



Modelling the performance of road mitigation strategies: Population effects of permeability for wildlife

Andreas Seiler, Julian Klein, Guillaume Chapron, Edgar van der Grift, Peter Schippers

SAFEROAD
Technical report 3



Conférence Européenne
des Directeurs des Routes
Conference of European
Directors of Roads



CEDR Transnational Road Research Programme Call 2013: Roads and Wildlife

funded by Austria, Denmark, Germany,
Ireland, Norway, Sweden, Netherlands and UK



Conférence Européenne
des Directeurs des Routes
Conference of European
Directors of Roads

SAFEROAD

Safe roads for wildlife and people

Modelling the performance of road mitigation strategies: Population effects of permeability for wildlife

Technical report No. 3
October, 2016

Partners:

Wageningen Environmental Research, Wageningen University and
Research Centre

Swedish University of Agricultural Sciences

Minuartia

Calluna AB

Institute for Natural Resource Conservation, Kiel University

Roughan & O'Donovan Innovative Solutions

Norwegian Institute for Nature Research



CEDR Call 2013: Roads and Wildlife
SAFEROAD
Safe roads for wildlife and people

**Modelling the performance of road mitigation
strategies: Population effects of permeability for
wildlife**

Due date of deliverable: 04/30/2015
Actual submission date: 06/26/2016

Start date of project: 01/05/2014

End date of project: 31/10/2016

Author(s) this deliverable:

Andreas Seiler, Swedish University of Agricultural Sciences, Sweden
Julian Klein, Swedish University of Agricultural Sciences, Sweden
Guillaume Chapron, Swedish University of Agricultural Sciences, Sweden
Edgar van der Grift, Wageningen Environmental Research, The Netherlands
Peter Schippers, Wageningen Environmental Research, The Netherlands

PEB Project Manager:

Lars Nilsson / Anders Sjölund, Swedish Transport Administration

Version: final, 10.2016

Table of contents

Executive summary	i
1 Introduction	1
2 Objectives	3
3 Methods	4
3.1 General approach	4
3.2 Model landscape	6
3.2.1 Generalized version	6
3.2.2 Realistic version	8
3.3 Model routines	9
3.3.1 Population routine	9
3.3.2 Permeability routine	9
3.4 Species characteristics	13
3.4.1 Behavioural responses to traffic	13
3.4.2 Life history	15
3.4.3 Simulated profiles	16
3.5 Model scenarios	18
4 Results	19
4.1 Population growth rates	19
4.2 Local extinction and re-colonization probabilities	21
4.3 Real species examples	24
5 Discussion	26
5.1 General patterns	26
5.2 Genetic effects	26
5.3 Species' characteristics	27
5.4 Implications for mitigation	28
6 Conclusions	30
7 Acknowledgements	31
8 References	32
Annex A: Calculation of Encounter rate E	A.1

Executive summary

Traffic mortality and barrier effects of infrastructure and traffic are recognized impacts of road transportation on wildlife populations. Collisions with larger animals can cause substantial socio-economic losses and human injuries as well as the death of most animals involved. Infrastructure managers have long been asking for effective mitigation of barrier and mortality problems and wondering whether it may be better to invest in fauna passages that provide connectivity but may not effectively reduce collision risks or in fences that prevent mortality but increase barrier effects. Clearly, the correct answer is a combination of both, but at what proportions and at what costs?

We developed a simulation model that combines metapopulation dynamics with road permeability routines to assess the cumulative effect of varying degrees of barriers and passages, traffic and fragmentation on the population viability of selected species. We developed two versions of this model, a generalized version to isolate the generic effects of mortality and isolation; and a more realistic version that can be applied to real-world situations and used in mitigation planning. In this report, we present results from the generalized version only.

The starting point of the model is the definition of the road network and the contiguous areas in between the roads, i.e. its meshes that comprise the habitats of local populations. The severing roads between these local populations are evaluated with respect to their permeability and mortality risk for wildlife. The model assumes that animals migrating between local populations either experience a certain probability of being killed or repelled by traffic or successfully reach the adjacent target patch. These probabilities depend on the species' behavioural response towards traffic and are modified by traffic volume and the proportion of the road that is mitigated by either exclusion fenced or crossing structure, i.e. safe passages. We tested the model on four principally different response profiles, i.e., non-responders, pausers, speeders and avoiders, in a variety of mitigation scenarios.

Effects on metapopulation viability were simulated for different fragmentation scenarios, i.e. different mesh sizes and road densities. In addition, we compared the influence of different life-history strategies, r and K , on the cumulative effect on viability. The results on metapopulation growth rate and local extinction probabilities were averaged over 1000 iterations for each combination of species strategy, response profile and mitigation and fragmentation scenario. The model was also applied to two real species, the moose (*Alces alces*) and the badger (*Meles meles*). Factors were parameterized with reference to empirical data from south-central Sweden.

The results clearly illustrated the significant impact of traffic mortality on population viability, whereas barrier effects were of lesser importance. In all scenarios, 'non-responders' and 'pausers' were the most sensitive response profiles and suffered most from traffic mortality. 'Speeders' and, especially, 'avoiders' were better able to cope with traffic and avoid being killed, but could suffer from barrier effects. As expected, K -strategists, characterized by large home ranges, slow reproduction and small population sizes, were generally more affected by roads and fragmentation than r -strategists, irrespective of their response profile. Thus, the simulated metapopulations were most severely affected in scenarios with high road densities and intermediate traffic volumes. In other words, roads of intermediate size with little mitigation created the most dangerous environment, whereas low degrees of fragmentation and roads with extremely low and high traffic volumes produced much more viable conditions.

These findings suggest that in most circumstances and for most species, mitigation efforts should primarily focus on reducing animal-vehicle collisions. Provisions to restore connectivity should be primarily planned and designed to optimize accident prevention, unless a significant isolation stress on population size makes connectivity measures compulsory. It is also evident that a better understanding of where and when wildlife-vehicle accidents occur and of how species behave in both traffic- and human-dominated environments is essential in developing effective accident-prevention approaches.

1 Introduction

There are a variety of mitigation options to prevent wildlife-vehicle conflicts and reduce the barrier effects of roads (Huijser et al., 2008; Iuell et al., 2003; Putman et al., 2004; van der Ree et al., 2015). Planners ask, however, which set of measures performs best under given local conditions and how much mitigation is needed to comply with the legal requirements and policy objectives. There may be circumstances in which most effort should be made to reduce traffic mortality, while in other cases barrier effects and isolation may be of greater concern. How does this translate into the efficacy, size and number of crossing structures, length of fences and other mitigation measures?

Two overarching objectives for biodiversity in Europe are to keep species at a favourable conservation status and to safeguard biodiversity values and ecosystem services (Helldin et al., 2016). This implies that wildlife populations should be able to maintain a large enough size and exert a large enough exchange of genes and individuals in order to maintain not only viable but thriving populations that produce valuable ecosystem services (Van Der Grift et al., 2016). Roads and traffic directly affect two key factors that drive population viability: mortality and dispersal, i.e. migration between populations (Fahrig, 2003; Forman et al., 2003; Jaeger and Fahrig, 2004). Both factors are intrinsically linked by their effects on population demography but can also partly compensate each other. Barrier effects and traffic mortality may be addressed by complementary types of mitigation (bridges versus fences), but they may also influence each other since mortality contributes to isolation while barrier effects may reduce mortality.

There are thus two critical questions:

1. how strong of a barrier effect (isolation) is acceptable?
2. and how great of a loss of individuals (mortality) can be tolerated in a given area/population/species that is exposed to road development?

Clearly, the answer will depend very much on the local conditions, but there may also be more general patterns that can be linked to the species' ecology and behaviour as well as to road density, road design and traffic. These dependencies can be assessed and simulated in mathematical models that help us to explore potential outcomes and to draw conclusions for mitigation planning (Ascensão et al., 2013; van Langevelde and Jaarsma, 2009).

Studying this empirically is difficult because it requires extensive and long-term monitoring and experimentation (Rytwinski and Fahrig, 2015). Not surprisingly, there is little empirical data on whether wildlife crossing structures effectively restore population connectivity, decrease genetic differentiation and eventually improve population viability (Corlatti et al., 2009). While complete exclusionary fencing of roads will inevitably decrease population connectivity (Jaeger and Fahrig, 2004), it is unclear how more realistic partial fencing affects populations (Ascensão et al., 2013; Huijser et al., 2016). Thus, road and population managers will benefit from an exploration of the relative effect of the fencing and bridging of roads on population demography and viability.

We have developed a connectivity model (PERM) that combines population routines with road permeability routines to assess the cumulative effect of varying degrees of fencing (= barriers), bridging (= crossing structures), traffic volumes (= mortality) and fragmentation on the viability of selected species. We have developed two versions of this model: a generalized version to isolate the generic effects of mortality and isolation irrespective of differences between local populations and between road sections; and a more realistic version that can be applied to real-world situations and be parameterized with case-specific

landscape, road, traffic and wildlife population data. In this report, we present results from the generalized version only. We focused exclusively on the demographic impact of roads and chose not to include genetic effects, but acknowledge that barrier effects can cause genetic drift and differentiation in wildlife populations (Coulon et al., 2006; Holderegger and Di Giulio, 2010; Wilson et al., 2015).

The main questions we addressed were how a change in road network permeability affects population viability and how this effect depends on the level of fragmentation and on the behaviour and life history of the target species. Changes in permeability can be produced by building wildlife crossing structures (providing safe movements) and fences (increased barrier but reduced mortality) and by traffic calming (reduced barrier and mortality). Population viability can be assessed by measuring changes in population growth rates and the risk of local extinctions. Model predictions can be translated into quantitative expectations on, for example, crossing rates, road kills and population sizes; measures that can be validated by monitoring and thus be included in outcome-based specifications for road mitigation projects.

2 Objectives

The objective of this project was to evaluate the combined effects road barriers and traffic mortality on different wildlife species or “profiles”, exhibiting different response behaviours towards vehicles and traffic and showing different life-history strategies. For this, we developed a metapopulation-road permeability model (PERM) that estimated the effects of changes in road design and traffic on population viability in medium-sized to large mammals such as ungulates and carnivores. The results of these estimations will ultimately help to develop better mitigation strategies.

3 Methods

3.1 General approach

PERM is an extended metapopulation model in which the viability of local populations is the result of two model routines (Figure 1): a) an individual-based local population routine that calculates local population growth from the species-specific life-history traits, local area size, and immigration rates, and b) a connectivity routine that estimates the degree of connectivity between adjacent populations based on the effect of traffic mortality, traffic avoidance and the presence of mitigation measures on road permeability for the given species. Both are linked through dispersal since successful emigrants from one population become immigrants in adjacent population. In other words, the population routine calculates an individual's likelihood to disperse and to encounter a boundary road, while the permeability routine calculates the individual's likelihood of successfully immigrating into the adjacent population.

We define local populations as the patches between roads, i.e., the meshes of a closed road network, whereby roads of a certain size or character comprise the patch boundaries. In the following, we use *patch*, *local population* or *mesh* as synonyms. Smaller roads or road segments within the patches are not considered to cause any barrier effect and may only increase the mortality of the local populations in general terms. Traffic volume on boundary roads and the presence of mitigation measures such as fences (barriers) and wildlife passages define the overall permeability of the boundary roads and determine the likelihood of a disperser being repelled, killed or successful in its migration into an adjacent population (Jaeger and Fahrig, 2004). Thus, high permeability will functionally merge local populations, whereas strong boundaries, produced by busy or fenced roads, will cause isolation and/or high mortality.

