

MODELING THE EFFECTS OF ROAD NETWORK PATTERNS ON POPULATION PERSISTENCE: RELATIVE IMPORTANCE OF TRAFFIC MORTALITY AND 'FENCE EFFECT'

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Abstract: Roads affect animals in three adverse ways. They act as barriers to movement ('fence effect'), enhance mortality due to collisions with traffic, and decrease habitat size. We study the relative importance of the first two effects using a spatially explicit individual-based model of population dynamics. We discuss our results with respect to the suitability of fences along roads as a measure to reduce road mortality. The results reveal a much stronger effect of road mortality than of the 'fence effect'; the influence of traffic mortality is always much more significant when the proportions of individuals avoiding the road and those that are killed on the road (in relation to the number of individuals encountering roads) in the two situations compared are the same. The results indicate that putting up fences along roads might be a useful interim mitigation measure until more suitable measures will be applied. However, fences must be used with caution because they could increase extinction risk for species that have large area requirements and small population sizes. In the second part of this paper, we outline a comparison of different configurations of road networks. We ask if different spatial arrangements of the same amount of roads (e.g., 'bundling' of roads) have consequences for the strength of both the 'fence effect' and road mortality. The model results indicate longer times to extinction in case of a 'bundling' of roads but the proportion of populations going extinct within 500 time steps does not change significantly.

Introduction

Should we put up fences along roads?

Nature conservationists, traffic planners, and landscape planners are increasingly concerned about the effects of roads on animal populations (e.g., Canters 1997, Glitzner et al. 1999, Trombulak and Frissell 2000, Lodé 2000). The discussion of the pros and cons of available mitigation measures includes the question of whether fences are a suitable measure to reduce traffic mortality due to collisions with vehicles.

Much data have been collected about absolute numbers of road kill (Trombulak and Frissell 2000, Knutson 1987). However, very few data are available on the proportion of animals killed related to total mortality. Such data exist for very few species; among these are otters in Eastern Germany (Stubbe et al. 1993) and hedgehogs in the Netherlands (Huijser and Bergers 2000).

The question arises as to whether fences along roads would be a helpful measure to prevent the animals from venturing onto the road even if we don't know how many individuals of a population are killed on roads in relation to total mortality in that population. On the other hand, fences would make road crossings impossible and lead to a complete separation of the habitats on either side of the road. 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. (*in press*). Currently, the use of fences is the subject of great controversy in traffic planning institutions and nature conservationists. Therefore, we wanted to compare the relative importance of both effects, isolation (the 'fence effect' of a road) and traffic mortality, in a simulation model.

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 present the results of our computer simulations and to outline the framework of which these simulations are a part. We address the following questions:

- Under what conditions is a fence expected to be harmful to population persistence?
- When does the 'fence effect' (due to road avoidance) have a recognizable effect on population density and persistence?
- What is the relative importance of the 'fence effect' and road mortality?

The larger project aims not only to examine the effects of a single road but also to compare different road network patterns with respect to their effects on population density and landscape connectivity. In addition, the project will develop a method to describe landscape connectivity as a function of network indices and species characteristics and to rank different road network patterns according to their predicted effects on landscape connectivity and population density and persistence.

Expectations about a road's 'fence effect' and traffic mortality

Research questions

Roads influence animal populations in three different ways (e.g., Jaeger et al., *in prep.*): (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 ('fence effect'). As the notion of the "barrier effect" means reduction of movements across the road and includes both road avoidance behavior and traffic collisions, we prefer the notion 'fence effect' as used by Krebs et al. (1969) and Krebs (1996). 'Fence effect' denotes the effect that animals encountering a road don't try to cross it and, therefore, are separated from the habitats on the other side of the road. We describe traffic mortality and 'fence effect' by the two variables ρ for the degree of road avoidance and κ for the proportion of animals killed on the road (Fig. 1).

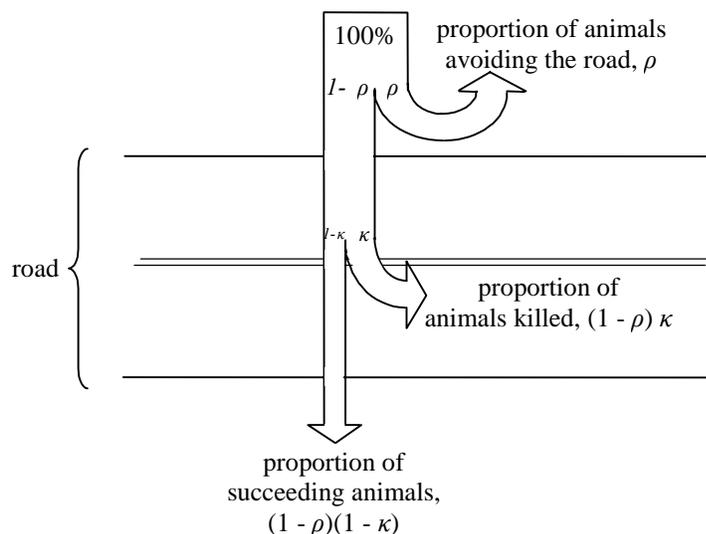


Fig. 1. The degree of road avoidance, ρ , and the proportion of animals killed on the road, κ , are specified independently of each other between 0 and 1.

