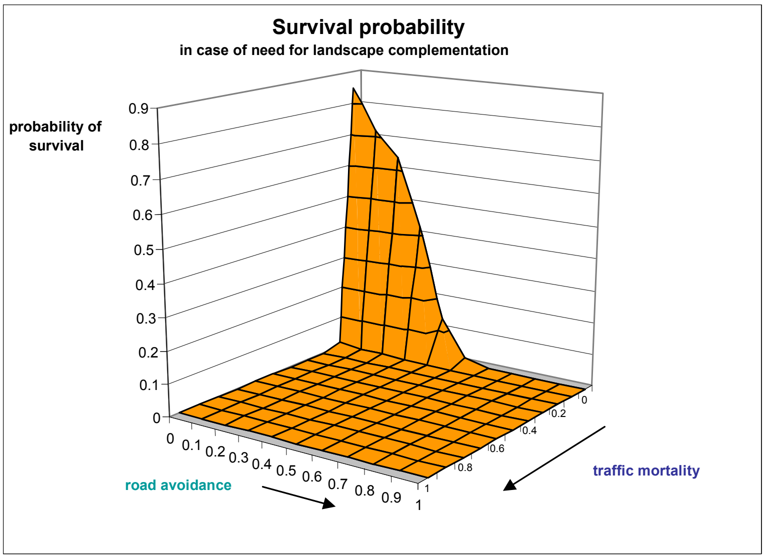


Figure 16:
Persistence probability in the case of landscape complementation (see Fig. 15). Probability of population persistence is shown as a function of road avoidance, ρ, and road mortality, κ, based on 500 runs for each parameter combination (500 time steps).



Discussion

Our objective was to characterize the conditions under which the use of fences provides an advantage for the persistence of animal populations. We compared persistence probability for situations without fences with persistence probability for the situation with fences and identified the conditions of when fences enhance population persistence. The conditions are characterized by two factors: traffic mortality, κ, understood as the proportion of animals killed on the road, of those that attempt to cross, and the degree of road avoidance, ρ, i.e., the proportion of animals avoiding the road when they encounter it.

Note that, in this paper, traffic mortality, κ, is defined as a proportion, of those that attempt to cross, and does not denote the absolute number of animals killed. κ can be inferred from the absolute number of road kill by

$$\kappa = \frac{D}{D + C}$$

where D is the absolute number of animals killed by collisions with vehicles within a certain time span and C is the absolute number of animals that successfully crossed the road within that time span (C can be obtained from telemetry data).

Our results underline that the influence of road mortality can be much stronger and more immediate than the effect of road avoidance. They also indicate that small populations can be reduced by road avoidance and can go extinct as a consequence of a real fence.

Our results suggest that even very low additive mortality can severely limit population size. Gibbs and Shriver (2002) presented model results suggesting that in many regions of the United States more than 5% of land turtles and large pond turtles are likely to die while crossing roads which is more than the populations can sustain. Other studies have shown that most turtle species cannot withstand death rate increases of more that 2-3% (cited by Gibbs & Shriver 2002: 1649). Accordingly, land areas with > 1 km of roads/km^2 with traffic volumes of > 100 vehicles/lane/day, which characterize many of the eastern and central regions of the United States, were predicted to be sufficient to contribute excessively to the annual adult mortality rates of land turtles.

The suitability of fences is characterized by a threshold in the combined values of traffic mortality and road avoidance. Our results indicate that, in general, for high traffic mortality and low road avoidance, the use of fences enhances population persistence probability and for low traffic mortality and high road avoidance, fences reduce population persistence. In the zone between these two situations, the suitability of fences depends on both traffic mortality and road avoidance. The higher traffic mortality, κ, the higher is the corresponding critical value of ρ distinguishing whether or not fences are suitable.

It is important to realize that our results are qualitative, not quantitative. Several factors will shift the fence threshold line downwards or upwards by affecting how often animals will encounter roads. This implies that the threshold line (Fig. 13) will be different for different species and even for the same species in different landscapes with different amounts of roads; see the discussion in Jaeger and Fahrig (subm.).