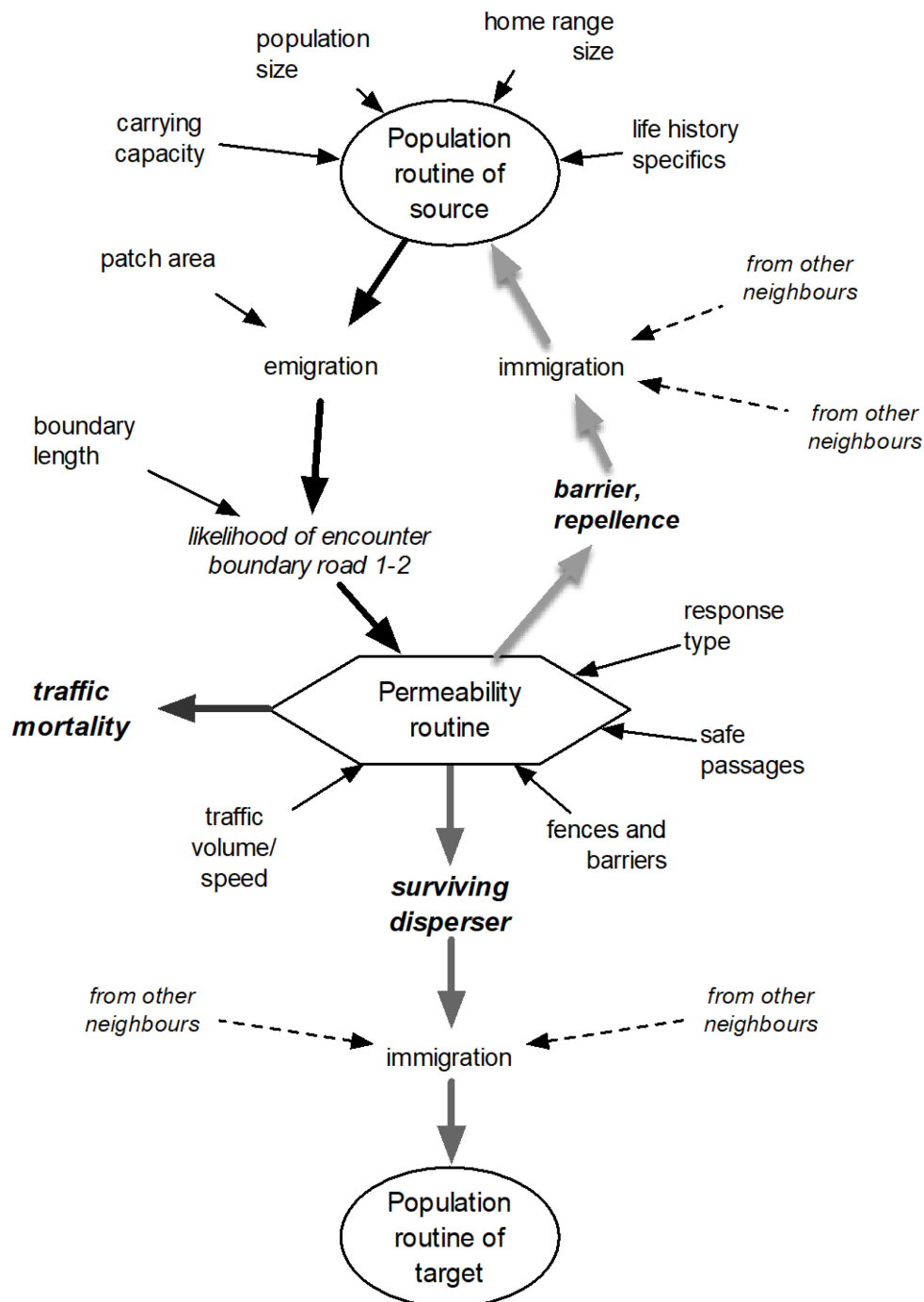


Figure 1. Sketch of the major components and their relationships in the PERM model.

Effects on population viability are measured by:

1. Changes in the growth rate of the entire metapopulation within the simulated timeframe.

2. The averaged probability for any local population to be empty in any given year within the simulated timeframe of 50 years; calculated as the number of years in which a patch is empty divided by all simulation years.

Each of these effects was simulated in a set of scenarios (see below) with respect to:

- the degree of fragmentation (five levels, see Figure 2)
- the species' life-history strategies (K- or r-strategies, see 4.4.2)
- the species' responses to vehicular traffic (see 4.4.1)

PERM was developed in two versions:

- i. Generalized version - a generalized model intended primarily for scientific use that allows for the exploration of general patterns across different species.
- ii. Realistic version - a spatially explicit version that allows for the manual input of empirical data on local populations and roads, which can thus be applied to real- world scenarios.

Both versions share the same programming language and can be rerun and applied by anyone with a basic knowledge of R. The code is written and executed in the open-source software R (R Development Core Team 2015). Graphs were created using the packages *ggplot* (Wickham 2011a), *reshape* (Wickham 2007) and *plyr* (Wickham 2011b).

3.2 Model landscape

3.2.1 Generalized version

The **generalized version** of the model uses a highly simplified landscape with all local populations equally sized and with equal carrying capacities, just like hexagonal cells in a honeycomb. The road network comprises the cell boundaries and runs thus between each cell and its adjacent hexagons. All boundary roads exhibit the same level of permeability; thus changes in road characteristics affect the entire network.

Increased landscape fragmentation caused by the expansion and densification of roads is simulated by splitting the original model landscape into more and smaller hexagons while the overall total area remains the same. This is done in five steps, producing 1, 3, 12, 37 and 91 equally sized hexagons (Figure 2). In order to have realistic dimensions even in the generalized model, we set the size of the entire metapopulation area at 10,000 km², which is about the median size of Swedish counties or a third of the area of Belgium. At the highest level of fragmentation (91 hexagons), local areas are reduced to 110 km², which approximates the average size of meshes within the public road network in south-central Sweden or the median effective mesh size in Europe (Jaeger et al., 2011). Thus, even the smallest area in this model should be large enough to host a small but still viable population of ungulates such as roe deer (*Capreolus capreolus*) or wild boar (*Sus scrofa*). They may, however, not be sufficient to support populations of large carnivores such as wolves (*Canis lupus*) or brown bears (*Ursus arctos*).

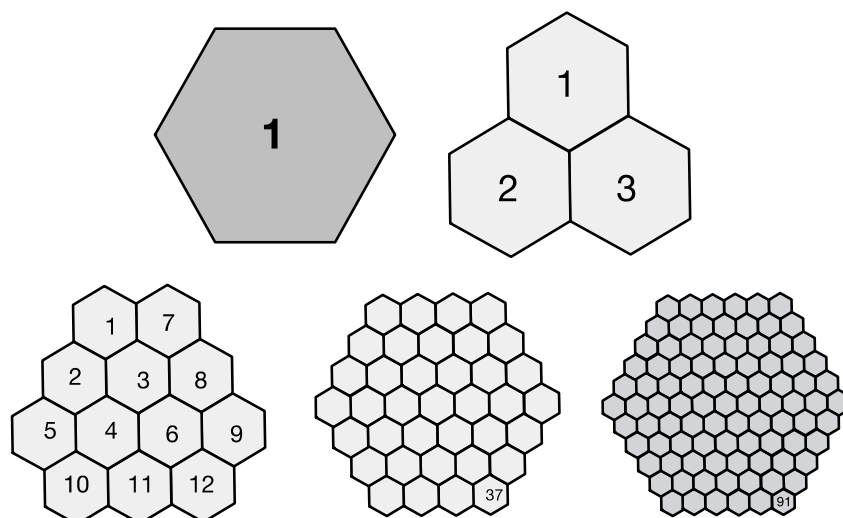
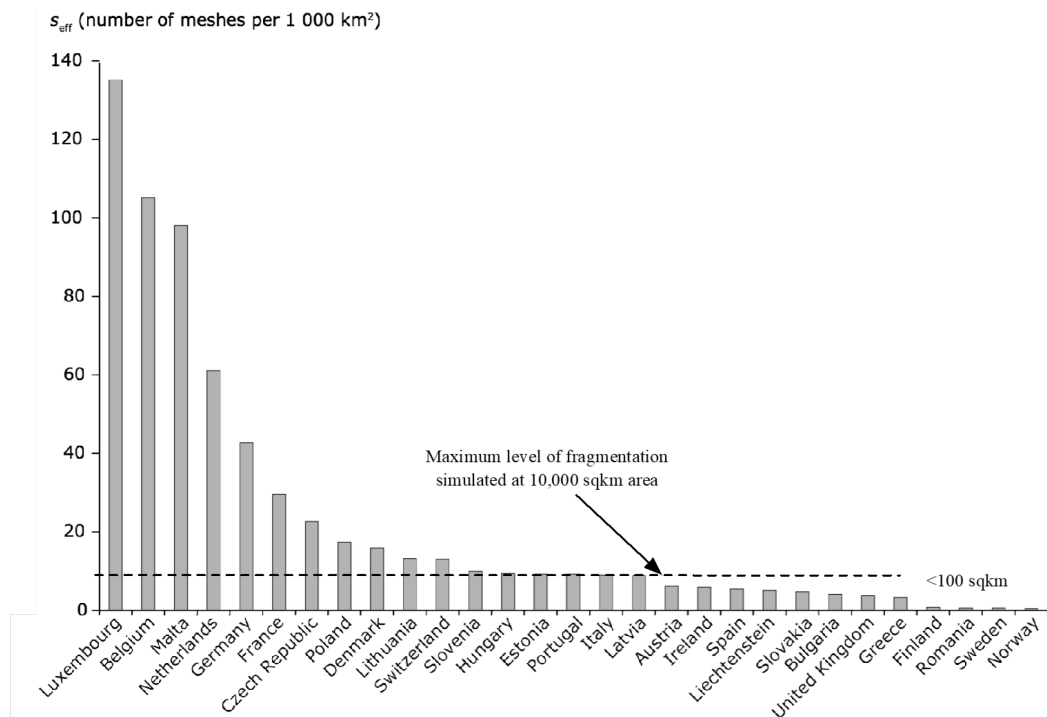


Figure 2. Model landscapes illustrating the placement of local populations represented by hexagons in a honeycomb-like model landscape. Hexagon borders are comprised of roads that separate local populations. An increased level of fragmentation is represented by five model landscapes with the number of cells increasing from 1, 3, 12 and 37 to 91, but the total overall size remains unchanged.



Source: EEA/FOEN 2011 (adapted from Jaeger et al. 2011)

Figure 3. Effective mesh density values in the major road networks per European country in 2009 according to Jaeger et al. 2011. We chose the median mesh size per country ($\approx 100 \text{ km}^2$) as the highest level of fragmentation in our simulation even though this level of fragmentation is still rather low for countries like Luxembourg, Belgium, Malta, Netherlands, Germany or France.

All populations share the same density, sex ratio, age structure, fecundity and dispersal rate. We did not include density-dependence traits or define a carrying capacity for each population because we wanted to focus on the relative effects of permeability on population viability only. The growth rate (λ) of the entire metapopulation in the roadless, unfragmented landscape (scenario 1 in Figure 2) was therefore set at $\lambda \cong 1$.

We further assumed that individuals are homogeneously dispersed with overlapping home ranges within a patch (hexagon). The likelihood of a disperser encountering patch borders and attempting to cross the boundary roads depends on the relation of home range size to patch size as described below. Dispersal was limited to occur only between adjacent populations.

Simulating the effects on metapopulation viability requires some parameterization of the dependencies between mortality, isolation, traffic volume and mitigation measures. We built these parameters from a combination of empirical data and expert opinion mainly representing conditions found in Sweden. However, the particular values should be seen as relative values and do not express any universal standard.

3.2.2 Realistic version

In the **realistic version** of the model, patches, i.e. the meshes in the road network, vary in size and quality (carrying capacity) depending on the overall shape of the road network and the composition of the landscape (Figure 4). Each boundary road has specific dimensions and characteristics of design and traffic that define its permeability. Local populations communicate with a variable number of adjacent neighbours. As in the generalized version, dispersal is limited to occur only between adjacent patches. The realistic version allows for the prediction of changes in population viability resulting from parameter changes in individual boundary roads. However, it was not possible to apply the realistic version to a real-world planning case within scope of the CEDR-Saferoad project.