Both range between 0 and 1. Barrier strength, β , denotes the sum of both effects and ranges from 0 to 1 as well. Note that 'fence effect' denotes the effect of a road (with ρ between 0 and 1) and should not be confused with 'effect of a fence' (with $\rho = 1$). Putting up fences reduces the proportion of animals killed but substantially enhances ρ , i.e., it enhances the 'fence effect' to its maximum. We investigate the following research questions:

- At which values of road avoidance would we expect to observe an effect of road avoidance ('fence effect') alone on population density and persistence?

- At which values of traffic mortality would we expect to see an effect of traffic mortality alone on population density and persistence?
- Which one is more important?
- Under what conditions would we expect a mitigation of traffic mortality by putting up a fence?
- When would we expect an aggravation due to the fence?

What would we expect?

Theoretical considerations show that, in principle, both cases are possible (mitigation or intensification due to a fence), 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 assumed to be constant, we expect to obtain a curve like the one in Figure 2. (If road avoidance increases as well, the curve may look different.)

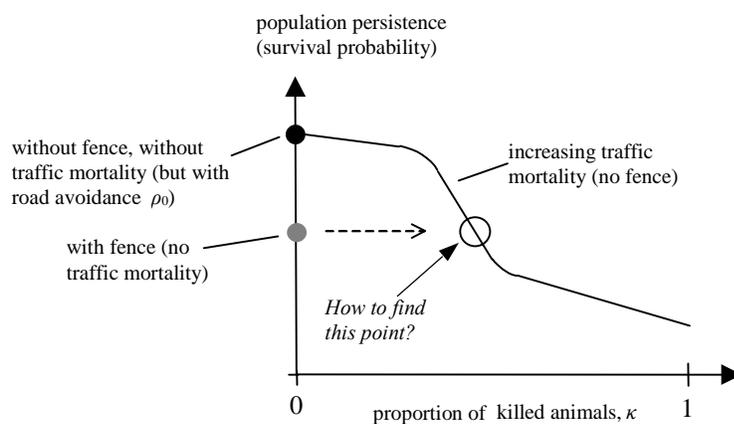


Fig. 2. Expectation for the effect of increasing road mortality, κ , as compared with the effect of a fence. At some value of κ , the curve for population persistence (as a function of traffic mortality) assumes the value of population persistence for putting up a fence. The situation where all animals crossing the road are killed is always worse than the effect of a fence (the animals return but are not killed).

At what values of κ does a fence act as a mitigation, i.e., when is population persistence higher for the situation with a fence than for the situation without the fence? We expect the fence to always reduce population persistence (as opposed to no fence and no traffic mortality) because of three closely related mechanisms:

- Separation of a population into smaller sub-populations: smaller populations have higher demographic stochasticity and, therefore, a higher extinction risk. In general, this can not be compensated for by a *larger number* of (small) populations because of the following two mechanisms.
- Lack of re-colonizations of empty habitats where the former population has gone extinct: this results in the loss of habitat because habitat that cannot be accessed is not inhabitable.
- Lack of density-dependent dispersal (for population regulation): missing the option of leaving the present habitat when the population has grown to carrying capacity. This means that the population in this particular habitat cannot grow any further because of a lack of balancing between (temporarily) growing and declining populations.

There are more mechanisms that explain why the isolation of habitats can be harmful for the persistence of animal populations (see the discussion), but we focus on these three mechanisms in the model used in this study.

A given probability of traffic mortality is always worse than the same probability of not crossing the road because when an animal is killed is also does not cross the road (i.e., two effects). Therefore, the curve for population persistence as a function of traffic mortality eventually has to go below the value for the fence (Fig.

2). Fig. 3 (a) and (b) show the situations that are possible. Either the fence reduces population persistence to a value > 0 , or the fence reduces the population persistence to 0 (and the curve goes down to the x -axis).