Mechanisms that may enhance the effect of road avoidance include inbreeding effects in smaller populations, and the Allee effect, i.e., reduced per capita growth rate at low population density, e.g., Hanski (1999: 31f), including difficulties in finding mates, unbalanced sex ratios in smaller populations. These mechanisms should be tested independently in future model simulations. If several of them apply at the same time, the effect of road avoidance might be much more important. However, a strong argument supporting our results is related to the concept of effective population size (e.g., Lande and Barrowclough 1987). This means that the mechanisms mentioned above correspond to an effective population size that is lower than what would be indicated by the number of individuals. Therefore, our result with regard to the question of when we would observe an effect of road avoidance will change quantitatively but not qualitatively.

Further issues that may have an influence on the results concern mechanisms that buffer the effect of road mortality and the choice of model characteristics. In some populations, birth rate may be density dependent. An increase of birth rate (as a reaction to reduced population density) may partly compensate for road mortality. However, this can only occur when birth rate is not at its maximum possible value. Endangered species may be already at a low population density, so their birth rate would probably not increase but dwindle when the population size further decreases (Allee effect).

In our simulations, breeding habitat was everywhere. Therefore, wherever the individuals move to (whether or not they cross the road), they always find breeding habitat. This is different from the study by Fahrig (1997, 1998), where breeding habitat was fragmented. In her study, fragmentation of breeding habitat curtailed population growth by a reduction of both reproductive and survival rates because more individuals move into non-breeding habitat where survival rate is lower and the animals cannot reproduce.

An increasing degree of road avoidance makes the dynamics of the two adjacent patches more and more independent until they are isolated (enhanced extinction risk in smaller populations due to demographic stochasticity). If two patches are connected, their populations can survive even if each of them becomes extinct from time to time, because the connections provide for re-colonization.

Our model results indicate that the time lag of road effects can be rather long. Therefore, effects after building a road may only be visible after tens of years, as discussed by Findlay and Bourdages (2000). According to our results, the time lag for the effect of road avoidance is greater than for road mortality.

Recommendations for the use of fences

According to the results of this study, we suggest the following general hierarchy of mitigation measures:
1. Remove road,
2. Close road (completely or at certain times),
3. Reduce traffic and build overpasses/underpasses,
4. Use fences in combination with overpasses/underpasses,
5. Use fences (as an interim measure) or do nothing, depending on the degree of road avoidance and traffic mortality (see below).

In many cases, fences can be better than nothing but, ultimately, crossings are required. Fences can be useful as an interim measure that, even though they also have a negative impact, prolong the time to extinction. The result that the population on one side of the road went extinct with a high probability underlines the need for overpasses or underpasses to allow for re-colonization.

We propose the following rules of thumb for the use of fences:
1. 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 mortality plays an important role in the population decline then fences are very likely to be a useful measure to reduce traffic mortality and slow down population decline.
   - On the other hand, if population size is stable or increasing and there is evidence that some animals are successfully crossing the road adding fences could be harmful.
   - 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.

   When none of the abovementioned information is available for the species of concern, fences should be used in combination with wildlife crossing structures (Groot Bruinderink & Hazebroek 1996).
2. For a road in the planning stages:
   - If the species of concern does not show any road or traffic avoidance behavior (e.g., noise avoidance, road surface avoidance, or car avoidance, see Jaeger et al. *in prep.*), mortality due to traffic collisions is expected to be high. Thus, fences should be included in the road construction plan even though it may only be useful as an

interim measure. This necessitates a study to investigate whether or not the animals show some degree of road avoidance. 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 are beneficial.

- In the case that there is no information about the species of concern available there is no general rule for the use of fences. It may be equally harmful to not put fences along the road when they should, or to put fences when they should not. In this case, fences should be used in combination with crossing structures. Reducing traffic amount, however, should always be beneficial (see above).

Note that these recommendations apply only if the species of concern do not require access to resources on eboth sides of the road (i.e., in the case of landscape complementation, see above).