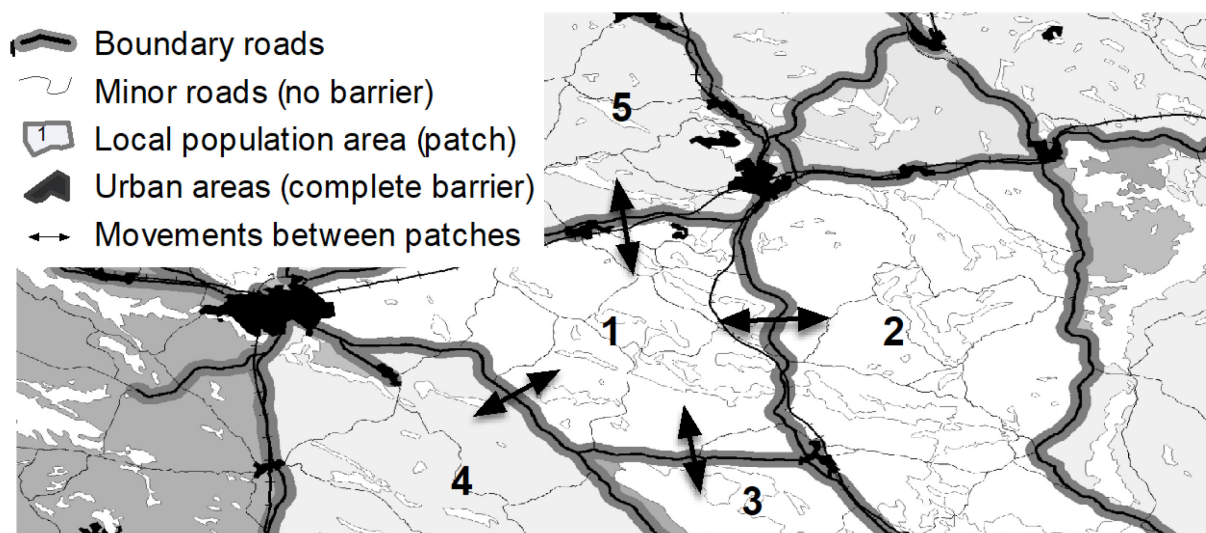


Figure 4. Example of a real-world landscape from southern Sweden that can be used in the realistic version of the model. Boundary roads consist of primary and secondary roads that constitute a closed network with its meshes representing the local population areas. Area sizes in southern Sweden average 28 km² with a range from 1-132 km².

3.3 Model routines

3.3.1 Population routine

Basically, the population routine calculates the likelihood of an individual dispersing and attempting to cross the boundaries of its native patch.

The simulation model for the population routine was developed in the language C (Kernighan and Ritchie, 1978) and uses functions from the Glib library (Wilmet, 2014). It simulates a population of individuals in a landscape organized in patches. The population dynamics emerge from events occurring at the individual level according to biological rules and parameters. All parameters serve as stochastic parameters following probabilities distributions. The random number generator in the model is the *Mersenne-Twister* in R (R Core Team, 2015). The model does not include feedback on parameters, and their values remain constant during simulations. Probabilities are passed as parameters with mean and standard deviations and converted to shape parameters of a binomial distribution through moment matching. Positive rates are also passed as parameters with mean and standard deviations and converted to shape parameters of a Gamma distribution through moment matching (Hobbs and Hooten, 2015). Individuals are characterized by the state variables identity number, living status, age and patch where they are located.

The model proceeds in yearly time steps; each year, the following sequence of events takes place: survival, reproduction, ageing and senescence, movement between patches and density dependence. The survival follows a Bernoulli distribution with a monthly stage-specific survival probability as a parameter. Reproduction is modelled following a Poisson distribution. All animals older than the maximum age are removed. The probability of moving between patches follows a multinomial distribution parameterized with the probabilities of moving. Moreover, the successful outcome of the multinomial draws triggers an additional mortality also modelled as a Bernoulli distribution. Finally, density dependence is implemented by removing all animals in excess of the carrying capacity in each patch. The entire routine is available as the R-package “Population”¹.

Time steps in this model were set at one year during which reproduction and dispersal takes place and individuals age into the next age cohort. Simulations were run over a period of 50 years.

3.3.2 Permeability routine

The connectivity routine, which is the central part of the model, calculates the chance that a disperser encounters a (particular) boundary road of a patch and successfully migrates into the adjacent population. Dispersers that fail will either die in traffic or be repelled by the boundary road and re-enter their native population as immigrants.

3.3.2.1 Dispersal / Migration

All individuals experience a certain probability of dispersal from their native home range in search for a new place to settle down. Some of these dispersers will encounter the patch borders and attempt to migrate into neighbouring patches, while others may only move within their native patch. Given that individuals are homogeneously distributed throughout the patch and have overlapping home ranges, the chance (E) that an individual encounters any patch boundary will be a function of patch area (A) relative to the animal's average home range area (H) that relates to its average dispersal distance (D) as $D = 7\sqrt{H}$ (Bissonette and Adair,

¹ <https://cran.r-project.org/web/packages/population/index.html>

2008b; Bowman et al., 2002). Thus, in patches that are large in comparison to the average dispersal distance, fewer dispersers will face the boundary than in relatively small patches. In other words, if the scale of an animal's area requirements and movements is large compared to the mesh size of the road network (as in the hypothetical K-strategist at high fragmentation levels, see chapter 4.4.3) most individuals will be exposed to road barriers during their dispersal. If the scale is small (such as in the model's r-strategist at low fragmentation levels, see 4.4.3), only a fraction of the dispersing individuals will ever confront roads and be able to migrate to neighbouring patches, while the majority will move only within the native patch.

Also non-dispersing, stationary animals have a certain chance of encountering the road boundaries and being killed in traffic. The smaller the patch size, the greater the loss in stationary animals due to traffic on boundary roads. To estimate this, we calculated the average moving distance in the population (M) as the weighted (x) average of all stationary individuals' home range radius (h) and all dispersing individuals' dispersal distances (D).

$$\text{Eq. 1} \quad M = (1 - x) \sqrt{\frac{H}{\pi}} + x * 7\sqrt{H}$$

3.3.2.2 Encounter rate

The proportion of all dispersers that may encounter a specific boundary road also depends on the relative length of this border (L) compared to the entire patch circumference (C). Thus, on average all individuals in patch/population 1 have a given likelihood of encountering the border to patch 2. In the generalized version, where all patches have the same hexagonal shape, this likelihood is calculated as

$$\text{Eq. 2} \quad E_{12} = \frac{M}{K * \sqrt{A_1}} * \frac{L_{12}}{C_1} \quad \text{or} \quad E_{12} = \frac{(1-x) \sqrt{\frac{H}{\pi}} + x * 7\sqrt{H}}{K * \sqrt{A_1}} * \frac{L_{12}}{C_1}$$

with

$$\text{Eq. 3} \quad K = \sqrt{\frac{(1-\sqrt{0.5})^2}{\pi}} \cong 0.16525$$

3.3.2.3 Permeability

Of all individuals that encounter a given boundary road, only a certain fraction will successfully cross the road: some will be repelled by adverse road features or high traffic volumes ($r(T)$), while others will experience physical barriers and be likewise hindered in moving further (f). In both cases, these individuals are "reflected" back into their native patch (Figure 5).

Of those individuals that continue across the boundary road, some will be killed in traffic ($k(T)$), while others eventually succeed ($s(T)$) into the adjacent patch. These survivors join the new population and reproduce. In the realistic version of the model reproduction is controlled by the population's carrying capacity. If carrying capacity is reached, further immigrants and offspring will die. In the generalized version, carrying capacity is not considered because only the relative effects on metapopulation growth rate are studied.

On open, unmitigated, unprotected road sections (U), repellence ($r(T)$) and mortality ($k(T)$) are considered to be species-specific responses to traffic volume alone (T) (compare 4.4.1). Vehicle speed is not included yet; it is often linked to traffic volume since larger and busier roads tend to allow for higher speed limits. Physical barriers such as fences (F) and safe

passages provided by bridges (B) are characteristics of mitigated, protected roads. The length of these mitigated sections is given as a ratio of the boundary road length. In the generalized version of the model, we define a fenced road section as a complete barrier, although in reality, fence efficacy varies widely with the design of the fence and fence openings, gates and fence length (Elvik et al., 2009; Huijser et al., 2016; Seiler and Olsson, 2015). Reduced fence efficacy can be incorporated into the realistic version model and will translate to a reduction of the length of the fenced road section.

The mitigating effect of bridges can be interpreted from bridge efficacy and species mobility as proposed in Seiler et al. (2015): a bridge can be assumed to alleviate the barrier effect of the road not only at its particular location but even at the distance animals can be expected to travel alongside the barrier to detect the passage. This distance may be assessed from their daily movements and has been suggested to approximate the square root of the species' average home range (H) area (Bissonette and Adair, 2008a). Seiler et al. (2015) proposed to use half of this distance on either side of a passage to assess the effectively mitigated road length. Thus, the length of the effectively bridged and permeable road sections can be defined as $B = e * 0,5\sqrt{H}$. Bridges that are well adapted to the species' requirements and achieve a full mitigation effect ($e = 1$) will maximise the B . Less effective bridges mitigate proportionally shorter distances, and B will be shorter.

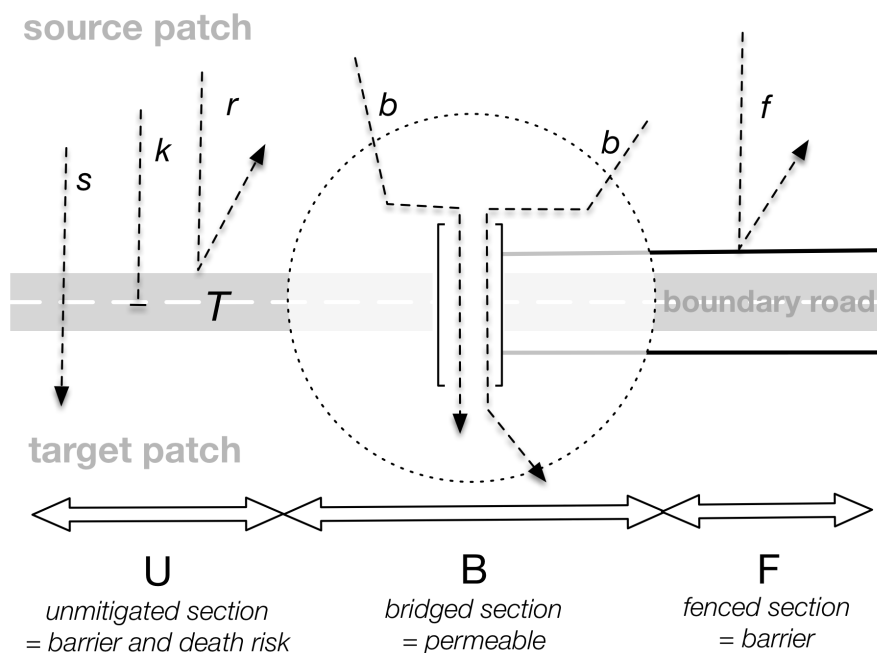


Figure 5. Sketch of the calculation of the permeability of a road separating two populations based on the proportional length of the fenced, bridged and unmitigated sections. Animals moving from the source patch to the target patch experience proportional and species-specific likelihoods of being repelled ($r+f$) or killed (k) or successfully crossing the road ($s+b$) during their migration.

We thus define the permeability (P) of a boundary road as its proportion that is fully permeable:

$$\text{Eq. 4} \quad P = B*b + F*(1-f) + U * (1-k(T) - r(T)) \quad \text{Permeability}$$

with

$$\text{Eq. 5} \quad U = 1-(B*b + F*f)$$

where B is the proportion of the road that is mitigated by safe passages and thus provides full permeability ($b = 1$); F is the proportion of the road fenced, thus providing a full repellence but no mortality ($f = 1$); U is the proportion of the road that is unmitigated and where its permeability is inversely related to the killing (k) and repelling (r) effect of traffic volume (T) (Helldin et al., 2010; Jacobson et al., 2016; Seiler, 2005). B , and consequently also F and U , are dependent on the number, distribution and efficacy of bridges (Seiler et al., 2015). To obtain a given B , one may either install many smaller and less effective passages or a few larger, highly effective passages.

The probability that dispersers encountering a given boundary road are reflected back into their native population is thus:

$$\text{Eq. 6} \quad R = F*(f) + U*r(T) \quad \text{Reflection}$$

while

$$\text{Eq. 7} \quad K = U*k(T) \quad \text{Traffic kill rate}$$

is the probability that dispersers encountering a given boundary road are killed by traffic and

$$\text{Eq. 8} \quad I = B*b + U * (1-k(T) - r(T)) \quad \text{Survival to immigration}$$

is the probability that the dispersers encountering a given boundary road successfully immigrate into the adjacent population. This is practically identical to the measure of permeability above.

3.3.2.4 Connectivity matrix

Based on the above calculations, each boundary road will produce a certain level of connectivity between adjacent patches. These connectivity levels add up to the overall degree of connectedness of an individual patch to all its adjacent neighbours. The more connected a patch, the higher the likelihood for any disperser to migrate to an adjacent patch (Table 1).