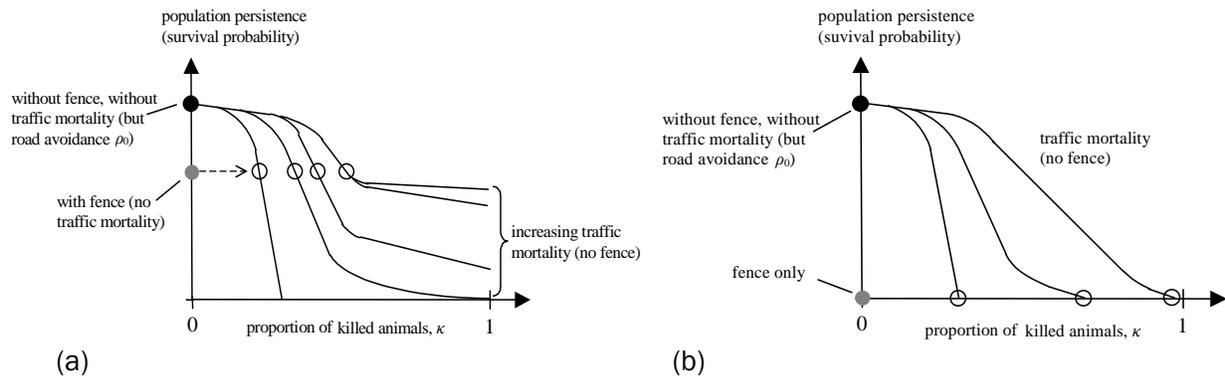


Fig. 3. Scenarios that can occur: (a) Possible scenarios if the fence alone does not lead to a 100% extinction risk. (b) Possible scenarios if putting up the fence ($\rho = 1$) leads to a 100% probability of extinction of the population: the points of intersection on the x -axis. In this case, the curve will go 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 animals would be better off with a fence. However, there is also a section with lower values of κ where the influence of the fence on the population is more adverse than the traffic mortality. This leads us to the question: At what magnitude of road mortality is a fence expected to be advantageous?

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 and different kinds of animal behavior at the roads during the movement phase (cmp. Schippers et al. 1996). Fig. 4 and 5 show the structure of the model. For subroutines 2, 3, and 4, see Fahrig (1998).

Accordingly, our model has three more parameters than the original GRID model:

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

The 'barrier effect' with barrier strength β includes 'fence effect' and road mortality. The barrier strength, β , describes the reduction of successful movements across the road ($\beta = \rho + \kappa - \rho \cdot \kappa$).

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. On its way to the new habitat cell, an animal may encounter a road and a decision is necessary if it wants to cross the road or not. This is done randomly with probability $(1-\rho)$. Three different types of behavior at the road are available when the individual encounters a road and does *not* want to cross it:

- it stops at the road and waits for the next round of movement;
- it moves along the road for the remaining portion of the dispersal distance;
- it goes to the road and tries to move a second step away from the road with the remaining part of the dispersal distance.

On the road, the animals are killed with probability κ .

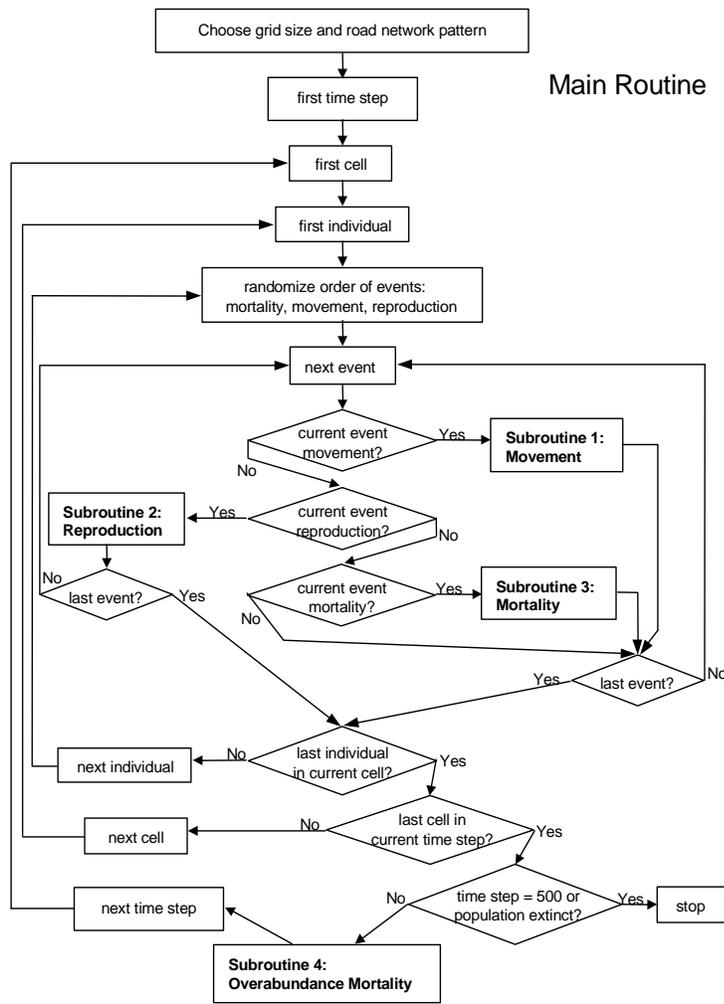


Fig. 4. Flow diagram of the main routine in the simulation model.

If the dispersal path would require an animal to cross more than one road the animal decides if it wants to cross the road or not for each road separately. If it once decides to avoid a road it will avoid all the other roads it encounters during this round of movement as well (not shown in Fig. 5).