Figure 17:
Comparison of mitigation measures in the diagram of population persistence (modified after Jaeger and Fahrig, subm.).

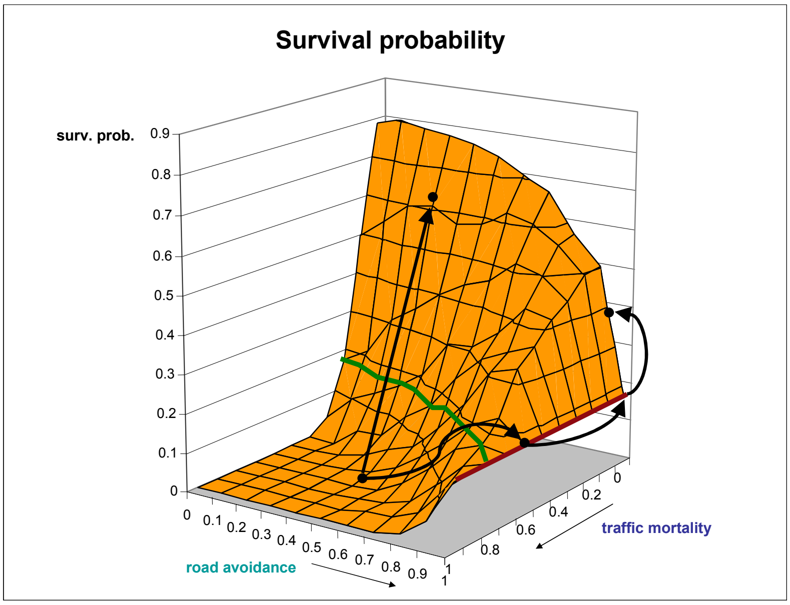
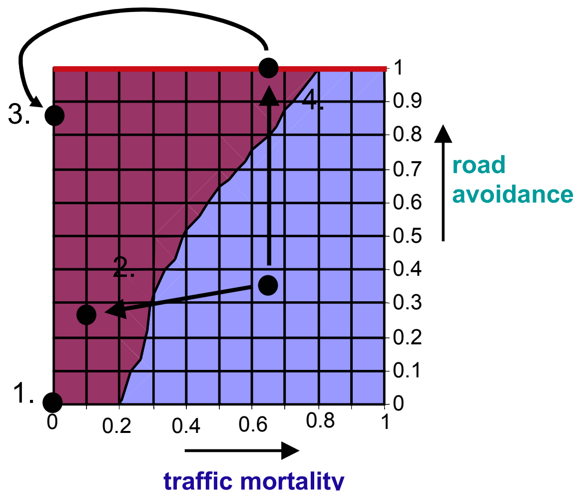


Figure 18:
Comparison of mitigation measures in the fence threshold diagram (modified after Jaeger and Fahrig, subm.). 1 = remove road, 2 = reduce traffic and build overpasses/underpasses, 3 = use fences in combination with overpasses/underpasses, 4 = use fences.



Finally, it is important to remember that traffic mortality and the degree of road avoidance depend on traffic amount; both increase when traffic amount increases. In addition, they will depend on the speed on the vehicles (Allen and McCullough 1976, Bertwistle 1999, Case 1978, Frank et al. 2002, Hels & Buchwald 2001, Hubbard et al. 2000, Hummel 2001, McCaffery 1973, Science 2002) and on the number and location of crossing structures. Reducing traffic amount and speed and adding crossing structures will reduce ρ and κ for this stretch of the road and, therefore, the negative effects of the road on persistence probability will be reduced (Fig. 17 and 18). Reducing traffic amount and traffic speed may obviate the need for fencing and crossing structures.

Outlook

The next step of our work will include a comparison of different spatial configurations of transportation networks in the landscape. The question is whether or not different spatial arrangements of the same amount of traffic lines (e.g., 'bundling' of traffic lines) have different consequences for the effects of both road avoidance and road mortality as well as for their relative importance. The results are expected to have important consequences for the conditions under which fences would be advantageous.

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