We define *connectedness* as a property of a patch or local population expressing the summed connectivity to all of its adjacent neighbours. Low connectedness implies a high degree of isolation and thus a low chance of being recolonized if the local population becomes extinct.

Connectivity is the property of a functional linkage between two patches and is dependent on the permeability of their shared boundary road and its length relative to the perimeter of the source population patch. High connectivity between patch A and B can be achieved through a long common border but also through a permeable boundary road.

Permeability is defined as a property of the boundary roads, measured as the ratio of successful crossings to all encounters of the road. In the model, only patch borders that are shared with other patches can be permeable. Patches at the perimeter of the metapopulation are therefore less connected than patches in its centre. This edge effect should be compensated for when the model is applied to a real landscape; in the generalized version of the model, this is of lesser concern.

Table 1. Example of connectivity matrix.

Patch	Patch 1, target	Patch 2, target	Patch 3, target	Summed connectedness
Patch 1, source	proportion of individuals in patch 1 that never encounter its patch border + individuals from patch 1 that are reflected from all surrounding borders of patch 1 to its neighbours	prop. of individuals that encounter the border between patch 1 and 2 and successfully manage to cross into patch 2	prop. of individuals that encounter the border between patch 1 and 3 and successfully manage to cross into patch 3	total sum of proportions of all dispersers that encounter any border of patch 1 <i>minus</i> those that are reflected by the barriers and those that are killed in traffic
Patch 2, source	same as patch 1-2	patch 2	patch 2-3	
Patch 3, source	same as patch 1-3	same as patch 2-3	patch 3	

3.4 Species characteristics

3.4.1 Behavioural responses to traffic

How species respond to roads and traffic varies widely, and this certainly affects the resulting permeability of the boundary roads in our model. The effect of traffic on wildlife is clearly non-linear (Hels and Buchwald, 2001; Jacobson et al., 2016; Jaeger et al., 2005; McGregor et al., 2007; Müller and Berthoud, 1997; Seiler and Helldin, 2006), but most mammals may at some point be able to recognize the danger in heavy traffic or be repelled by its noise, light, movement or smell. Thus, at very high traffic volumes, most mammals may avoid crossing a road, and those who try will be run over and the resulting barrier effect will be complete. As a rule of thumb, the European Handbook (Iuell et al., 2003) recommends a minimum of 10,000 vehicles a day as a general threshold to define the traffic volume at which most wildlife species will experience an effective barrier due to a high death risk and/or high repellence (Table 2). In the generalized model, we arbitrarily set this threshold at 14,000 vehicles to account for known movements of ungulates across even busier roads. The true threshold may in fact lie even higher, but the actual figure has little effect on the performance of the generalized model. The important aspect is that at intermediate traffic volumes, animal responses will differ considerably; these differences will be linked to the animals' cognitive ability to recognize vehicles as a threat and to their typical antipredator behaviour, which may result in either flight or fight responses (Lima et al., 2015).

To account for this, we employed four principal response profiles suggested by Jacobson et al. (2016), i.e., '*non-responders*', '*avoiders*', '*pausers*', '*speeders*' (Figure 6), and studied how differently these profiles affect the overall impact on metapopulation dynamics. These profiles are not meant to represent true animals nor can they be interpreted as distinct categories; instead, they are the stages on a gradual scale at which non-responders and total avoiders comprise the outer limits. In reality, species will most likely exhibit intermediate stages or a combination of these response types, all depending on the individual and the context.

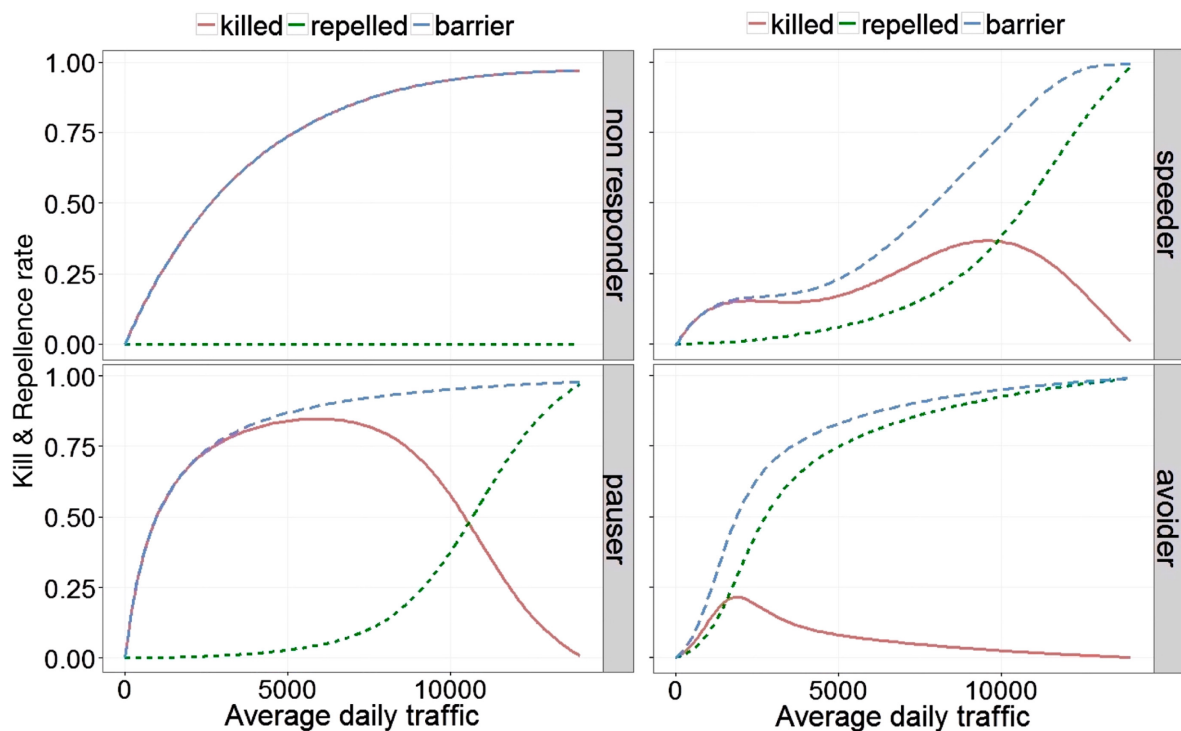


Figure 6. The four response types according to Jacobson et al. 2016, parameterized to fit a maximum traffic volume of 14,000 vehicles a day, at which point the resulting barrier effect reaches 100%. The chosen scale of traffic may differ for different species.

Non-Responders do not recognize moving vehicles as threats and are thus unable to avoid mortality regardless of traffic volume. Amphibians are a typical example of non-responders because they are hardly able to become aware of vehicles and avoid collisions at all (Hels and Buchwald, 2001).

Pausers respond to a perceived threat (of predation) not by flight but rather by crypsis or counter-threat, which increases the time spent on the road and likewise the risk of being killed in traffic. However, when traffic has reached sufficient volume for the animal to pause before attempting to cross, the probability of avoidance becomes greater than the probability of mortality. Examples of pausers are badgers (*Meles meles*) (Jaarsma et al., 2007; Seiler et al., 2003; van Langevelde and Jaarsma, 2004), but also cryptic snakes and some amphibians (Clarke et al., 1998) and turtles (Jacobson et al., 2016).

For *speeders*, flight is the primary response to threat. Speeders may be able to exploit gaps between vehicles even at higher traffic volumes, but as traffic increases and gaps become shorter, the probability of being hit by vehicles increases steeply until traffic provokes avoidance. Speeding behavior may be observed among several deer species such as fallow deer or roe deer (Helldin et al., 2010; Seiler, 2005; Seiler et al., 2011).

Avoiders, may be typically found among large carnivores such as bears (*Ursus arctos*) or lynx (*Lynx lynx*), who may more easily recognise and avoid approaching vehicles even at farther distances than species with a typical panic & flight response as found in many ungulates. In result, avoiders will suffer less from mortality than the other response profiles,

but may experience a generally stronger barrier effect (Huber et al., 1998; Kaczensky et al., 2003).

In our simulations, we parameterized the conceptual profiles proposed by Jacobson et al. (2016) with reference to Swedish studies on moose, roe deer and badger mortality (Seiler, 2004; Seiler, 2005; Seiler et al., 2003; Seiler and Jägerbrand, 2016), setting the maximum traffic volume at which the resulting barrier effect reaches 100% at 14,000 vehicles a day (Figure 6). This scale may not be adequate for other species, but it also resembles the general recommendations given in Luell et al. (2003) (Table 2).

Table 2. The relationship between traffic volume and the barrier effect on mammals. Fences along infrastructure increase the barrier effect of infrastructure. However, fences near passages can be used to lead animals safely to fauna passages. Adapted from (Helldin et al., 2010; Luell et al., 2003; Müller and Berthoud, 1997).

TRAFFIC DENSITY	PERMEABILITY	MORTALITY
Roads with traffic below 1,000 vehicles/day	Permeable to most (larger) wildlife species	Only a few casualties in most larger species
Roads with 1,000 to 4,000 vehicles/day	Permeable to some species but avoided by more sensitive species.	Increased numbers of casualties among those animals that attempt to cross the road
Roads with 4,000 to 10,000 vehicles/day	Stronger barrier, noise and movement will repel many individuals.	High mortality rate, most animals trying to cross the road are killed
Roads with traffic levels above 10,000 vehicles/day	Impermeable to most species. Most animals will refrain from crossing the road.	Fewer casualties despite an almost absolute death risk for those who dare to enter the roadway

3.4.2 Life history

Not only do species show different responses to traffic, but they also pursue different feeding and life-history strategies and they differ in their reproduction, mean survival and area requirements. Species that inhabit large home ranges often occur in low numbers, reproduce relatively slowly and have a long life expectancy (such as bears). Such species will therefore be more often exposed to roads and more sensitive to road density and traffic mortality than species that manage with smaller home ranges, exist at higher densities and produce more offspring (such as roe deer) (Rytwinski and Fahrig, 2011). These strategies are traditionally described as either K-strategy (long life, low reproduction, large home ranges) or r-strategy (high reproduction, short life, smaller home ranges) (Pianka, 1970). Typically, carnivores are more often classified as K-strategists, while herbivores show more of the r-strategist traits if compared to carnivores. In comparison with hares or rabbits, however, any ungulate would be classified as K-strategist. Thus, the scale is continuous and the classification merely relative.

Thus, we expect that road network permeability and habitat fragmentation will affect population viability differently in different species due to differences in their life history and their behavioural response. Consequently, different species may benefit from different mitigation strategies (Jaeger and Fahrig, 2004).

3.4.3 Simulated profiles

To test the effect of life-history traits and behavioural responses on the sensitivity to road barriers and road mortality, we simulated a hypothetical r-strategist and a hypothetical K-strategist for each of the four response profiles. The r-strategist has traits similar to species such as wild boar utilizing home ranges of less than 1 km², while the K-strategist resembles species such as brown bear or lynx.

In addition, we exemplified the generalized model in two real species for which empirical data is available: moose, representing both 'avoider' and 'speeder' profiles and the European badger, representing the 'non-responder' and 'pauser' profiles (Table 3).

Both species have previously been the focus of mitigation actions: the moose mainly in respect to traffic safety (Rea, 2004; Rea et al., 2014; Rolandsen et al., 2011; Seiler, 2005) and game management, and the badger mostly in respect to species protection (Dekker and Bekker, 2010; Van Apeldoorn et al., 2006).

Swedish studies have shown that moose mortality is highest on intermediate roads and drops as traffic increases above 6000 vehicles per average day, presumably as a result of road avoidance by the animals (Seiler, 2005). This pattern clearly resembles the response profile of an 'avoider' (Figure 7).

Badger casualties, on the other hand, tend to be more frequent as traffic increases, suggesting a more linear response and a lack of avoidance at lower to moderate traffic volumes (Lankester et al., 1991; Seiler et al., 2003; van Langevelde et al., 2009). It is likely, although not yet supported by empirical data, that at very high traffic volumes, even badgers will eventually refrain from entering the roadway and mortality will thus decline. In the Netherlands, however, badger casualties still occur on roads as busy as 100,000 vehicles a day (Hans Bekker, Rijkswaterstaat, NL, pers. comm.). We thus chose to employ a 'non-responder'-profile combined with a low level of repellence to simulate effects on badger populations (Figure 7).