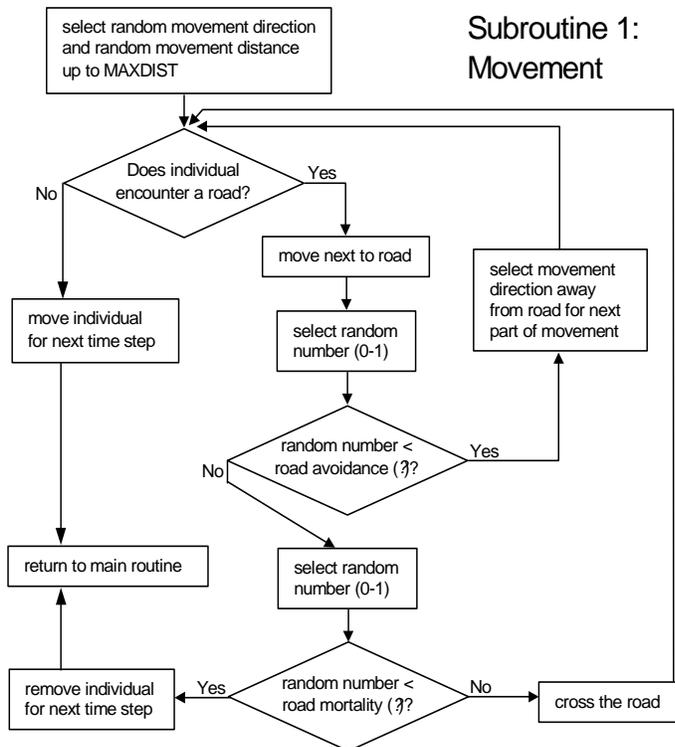


Fig. 5. Flow diagram of the model subroutine for individual movement.

Parameters used in the simulation are given in Tab. 1. All cells were breeding habitat. In the 25x25 grids we applied the results of Bowman et al. (*in press*) for the dispersal distances. Throughout the simulations we used reflecting boundaries and movement type (3) at the road, i.e., moving away from the road (at any angle chosen randomly) for the remaining part of the dispersal distance. We chose parameter combinations where we would observe an extinction risk slightly higher than 0 when there is no road present because we are especially interested in the effects of additional roads on species that already have some extinction risk, e.g., endangered species. We then conducted 1760 model simulation runs with 20 runs for each parameter combination. We varied both proportion of animals avoiding the road, p , and traffic mortality, κ , independently between 0 and 1 in steps of 0.1. Road configurations are shown in Fig. 6 and 7.

Table 1
Parameter values held constant through all simulation experiments

Parameter	Value	
Model / landscape size	4 x 4 grid (16 cells)	25 x 25 grid (625 cells)
Starting number of individuals	40	300
Time steps in simulation	500	500
Reproduction probability (RPROB)	0.5/individual/timestep in breeding habitat cell	0.5/individual/timestep in breeding habitat cell
Mortality probability in breeding habitat	0.35/individual/timestep	0.4/individual/timestep
Movement probability in breeding habitat	1.0/individual/timestep	1.0/individual/timestep
Offspring per reproduction	1	1
Maximum cell occupancy	5 individuals	25 individuals
Maximum movement distance	1 cell	8 cells
Type of movement distance distribution	uniform distribution	exponential distribution (with median movement distance of 1.4 cells)

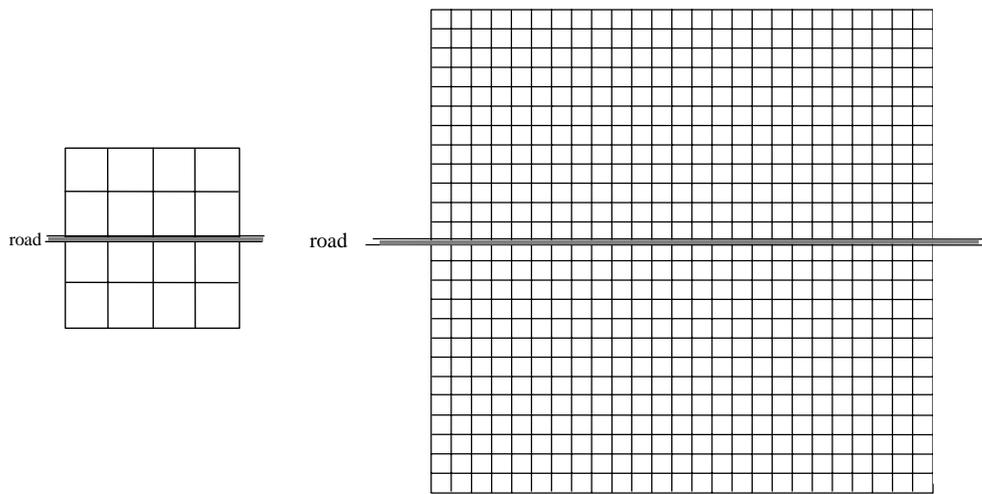


Fig. 6. Positions of the roads in the first series of model runs. (a) 4x4 grid model; (b) 25x25 grid model.