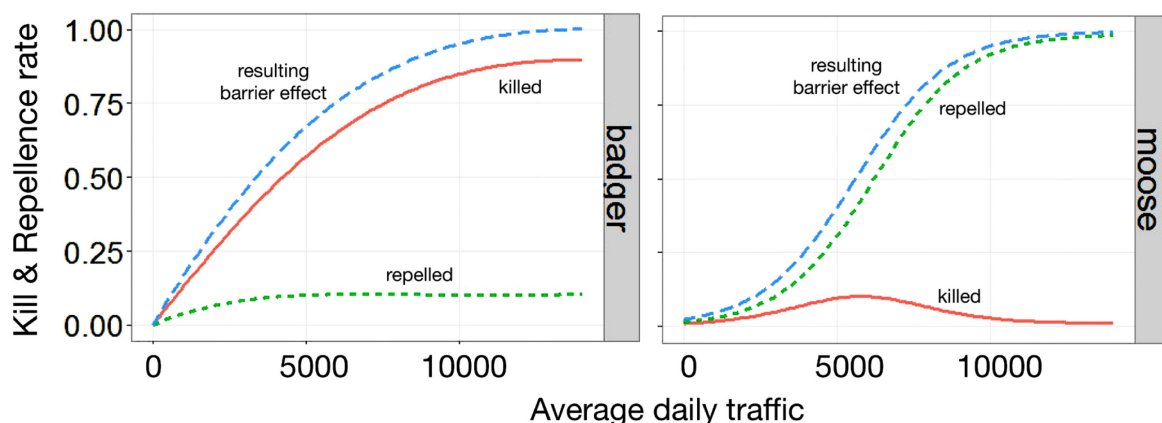


Figure 7. Conceptual model based on observed pattern in traffic mortality in moose and badger in Sweden (Helldin et al., 2010; Seiler, 2005; Seiler et al., 2003).

Table 3. Life-history traits in r- and K-strategists, moose and badger, as used in the simulation model. Life-history data was adjusted to produce stable populations under baseline conditions (population growth rate ≈ 1 and extinction rate = 0 in 50 years).

Life-history trait	r strategist	K strategist	Moose	Badger
metapopulation area (km ²)	10	10	10	10
home range (km ²)	1	100	20	1
animal density (ind/km ²)	1	0,02	0,5	1
average dispersal rate (%)	50	15	25	30
No. of iterations	1000	1000	1000	1000
Survival rates				
Age class 1	0,2	0,7	0,6	0,35
Age class 2	0,3	0,6	0,5	0,6
Age class 3	0,5	0,9	0,9	0,6
Age class 4	-	0,8	0,8	0,6
Age class 5	-	-	-	0,6
Litter size				
Age class 1	2	0	0	0
Age class 2	6	0	1	2,15
Age class 3	8	1,5	2	2,33
Age class 4	-	1,5	1	2,4
Age class 5	-	-	-	2,05
Initial metapopulation size				
Age class 1	10000	200	5000	10000
Age class 2	6000	60	2000	5600
Age class 3	3000	40	1500	2100
Age class 4	1000	60	1000	1200
Age class 5	-	40	500	700
Age class 5	-	-	-	400
Response profiles				
non-responder	+	+		+
pauser	+	+		+
speeder	+	+	+	
avoider	+	+	+	
traffic volume (range)	0 - 14000 vehicles per average day			
percentage fenced	0 %, 40 %, 80 %			
percentage passage	0 %, 20 %, 40 %			
number of patches	1, 3, 12, 37, 91			

3.5 Model scenarios

We developed a series of simulations for the two life-history strategies and four response profiles and for the real-species examples on moose and badger. These simulations were run for the five scenarios with varying degrees of fragmentation and road permeability.

Fragmentation scenarios:

We included five levels of fragmentation (Figure 2): 1 patch as the unfragmented baseline), plus 4 fragmented scenarios with 3, 12, 37 and 91 patches. The total metapopulation area was kept constant at 10,000 km², while local patch area declined to 110 km² (Figure 3).

Mitigation scenarios:

Road permeability was simulated using three levels of road fencing (0%, 40%, 80% of boundary road fenced) and three levels of road bridging by wildlife passages (0%, 20%, 40% of boundary road made permeable), producing a combined number of 8 scenarios with the proportion of the remaining unmitigated, unprotected road ranging from 0% to 100% (Table 4).

Table 4. Scenarios developed to simulate different degrees in road mitigation by fences (F) and passages (B) and the resulting proportion of the unmitigated road (U). The overall length of the boundary road (F+B+U) is always 1.

F = proportion of road fenced	B = proportion of road bridged			
	0%	20%	40%	** 100%
0%	U = 100 %	U = 80 %	U = 60 %	U = 0 %
40%	U = 60 %	U = 40 %	U = 20 %	n.a.
80%	U = 20 %	U = 0 %	n.a.	n.a.
* 100%	U = 0 %	n.a.	n.a.	n.a.

* 100% fenced is represented by max traffic volume in all but the non-responders profile.

** 100% bridged is represented by zero traffic volume in all profiles.

Altogether, we ran 8 (Mitigation scenarios) * 4 (Fragmentation scenarios) * 28 (Traffic volumes) + 1 (No roads or one-patch baseline) = 897 scenarios, with each scenario iterated 1000 times for each of the four response types and the two real-species examples. Simulated time span was 50 years, which is within the range of the technical and economic life lengths of mitigation measures such as fences (20-30 years), bridges (40-60 years) and roads (50-100 years) in Sweden (Trafikverket, 2012b).

4 Results

The simulations revealed clear effects of the traffic volume, fragmentation and mitigation status of the roads severing local populations on growth rates, extinction risks and re-colonization probabilities. These effects, however, differed substantially between species' response profiles and also differ between r- and K-strategists. In all scenarios, 'non-responders' and 'pausers' were the most sensitive response profiles and suffered most from traffic mortality. 'Speeders' and, especially, 'avoiders' were more able to cope with traffic and avoid being killed. Consequently, however, they may also be more susceptible to the barrier effects of increasing traffic. As expected, K-strategists, characterized by large home ranges, slow reproduction and small population sizes, were generally more affected by roads and fragmentation than r-strategists, irrespective of their response profile.

Overall, the simulated metapopulations were most severely affected in scenarios with high road densities but intermediate traffic volumes. In other words, roads of intermediate size with little mitigation created the most dangerous environment for wildlife, whereas low degrees of fragmentation and roads with very low or very high traffic volumes produced much more viable conditions from a population-demographic point of view. This ignores, however, the long-term genetic effects of isolation by roads that, in very small local populations, may reduce viability due to inbreeding depression and thus induce genetic differentiation within the metapopulation.

4.1 Population growth rates

Growth rates of the simulated populations were clearly affected by increased fragmentation and increased traffic. The effect was, however, not linear but primarily reflected the rise and fall of mortality risks predicted by the response profiles (Figure 8). Growth rates dropped most evidently in the range of traffic volumes where most accidents occurred. In the 'avoider' profile, this was at low traffic volumes before repellence reduced accident risks. In 'speeders', the critical traffic volume was considerably higher. In 'non-responders' and 'pausers', and especially among K-strategists of these profiles, already low levels of fragmentation had already quickly led to the extinction of the entire metapopulation.

Interestingly, fencing and bridging performed very similarly in counteracting the decline in growth rate, suggesting that the observed similarity is mostly due to reduced mortality: if 40% of the boundary roads were fenced, the improvement was comparable to 40% of the road being effectively bridged. Both fencing and bridges prevent traffic mortality, but whereas fences increase barrier effects, passages resolve them. The immediate effect of barriers and isolation on metapopulation growth rate was only marginal. Long-term genetic effects on growth rates, however, were not considered in the model.

Also, as traffic volume was increased above the most 'critical' level assumed in the response profiles (except non-responders)(Figure 6), vehicle avoidance reduced mortality and metapopulation growth rate could increase again. Eventually, when high traffic volumes produced a complete barrier effect due to avoidance, metapopulation growth rates were back to the baseline level.

This suggests, that, as far as stochastic extinctions are considered in the simulated conditions, mortality is a much more severe problem than isolation. The further effects of isolation on allele frequencies, genetic drift and eventual inbreeding problems or of negative density dependence in growth rates have not been included in the model but will certainly add significance to barrier effects, especially in small, fragmented populations of K-strategists.

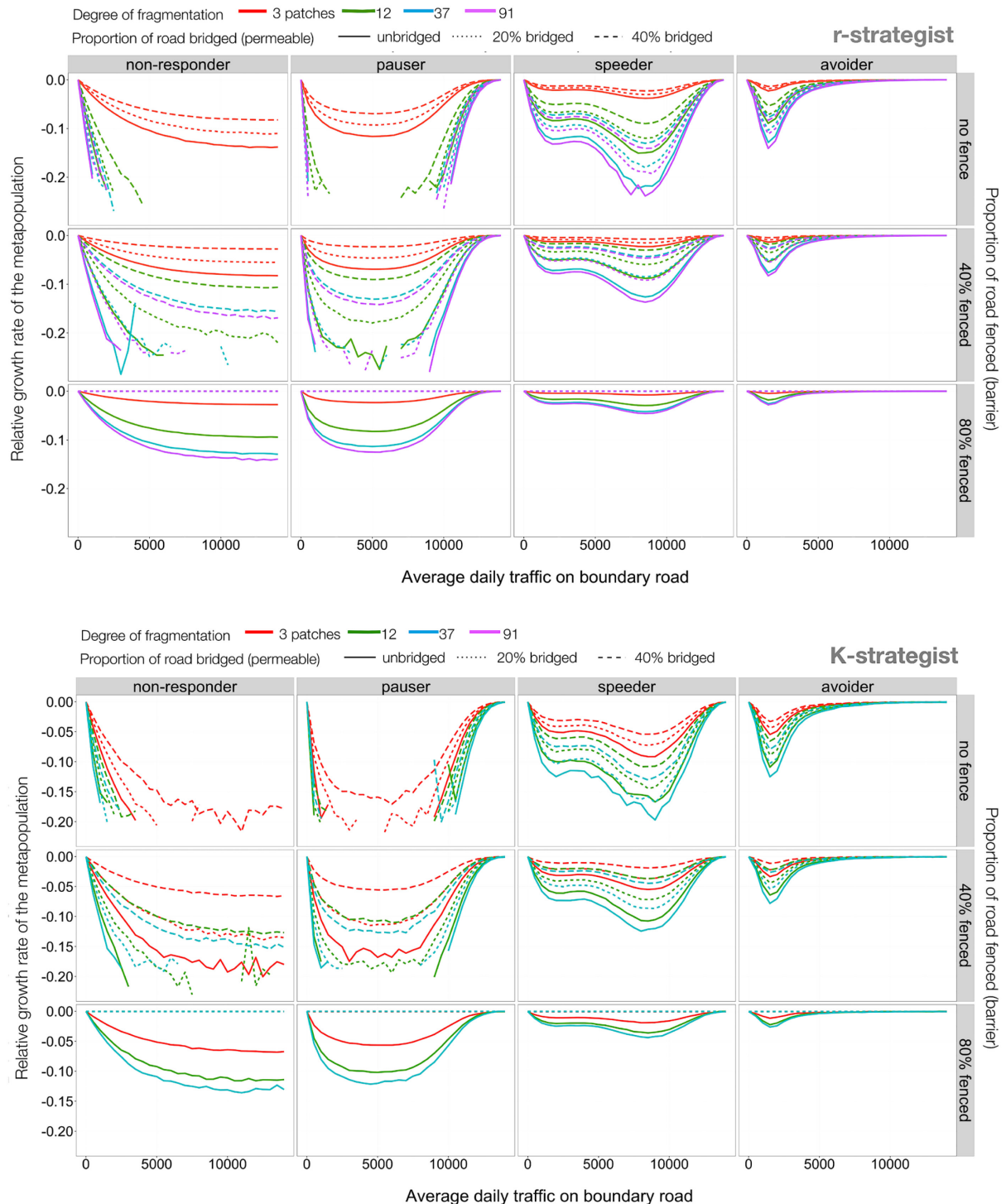


Figure 8. Changes in the averaged annual metapopulation growth rate (λ) for r-strategists (upper picture) and K-strategists (lower picture) over a period of 50 years compared to the baseline scenario (no traffic, no mitigation, one patch) and in relation to the effects of traffic volume, fencing, bridging and fragmentation. Missing lines, as in the non-responder, indicate that the metapopulation became extinct.

4.2 Local extinction and re-colonization probabilities

The second direct effect of fragmentation by road networks on population viability is the increased risk of stochastic extinction. The smaller the population and the lower its growth rate, the greater the risk that random events in the environment may cause a local population to become extinct. Overall, risk levels were generally higher for K-strategists because their population densities were substantially (10-times) lower than those of the r-strategist in the model.

In all of the four response profiles, patterns in extinction risks strongly reflected variations in profile-specific mortality on boundary roads (Figure 9). 'Non-responders' and 'pausers' quickly faced high extinction risks in local populations as either traffic volume or the degree of fragmentation increased. Partial fencing (from unfenced to 40% fenced) had comparably little beneficial effect as did partial bridging (from 0-20%). However, if fences were combined with bridges (40% each), extinction risk were nearly halved or, in low-fragmentation scenarios, practically eliminated. In contrast, 'avoiders' faced very small extinction risks even at high fragmentation levels and on completely unmitigated roads. Again, as for population growth rate, traffic mortality alone appears to be the major single factor driving the observed extinction pattern. Isolation effects first become evident at high traffic volumes, i.e., when road traffic imposes an already effective barrier (in our model: ADT >11,000). Under these conditions, extinction rates in 'pausers' and 'speeders' and in 'avoiders' increase again, presumably because the rescuing immigration events become too rare.

If a population in a patch has become extinct during one year, the patch can still be re-colonized by emigrants from neighbouring patches, provided that the patch is not too isolated. The probability of re-colonization is generally not dependent on the size or growth rate of the local population but on the patch's connectedness with its neighbours and their production of emigrants.

Re-colonization probabilities are hence directly linked to mortality on the boundary roads since high traffic mortality reduces the chance that emigrants successfully reach the vacant patch. In addition, re-colonization can only occur after a local population becomes extinct. Thus, re-colonization patterns inversely reflect profile-specific road kill as well as the patterns observed in the extinction probabilities (Figure 10).

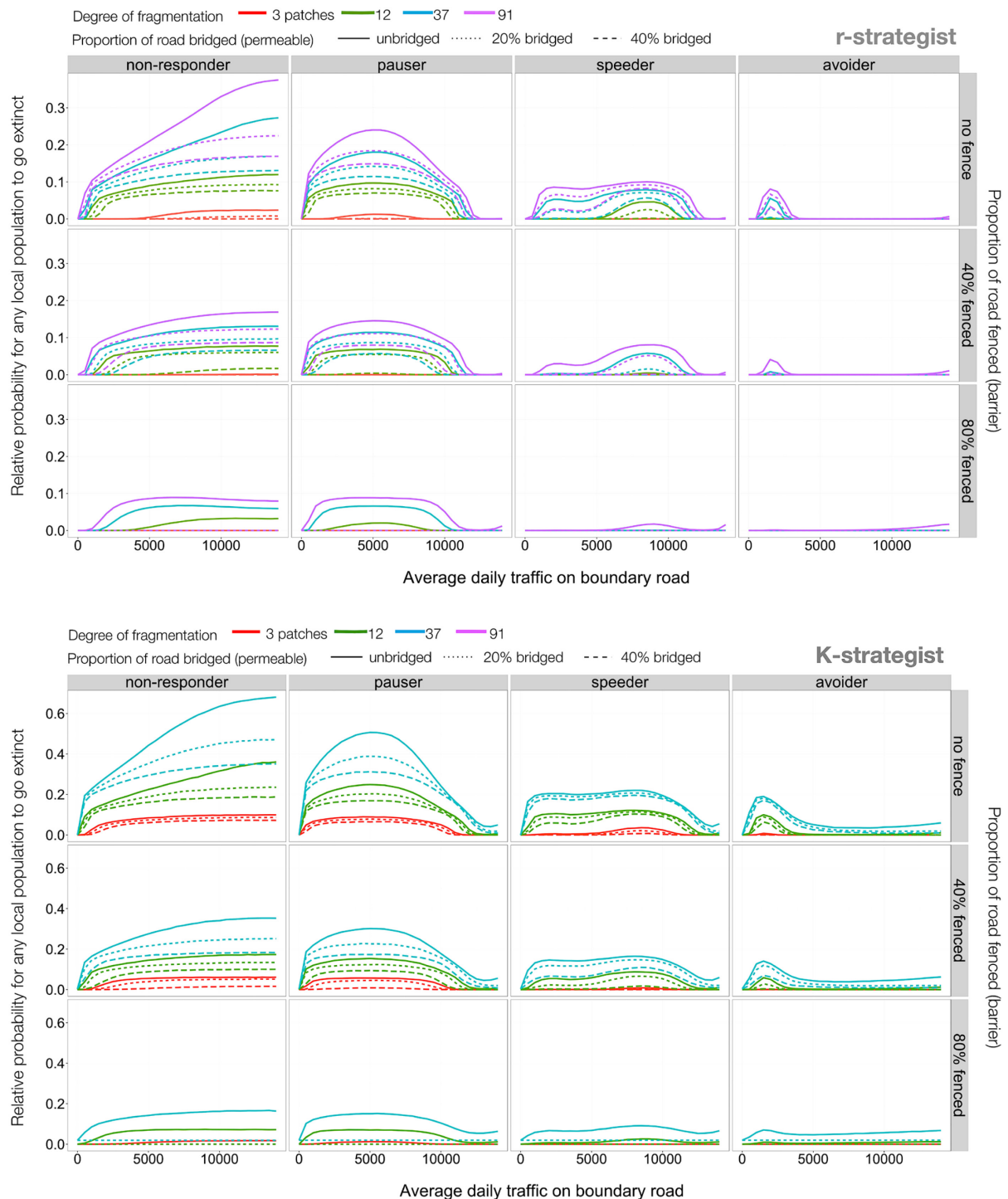


Figure 9. Changes in extinction probabilities of local populations of *r*-strategists (upper picture) and *K*-strategists (lower picture) compared to the baseline scenarios (no traffic, no mitigation, one patch) and in relation to the effects of traffic volume, fencing, bridging and fragmentation.

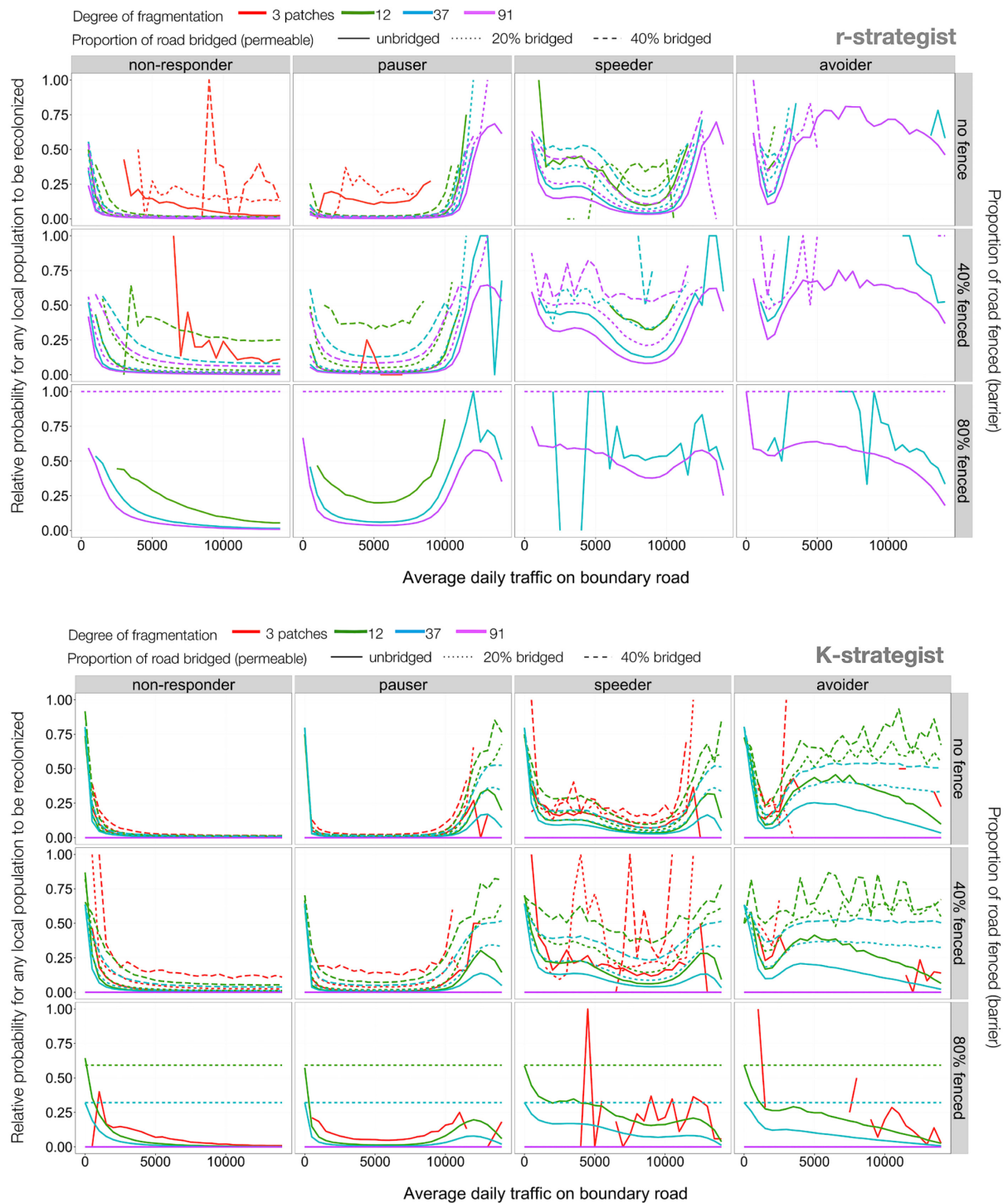


Figure 10. Changes in the relative probability of the re-colonization of any local population in r-strategists (upper picture) and K-strategists (lower picture) during a period of 50 years compared to the baseline scenario (no traffic, no mitigation, one patch) and in relation to the effects of traffic volume, fencing, bridging and fragmentation. Note that in a 3-patch scenario, the variation among individual iterations can largely be due to the rarity of re-colonization events.

4.3 Real species examples

The comparison of the two real-world species, moose and badger, reveal significant differences in their sensitivity to road traffic (Figure 11, 12). As in the general response profiles above, mortality appears as the single most important factor determining growth rates and extinction risks.

Badgers exemplified the 'non-responder/pauser' profile and were significantly affected by both traffic mortality and fragmentation. Population growth rates dropped by over 20% in the 12-patch scenario, but could be recovered by 15% if 80% if the roads were fenced or bridged. If fragmentation levels were higher (37- or 91-patch scenarios), even the entire metapopulation of badgers would become extinct.

Moose, on the other hand, resembled the 'avoider/speeder' profile and were much less affected than badgers. Population growth rates declined only slightly (< 6% at most) as traffic reached intermediate volumes where most of moose-vehicle collisions reportedly occur in Sweden. Neither the entire metapopulation nor local populations of moose faced any risk of becoming extinct during the simulated time scale.