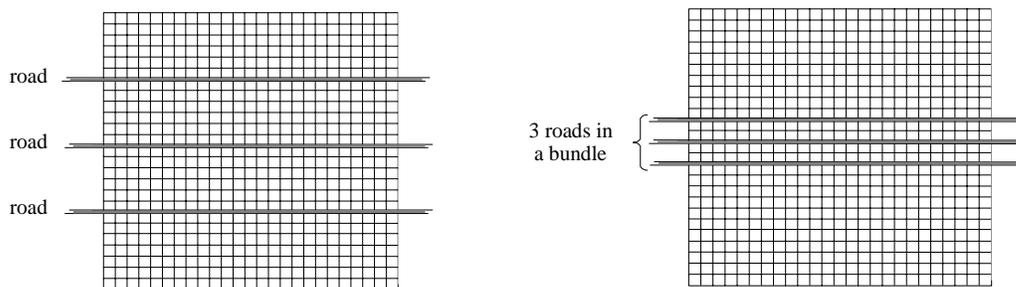


Fig. 7. Positions of the road in the second series of model runs (25x25 grid model). (a) even distribution; (b) bundling of roads.

Results

We recorded both the number of individuals in each habitat patch and in total, and the time to extinction in each habitat patch and in total. We also recorded the number of re-colonizations in each patch as well as the calculated extinction probability.

Small grid (size of 4x4), one road

Figure 8 shows an example of the number of individuals in the two habitat patches in a run of the 4x4 grid model (Fig. 6a). Traffic mortality has a much stronger effect on survival probability than road avoidance (Fig. 9). If κ equals 1, a fence would be better because even though the two habitats would be isolated no animals would be killed any more. However, a fence still would lead to extinction with a probability of 100%. The average extinction time in case of a fence is 230 time steps as opposed to 40 time steps in the situation with $\kappa = 1$. If $\kappa < 0.3$ a fence would be worse, if $\kappa = 0.3$ a fence would be an improvement because the time to extinction would be longer. In this situation, a fence could be a useful measure for a couple of years until a more effective mitigation measure will have been realized.

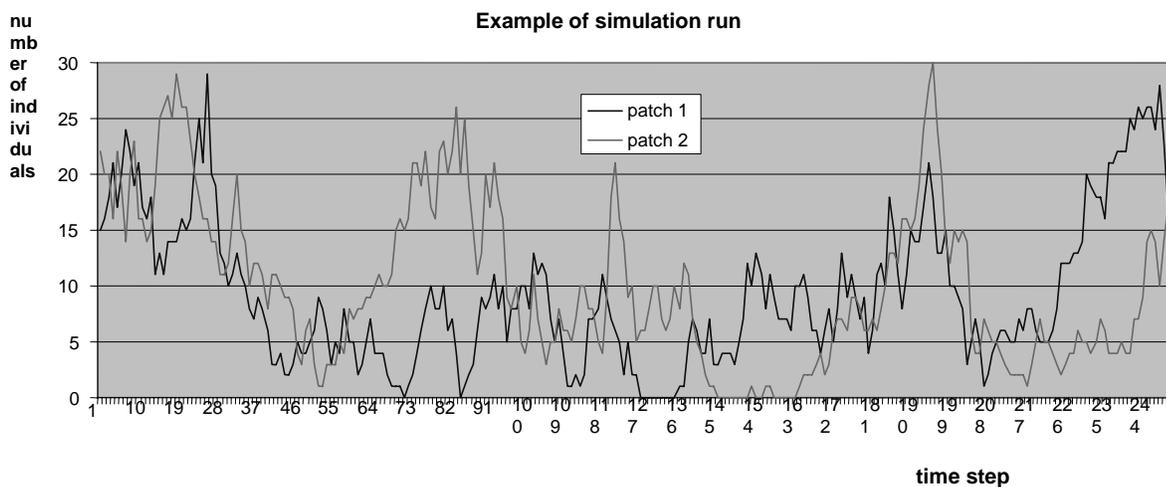
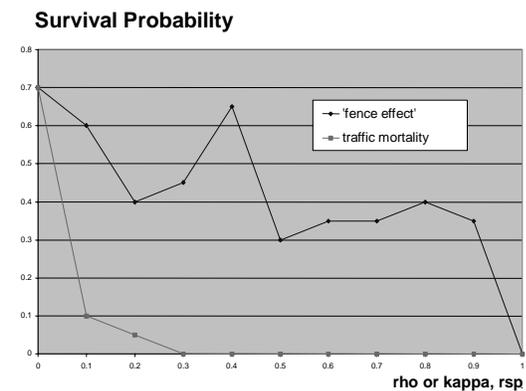
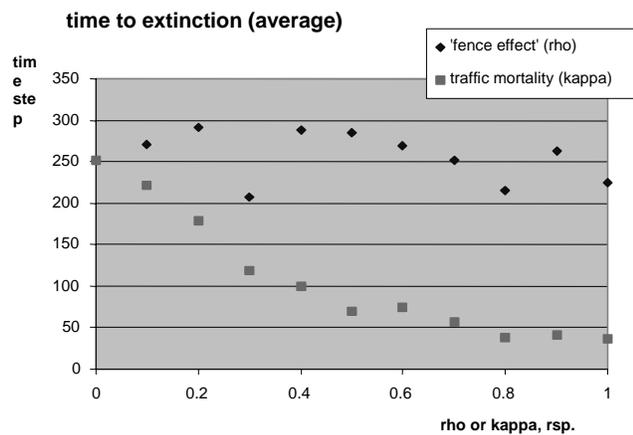


Fig. 8. Example of a simulation run for the 4x4 grid (270 time steps shown) with road avoidance of $\rho = 0.8$ ($\kappa = 0$): 3 re-colonizations in patch 1 and 3 re-colonizations in patch 2 are observed. (Number of individuals after 500 time steps = 30).