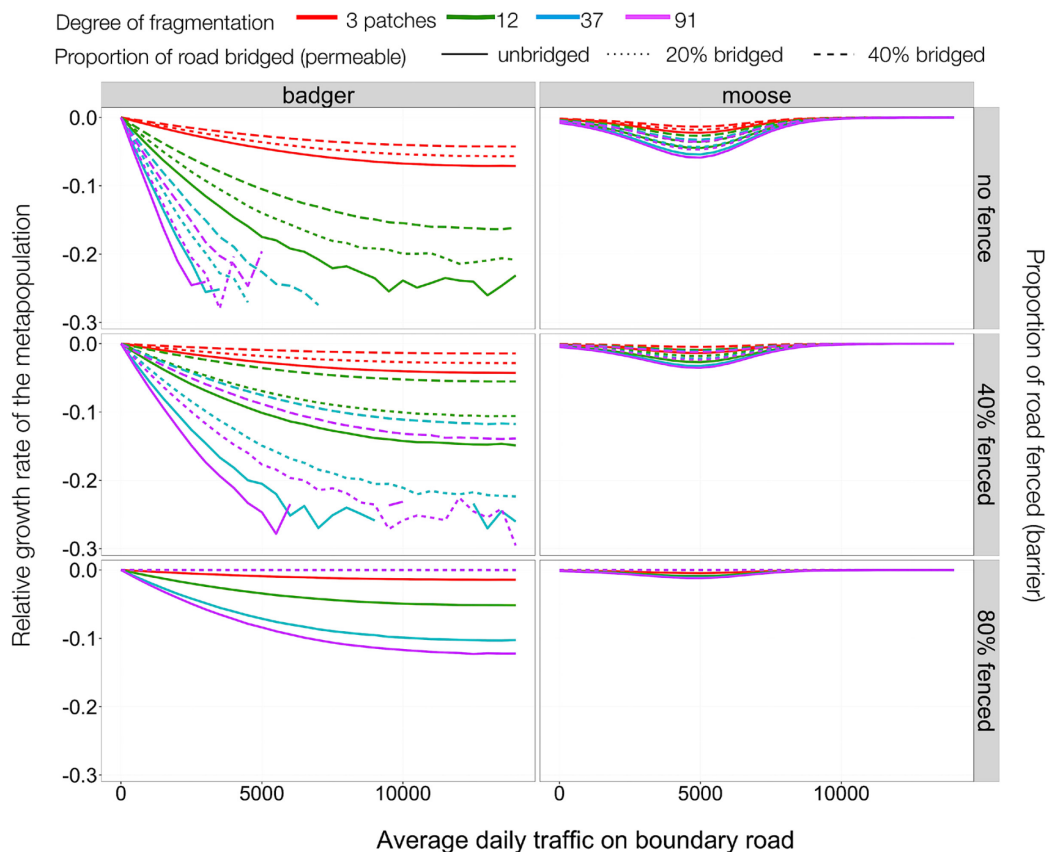


Figure 11. Changes in metapopulation growth rate in badger and moose compared to the no-impact baseline scenario and in relation to the effects of traffic volume, fencing, bridging and fragmentation.

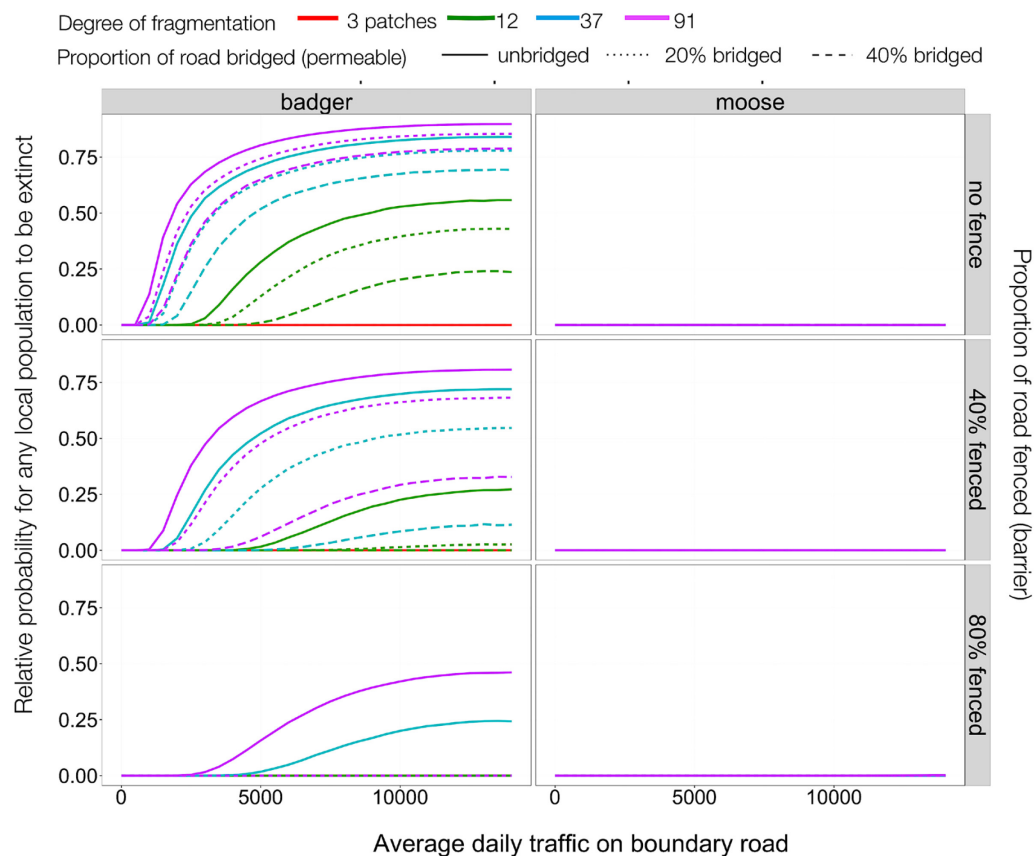


Figure 12. Changes in metapopulation local extinction probabilities in badger and moose compared to the no-impact baseline scenario and in relation to the effects of traffic volume, fencing, bridging and fragmentation.

5 Discussion

5.1 General patterns

The results from the generalized model simulations concur well with earlier studies that all underline the overarching significance of traffic mortality on population viability (Ascensão et al., 2013; Jaeger and Fahrig, 2004; Jaeger et al., 2005; van der Grift et al., 2003). Although we only considered mortality during dispersal to be traffic-related and disregarded any road-related mortality that may occur within a local population or during non-dispersal times, mortality was the single most influential factor producing the observed patterns in population growth rates and extinction probabilities. Barrier effects caused by road avoidance and fences primarily reduced mortality and were thus beneficial to the survival of local populations. From a demographic point of view and given the temporal and spatial scale of our simulations, local populations were rather resilient to isolation effects, and benefits from reduced mortality by increased barrier effects out-weighted the costs of reduced immigration. Only in situations where the metapopulation was already highly fragmented, i.e. local populations were small, did isolation effects become evident and extinction probabilities rise.

5.2 Genetic effects

The generalized model does not distinguish between dispersers that were repelled by the boundary roads and forced back into their native patch to breed or eventually die and those dispersers that successfully immigrated from neighbouring patches across the severing roads. All individuals (in a given age cohort) are assumed to be of equal value for the population, irrespective of their genetic background.

These assumptions, however, ignore the long-term effects of genetic drift or inbreeding depression caused by habitat fragmentation and road networks on population viability (Holderegger and Di Giulio, 2010; Sunnucks and Balkenhol, 2015). Other studies have shown that the barrier effects of road networks and other linear landscape structures can indeed lead to genetic differentiation in wildlife species. Evidence exists for amphibians (Reh and Seitz, 1990), ground beetles (Keller and Largiader, 2003) and also for large mammals such as moose (Wilson et al., 2015) and roe deer (Coulon et al., 2006). Reduced gene flows between populations may induce a decline in animal fitness and reproductivity due to increased inbreeding (e.g., (Crnokrak and Derek, 1999; Kenney et al., 2014). Yet, it is uncertain how many generations it takes before these genetic changes may begin to depress population growth or even endanger viability. If populations are effectively very small, as in the Scandinavian wolf population, inbreeding problems may manifest themselves rather quickly (Liberg et al., 2005), but under more favourable conditions, and especially in intensively managed ungulate populations, the risk of inbreeding depression caused by roads may be marginal.

Nevertheless, it is important to note that the model's predictions are inevitably biased towards an underestimation of isolation effects. Consequently, the model does not sufficiently acknowledge measures such as bridges, tunnels or other crossing structures for wildlife that specifically facilitate the exchange between local populations. Despite the similarity in the effect on population growth and regardless of the necessary focus in mitigation on reducing mortality, fences (barriers) are no true alternatives to crossing structures (bridges) to ensure the long-term viability of populations.

As noted in the Swedish guidelines (Trafikverket, 2012a; Trafikverket, 2014), fences should be regarded as a complement to passages for wildlife, not as a substitute.

5.3 Species' characteristics

The generalized model predicts that in situations where local population sizes are relatively large but traffic volumes on the boundary roads are critically high, meaning that they produce the maximum mortality in wildlife (predicted by the species' response profile), exclusion fencing may be the single most effective measure to protect wildlife – and vehicle drivers alike. Where traffic volumes exceed the critical levels and more animals are repelled by the busy roads than are killed, fencing may cease to be effective, and instead measures should be taken to provide safe and efficient passages across the boundary roads. However, this applies only to species that are able to respond to increased traffic by avoidance. If, in addition, local populations are very small relative to the species' area requirements, most dispersers will encounter the bordering roads and thus benefit from both fences and crossing structures. Also, in very small populations that face a substantial risk of stochastic extinction, bridges become especially important because only they allow for the rescuing effect of immigration and, in the long run, prevent inbreeding depression.

K-strategists are typically more sensitive than r-strategists to fragmentation by roads, simply because they produce fewer individuals, which also range over larger areas and are thereby more susceptible to traffic (Rytwinski and Fahrig, 2015). K- and r-strategies are no absolute classifications, but rather relative notions along a continuous scale (Pianka, 1970). Thus, in mitigation planning, any species with area requirements similar to or larger than the areas left over within the road network may be considered as K-strategists and hence require special concern to reduce road barrier effects. Moreover, if K-strategists have limited abilities to recognize the danger in vehicular traffic (as in the non-responders profile) and thus suffer increasing road mortality as roads become busier, the resulting barrier effect will be largely due to road kill.

The significance of road traffic during dispersal is clearly dependent on how animals respond to traffic. Whether an animal avoids or ignores traffic, flees or pauses when encountering vehicles not only determines the animal's chance of survival and successful migration but has also clear implications for mitigation planning (Jacobson et al., 2016; Kociolek et al., 2015). Avoiders and speeders are much less susceptible to road mortality than pausers or non-responders but differ in how much traffic they are able to cope with without noticeable population effects (Figure 8). Avoiders may be the most susceptible to traffic at rather low volumes, while speeders require a denser traffic to be repelled and thus avoid being killed. Pausers and non-responders, on the other hand, will suffer earlier and more severely from already moderate traffic volumes – and likewise benefit more from mitigation than avoiders.

For example, Swedish studies on badgers (representing the pauser/non-responder profiles) and moose (representing avoider/speeder profiles) suggest that badger road kills may be six times more likely to occur than accidents with moose (Seiler et al., 2003). Traffic probably outweighs hunting as the single most important cause of death in badgers (Seiler et al., 2003), while it comprises only about 10% of the annual game bag in moose (Seiler, 2004). In the Netherlands, badgers are also known to be heavily affected by road mortality (Schippers et al., 1996; Van Apeldoorn et al., 1998), and comprehensive conservation efforts have been made to reduce mortality and re-connect badger populations (Bekker et al., 1997; Dekker and Bekker, 2010).

On the other hand, moose, as many other ungulates in Europe, is intentionally managed for high growth rates in order to allow a sufficiently large annual harvest. Hunting is used to balance population numbers at the highest possible levels at which adverse effects on, for example, forest regeneration are kept at bay. An increase in road mortality may be

compensated by a decrease in harvest numbers. That is, road mortality will be largely compensatory, and its effect on population growth rates and extinction risks may therefore be grossly delayed if they are visible at all (Figure 11).

In both species, however, mitigation should primarily focus on reducing traffic mortality, although for different reasons. In badgers, road kills can impose a significant threat to the survival of local populations. Thus mitigation efforts should aim at securing the survival of badger populations. Fences and tunnels should be installed where they can be most effective in reducing badger road kill. Since badgers hardly avoid vehicles and mortality risks increase quickly as traffic volumes rise, local traffic calming may provide another very useful approach to protect badgers (Jaarsma and Willems, 2002; van Langevelde and Jaarsma, 2009). In moose, on the other hand, collisions with vehicles are primarily a traffic safety issue and hence strongly related to human injury, while conservational concerns, can in most cases, be left out of consideration. Thus, mitigation should primarily focus on reducing the severity and cost of moose-vehicle collisions and not necessarily on their numbers. Traffic accidents are generally more severe at higher vehicle speeds, irrespective of whether they involve wildlife or not (Elvik et al., 2009). Thus, mitigation may therefore be most effective if it aims at reducing vehicle speed, at least during those times and at those places where accidents occur specifically often (Bil et al., 2013; Seiler et al., 2016). The standard approach, however, is to fence any high-speed, high-traffic road. Inevitably, this increases the overall landscape fragmentation caused by road infrastructure and calls for the subsequent mitigation of the increased barrier effects. Yet, in moose and other deer species that fit the avoider's/speeder's profile, targets for maintaining a functional connectivity across fenced infrastructure networks may not need to focus on population viability; rather, they can be set with regard to political goals and practical constraints, as suggested in recent Swedish guidelines for the landscape adaptation of roads (Seiler et al., 2015; Trafikverket, 2015).