(a)

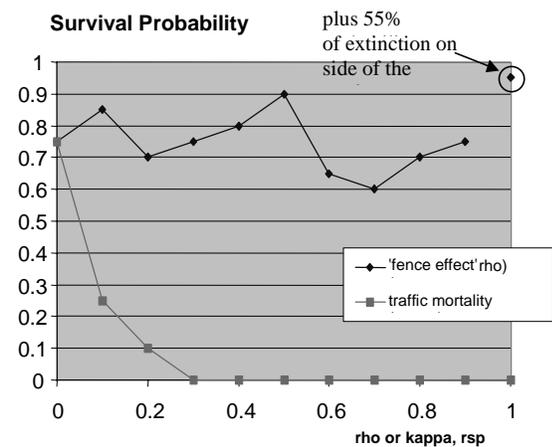


(b)

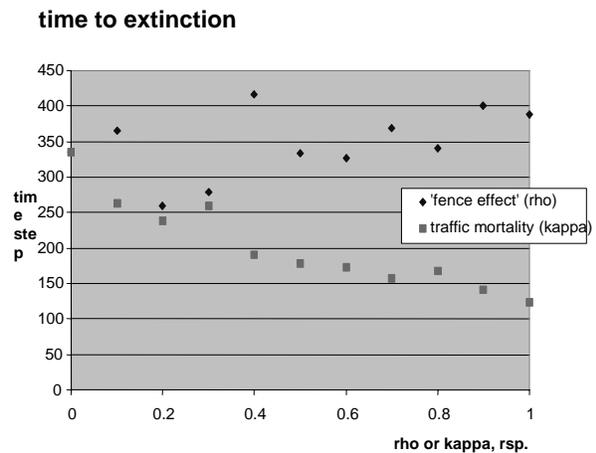
Fig. 9. Results for the relation between road mortality, κ , or road avoidance, ρ , respectively, and (a) survival probability, (b) average extinction times based on the runs that went extinct within the 500 time step limit of the simulations. (4x4 grid with one road; 20 runs for each parameter combination).

Larger grid (size of 25x25), one road

The results are shown in Fig. 10. The effect of traffic mortality on survival probability is very strong whereas the effect of the 'fence effect' is not significant. A fence would lead to higher survival probability than would traffic mortality for almost any value of $\kappa > 0$. However, in 55% of all runs with total road avoidance, the population on one side of the road went extinct. Such an event is equivalent to 50% habitat loss because the habitats are isolated and cannot be re-colonized.



(a)



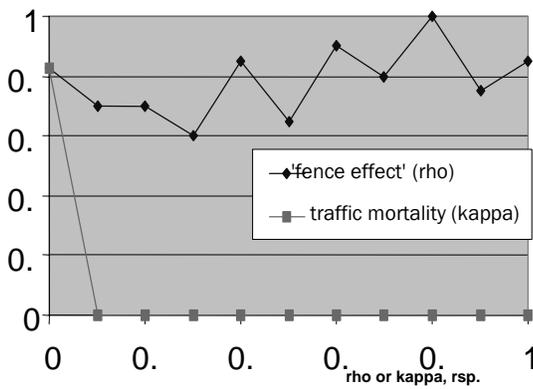
(b)

Fig. 10. Results for the relation between road mortality, κ , or road avoidance, ρ , respectively, and (a) survival probability, (b) average extinction times based on the runs that went extinct within the 500 time step limit of the simulations. (25x25 grid with one road, Fig. 6b; 20 runs for each parameter combination).

Bundling of roads

Next, we conducted a series of simulations with the two patterns shown in Fig. 7 with three roads to compare them with each other and with the results from the previous situation with just one road (Fig. 6). The results are shown in Fig. 11 and 12. They exhibit a stronger effect of traffic mortality than in the situation with one road whereas the 'fence effect' is not significant in either case. As before, a fence would lead to higher survival probability for almost any value of $\kappa > 0$. However, for total road avoidance in case of a uniform distribution of the road, one patch went extinct (or, equivalently, 25% habitat loss) in 15% of all runs, two patches went extinct (50% habitat loss) in 25% of all runs, and three patches went extinct (75% habitat loss) in 45% of all runs. When the roads were bundled in the center, the equivalent habitat loss in case of total road avoidance was 8% in 10% of all runs, 16% in 10% of all runs, and 50% in 35% of all runs (extinction occurred in 40% of all runs). As for traffic mortality, the average time to extinction was higher for the clumped arrangement of the three roads (e.g., twice as high for $0.5 < \kappa < 1.0$) as opposed to the dispersed distribution.

Survival Probability



Time to Extinction (average)

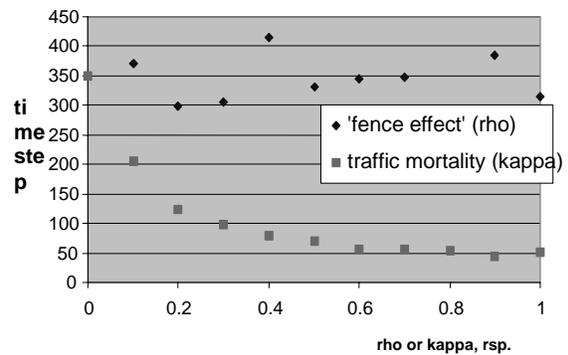
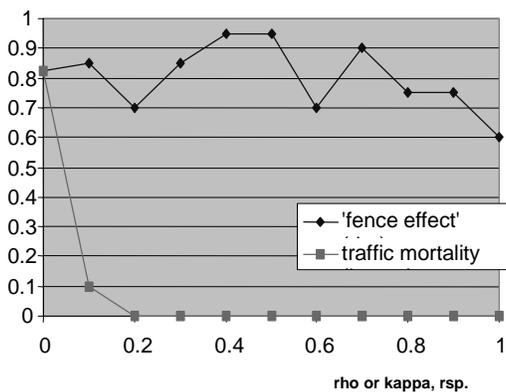


Fig. 11. Results for the relation between road mortality or road avoidance, resp. and (a) survival probability, (b) average extinction times based on the runs that went extinct within the 500 time step limit of the simulations. (25x25 grid with three roads distributed evenly, Fig. 7a).

Survival Probability



time to extinction (average)

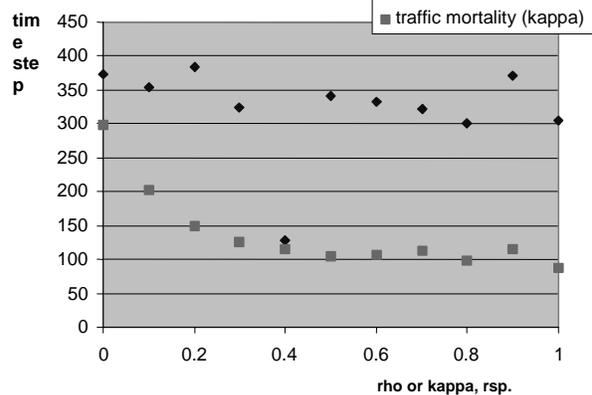


Fig. 12. Results for the relation between road mortality or road avoidance, resp. and (a) survival probability, (b) average extinction times based on the runs that went extinct within the 500 time step limit of the simulations. (25x25 grid with three roads bundled in the center, Fig. 7b).

Discussion

The results underline that the influence of road mortality can be much stronger than the 'fence effect'. Our results also indicate that small populations can be reduced by the 'fence effect' of a road and can go extinct as a consequence of a real fence. We don't know what the values of ρ and κ really are. In case of small populations, the results for the 4x4 grid indicate that a fence would not be a reliable measure if the strength of traffic mortality, κ , is not known. However, the simulation results of the 25x25 grid suggest that, for large, stable populations (that can be seriously affected by traffic mortality), a fence would not be harmful. Therefore, the use of fences seems appropriate if there are no large animals with a small population size around. In dealing with small, endangered populations, we need to know more about the extent of road mortality to be able to decide if a fence would be more harmful or not.

Mechanisms that may enhance the 'fence effect' or decrease the effect of traffic mortality

The 'fence effect' in our model includes enhanced extinction risk in smaller populations due to demographic stochasticity and reduction of re-colonization numbers, as well as reduced regulation of population density due to a reduction of density-dependent dispersal. However, as the individuals in the model act independently of each other, mechanisms such as the process of finding mates or unbalanced sex ratios in small populations are not included. In addition, the individuals in the model don't necessarily stay in the patch that they just have re-colonized. Individuals move in a randomly chosen direction and, therefore, may leave that patch over the next couple of time steps. The individuals don't perceive themselves to be immigrants into an empty habitat in which it would be important (for a higher population persistence) to stay. Therefore, we would expect re-colonization in nature to be more effective than in our model.

Mechanisms that may enhance the 'fence effect' of a road include the need for landscape complementation (e.g., breeding habitat, foraging habitat, and winter habitat), 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 'fence effect' 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 most of the mechanisms mentioned above correspond to an effective population size that is lower than would be indicated by the number of individuals. Therefore, our result with regard to the question of when we would observe a 'fence effect' will change quantitatively but not qualitatively. These changes also could influence the relative importance of the 'fence effect' and road mortality.

Further issues that may have an influence on the results concern mechanisms that might 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 only can occur when birth rate is not at its maximum possible value. (Otherwise we would expect an Allee effect.) 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.

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 Fahrig (1997, 1998), where breeding habitat was fragmented. In her study, fragmentation of breeding habitat curtailed population growth by a reduction in both reproductive and survival rates because more individuals move into non-breeding habitat where survival rate is lower and the animals cannot reproduce. The increasing avoidance of crossing the road (i.e., increasing ρ) makes the dynamics of the two adjacent patches more and more independent of one another until they are isolated. In our model, this is the only cause of the 'fence effect'. For example, if one patch is a sink (e.g., because it has a lower birth rate than death rate), it can be sustained by incoming

individuals from an adjacent source patch. When the avoidance of the road becomes stronger, the sink no longer has enough immigrants and the population will go extinct. (This is not demonstrated in this paper but could be shown in a configuration with a large and a small patch.) A second effect of this mechanism is a lack of re-colonization of empty habitats. If two patches are connected, their populations can survive even if each of

them becomes extinct from time to time, because the connections provides for re-colonizations. If they are separated, their populations will not be re-vitalized once they go extinct.

The model results indicate quite a long time lag of the road effects. Therefore, effects after building a road may not be visible instantly but after tens of years as discussed by Findlay and Bourdages (2000). According to our results, the time lag for the 'fence effect' would be greater than the time delay of road mortality. It would be interesting to add a road at some point in time during a simulation run and investigate the time delay in the model in more detail.

Recommendations

Not all animals have the same value of traffic mortality (κ). Thus, for some species a fence would be advantageous, while for others it is not. It may be good to accept a fence as an interim measure that has a negative impact but does not destroy a population if it saves populations that are on the edge of extinction. In accordance to our results, we propose the following hierarchy of measures:

1. Remove road,
2. Close road (completely or at certain times),
3. Use fences in combination with overpasses/underpasses,
4. Use fences (as an interim measure),
5. Do nothing.

In many cases, fences can be better than nothing but, ultimately, crossings are required. The result that the population on one side of the road went extinct with a high probability when road avoidance was total ($\rho = 1$) underlines the ultimate need for overpasses and/or underpasses to allow for re-colonization.

A major problem of fences is that they are there all the time (night and day, all year round) and affect all species larger than the mesh size of the fence that move on the ground. Traffic density, however, may vary considerably over time, and the animals might be able to cross successfully at certain times (low traffic periods) if there is no fence.

Because of the issues discussed above, recommending to put up fences along roads everywhere would be precipitate. However, our results indicate that, under certain conditions, a fence could be a very useful provisional measure to slow down the decrease of population density until more effective measures are implemented (if the roads cannot be closed or removed). There are conditions under which putting up fences is worsening the situation for some species. This means that putting up a fence is not generally useful and should not be misunderstood as a means to cushion pangs of conscience. However, under certain conditions that have to be explored in more detail in future studies (modelling and field studies), fences can be helpful for mitigation, e.g., in combination with other measures.

Outlook: network indices and landscape connectivity

In the next steps of our project, we will compare different configurations of road networks to derive landscape connectivity indices based on the effective mesh size, m (Jaeger 2000). The relative importance of 'fence effect' and road mortality may vary with different spatial arrangements of the roads. We describe road patterns, including the amount of traffic and the spatial distribution of the roads, using network indices. We estimate the effects of the road networks on landscape connectivity (Tischendorf and Fahrig 2000, Tischendorf 2001). The results are the basis for describing landscape connectivity as a function of network indices and species characteristics (such as dispersal distance, dispersal rate, reproduction rate, and mortality). This allows us to design ecologically scaled landscape indices (ESLI), as discussed by Vos et al. (2001), to rank different road network patterns. We will discuss the following research questions:

- Which indices are used in transportation science to describe road network patterns?
- Are these indices of any use for predicting the effects of different patterns of roads on landscape connectivity, species persistence, or population density?
- What other indices have a higher predictive value?
- Is it feasible and advantageous to design ecologically scaled landscape indices (ESLI) to predict landscape connectivity, species persistence, and population density? Which indices (network indices or ESLI) are better understood by traffic planners and more likely to be used?
- Can we derive some general rules for an ecologically sustainable design of road patterns?

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List of Illustrations

- Fig. 1: The degree of road avoidance, ρ , and the proportion of animals killed on the road, κ , are specified independently of each other between 0 and 1.
- Fig. 2: Expectation for the effect of increasing road mortality, κ , as compared with the effect of a fence. At some value of κ , the curve for population persistence (as a function of traffic mortality) assumes the value of population persistence for putting up a fence. The situation where all animals crossing the road are killed is always worse than the effect of a fence (the animals return but are not killed).
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Fig 12: Results for the relation between road mortality or road avoidance, resp. and (a) survival probability, (b) average extinction times based on the runs that went extinct within the 500 time step limit of the simulations. (25x25 grid with three roads bundled in the center, Fig. 7b).

Table 1: Parameter values held constant through all simulation experiments