To conclude, while traffic mortality appears to be a significantly more influential factor than the barrier effect due to road avoidance, not all mitigation efforts need to focus on preventing road kills. Especially in situations where populations are small and fragmentation intense, where traffic volumes exceed critical levels or where constraints other than population viability come into play, connectivity measures and alternative measure may be of greater advantage.

5.4 Implications for mitigation

By simulating dependencies between road traffic, mortality, isolation and population viability, we hoped to better understand how strong a barrier effect can be accepted and how great a loss of individuals can be tolerated in a given area/population/species that is exposed to road development and whether mitigation plans should focus on reducing mortality or increasing connectivity. With the generalized version of the PERM-model, we were able to develop generic rules and recommendations for mitigation based on the species' ecology, behaviour and road network characteristics. But we cannot provide specific thresholds for, for example, traffic or road kills. For this task, we also wrote the realistic version of the model to apply to real-world planning cases. Critical thresholds will likely be site- and case-specific. Nevertheless, some general guidelines or rules of thumb for the prioritization of mitigation approaches can be derived from the generalized model (Table 5).

Table 5. Examples of prioritization in mitigation approaches in relation to road, traffic and species characteristics.

Factors of concern to mitigation planning	relative levels / impacts					
Traffic volume	low			high		
Patch area relative to home range area	large		small	large	small	
Effective local population size	large			large	small	large
Life-history strategy	r-strategist	K-strategist		r-strategist	K-strategist	
Response profile to traffic	avoider / speeder	non-responder / pauser	avoider / speeder	non-responder	pauser / avoider / speeder	avoider / speeder
Preferred mitigation approach	none	fence	fence + bridge	fence	bridge	bridge

1. Fences and crossing structures should be considered as modules in a combined mitigation package. Fences keep animals off the road and lead them to passages where they can safely cross. Bridges provide a safe conduit but require fencing in order to be efficient. Thus, boldly speaking: no fence without a crossing structure and no crossing structure without a fence.
2. In most cases and probably for most species, mitigation works should focus primarily on reducing road mortality. Moreover, provisions to restore connectivity should be planned and designed to optimize accident prevention.
3. If the target populations are already at risk due to small sizes or isolation, connectivity measures should be obligatory and aim at increasing the exchange between populations. A few well-positioned bridges may suffice to achieve enough migration and reduce extinction risks.
4. Mitigation planning cannot be done solely from a local perspective but requires a regional or pan-regional perspective to encompass neighbouring populations in the meta-population complex. Setting the appropriate scale to evaluate effects on wildlife populations or traffic safety is imperative since it will strongly affect the outcome.
5. Statistics of traffic victims are likely to underestimate the barrier effect on wildlife because the data will be biased towards those species that are less repelled by busy roads and less able to avoid vehicles.
6. Designing effective mitigation strategies requires detailed knowledge about the ecology and behaviour of the target species. Whether a species ignores, flees or avoids traffic will influence the choice and efficacy of preventive measures. Here, more basic research is needed to increase the knowledge about species' responses to traffic and identify critical levels in traffic volume.

6 Conclusions

- In all scenarios, 'non-responders' and 'pausers' are the most sensitive response profiles, while 'speeders' and especially 'avoiders' suffer less from road mortality and barrier effects.
- As expected, K-strategists (large home ranges, slow reproduction, small population sizes) were generally more affected by fragmentation, i.e. patch size and road density, than r-strategists.
- Patterns in metapopulation growth rate and local population extinction risks closely resembled mortality patterns in the response profiles. Road avoidance, on the other hand, had much less effect. Its impact on extinction probabilities became visible only at very high traffic volumes and especially in the K-strategist scenarios.
- Fences and passages performed equally well in reducing stochastic extinction risks and increasing growth rates because they both were defined to prevent traffic mortality along the mitigated section of the road. The additional effect of increased connectivity due to bridges was visible only at high traffic volumes and high levels of fragmentation. Genetic effects of isolation were not considered in the model.
- Fragmentation or road density was another influential factor because it reduced local population sizes, increased the risk of stochastic extinctions in small populations and thus made populations more susceptible to mortality and isolation effects.
- Overall, traffic mortality conveyed by traffic volume on the unmitigated road sections appeared to be the major culprit for the adverse impact of road networks on the demography of the simulated metapopulations.
- In consequence, our model simulations suggest that the focus of most mitigation strategies should first and foremost be on reducing traffic mortality in wildlife. Providing connectivity by means of safe passages may come as a secondary objective, but it will be important at relatively high road densities and traffic volumes.
- Wildlife passages, ecoducts and other connectivity measures should thus be primarily designed and located to reduce the risk of wildlife-vehicle accidents rather than to provide connectivity. This may create new constraints on planning fauna passages, and it emphasizes the need to combine crossing structures with long enough fences that safely lead animals towards the passage. Fences and crossing structures should thus be considered as modules in a combined mitigation package.
- Alternative options to mitigate road mortality and increase (maintain) connectivity across the landscape should be studied in greater depth. Traffic calming and bundling infrastructure in transport corridors may produce busier but fewer and safer roads that can be easier targets for mitigation. Temporary and local speed reduction, increased driver awareness, wildlife warning systems (to induce adequate flight response in the animals), etc. may be cost-efficient complements to fences and bridges.
- To effectively target accident prevention methods and develop alternative, cost-efficient mitigation approaches, we need a better understanding of the spatial and temporal patterns in road kills and animal-vehicle collisions as well as of the behaviour of wildlife in relation to traffic and mitigation measures. New research projects and experiments that go beyond standard monitoring procedures should therefore be linked with ongoing or planned mitigation works.

7 Acknowledgements

The research presented in this report was carried out as part of the CEDR Transnational Road Research Programme Call 2013. The funding for the research was provided by the national road administrations of Austria, Denmark, Germany, Ireland, Norway, Sweden, Netherlands and the UK. The project was cofounded by the Swedish Transport Administration and through complementary research activities within the TRIEKOL research programme.

8 References

- Ascensão, F., Clevenger, A., Santos-Reis, M., Urbano, P. & Jackson, N., 2013. Wildlife-vehicle collision mitigation: Is partial fencing the answer? An agent-based model approach. *Ecological Modelling*, 257, 36-43.
- Bekker, G. J., Canters, K. J., Canters, K., Piepers, A. & Hendriks-Heersma, A., 1997. The continuing story of badgers and their tunnels. *Proceedings of the international conference on "Habitat fragmentation, infrastructure and the role of ecological engineering" Maastricht & DenHague 1995*. Delft, The Netherlands: Ministry of Transport, Public Works and Water Management, Road and Hydraulic Engineering division.
- Bil, M., Andrasik, R. & Janoska, Z., 2013. Identification of hazardous road locations of traffic accidents by means of kernel density estimation and cluster significance evaluation. *Accident Analysis and Prevention*, 55, 265-273.
- Bissonette, J. & Adair, W., 2008a. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation*, 141, 482-488.
- Bissonette, J. A. & Adair, W., 2008b. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation*, 141, 482-488.
- Bowman, J., Jaeger, J. & Fahrig, L., 2002. Dispersal distance of mammals is proportional to home range size. *Ecology*, 83, 2049-2055.
- Clarke, G. B., White, P. C. L. & Harris, S., 1998. Effects of roads on badger *Meles meles* populations in south-west England. *Biological Conservation*, 86, 117-124.
- Corlatti, L., Hacklander, K. & Frey-Roos, F., 2009. Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. *Conserv Biol*, 23, 548-56.
- Coulon, A., Guillot, G., Cosson, J. F., Angibault, J. M., Aulagnier, S., Cargnelutti, B., Galan, M. & Hewison, A. J., 2006. Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. *Mol Ecol*, 15, 1669-79.
- Crnokrak, P. & Derek, A. R., 1999. Inbreeding depression in the wild. *Heredity*, 83, 260-270.
- Dekker, J. & Bekker, H., 2010. Badger (*Meles meles*) road mortality in the Netherlands: the characteristics of victims and the effects of mitigation measures. 53, 81-92.
- Elvik, R., Høye, A., Vaa, T. & Sørensen, M., 2009. *Handbook of Road Safety Measures*, Bingley, UK, Emerald Group Publishing Limited.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, 34, 487-515.
- Forman, R. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., Fahrig, L., France, R., Goldman, C. R., Heanue, K., Jones, J. A., Swanson, F. J., Turrentine, T. & Winter, T. C., 2003. *Road ecology - Science and Solutions*, Washington, Island Press.
- Helldin, J. O., Broekmeyer, M., Campeny, R. & Kistenkas, F., 2016. *Roads and wildlife: Legal requirements and policy targets. SAFEROAD Technical report 1.*, Brussels, Conference of European Directors of Roads (CEDR).
- Helldin, J. O., Seiler, A. & Olsson, M., 2010. *Roads and railroads: barriers in the landscape (In Swedish: Vägar och järnvägar: barriärer i landskapet)*, CBM, Uppsala, Triekol report, CBM skrift 42.
- Hels, T. & Buchwald, E., 2001. The effect of road kills on amphibian populations. *Biological Conservation*, 99, 331-340.

- Hobbs, N. T. & Hooten, M. B., 2015. *Bayesian models: a statistical primer for ecologists*, Princeton University Press.
- Holderegger, R. & Di Giulio, M., 2010. The genetic effects of roads: A review of empirical evidence. *Basic and Applied Ecology*, 11, 522-531.
- Huber, D., Kusak, J. & Frkovic, A., 1998. Traffic kills in brown bears in Gorski Kotar, Croatia. *Ursus*, 10, 167-171.
- Huijser, M. P., Fairbank, E. R., Camel-Means, W., Graham, J., Watson, V., Basting, P. & Becker, D., 2016. Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife–vehicle collisions and providing safe crossing opportunities for large mammals. *Biological Conservation*, 197, 61-68.
- Huijser, M. P., McGowen, P., Clevenger, A. P. & Ament, R., 2008. *Wildlife-vehicle Collision Reduction Study: Best Practices Manual*, U.S. Department of transportation, Federal Highway Agency.
- Iuell, B., Bekker, H., Cuperus, R., Dufek, J., Fry, G. L., Hicks, C., Hlavac, V., Keller, J., Le Marie Wandall, B., Rosell Pagès, C., Sangwine, T., Torslov, N. & (Eds), 2003. *Wildlife and Traffic - A European Handbook for Identifying Conflicts and Designing Solutions. Prepared by COST 341 - Habitat Fragmentation due to Transportation Infrastructure*, Delft, The Netherlands, Ministry of Transport, Public Works and Water Management, Road and Hydraulic Engineering division, Delft, The Netherlands.
- Jaarsma, C., Van Langevelde, F., Baveco, J., Van Eupen, M. & Arisz, J., 2007. Model for rural transportation planning considering simulating mobility and traffic kills in the badger *Meles meles*. *Ecological Informatics*, 2, 73-82.
- Jaarsma, C. & Willems, G. P. A., 2002. Reducing habitat fragmentation by minor rural roads through traffic calming. *Landscape and Urban Planning*, 58, 125-135.
- Jacobson, S., Bliss-Ketchum, L., De Rivera, C. & Smith, W. P., 2016. A behavior based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere*, in press.
- Jaeger, J. & Fahrig, L., 2004. Effects of road fencing on population persistence. *Conservation Biology*, 18, 1651-1657.
- Jaeger, J., L.F., M., Soukup, T., Schwick, C. & Kienast, F., 2011. *Landscape fragmentation in Europe. A joint EEA-FOEN report.*, Copenhagen, European Environment Agency.
- Jaeger, J. a. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B. & Von Toschanowitz, K. T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling*, 185, 329-348.
- Kaczensky, P., Knauer, F., Krze, B., Jonožovic, M., Adamic, M. & Gossow, H., 2003. The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biological Conservation*, 111, 191-204.
- Keller, I. & Largiader, C. R., 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Proceedings of the Royal Society B: Biological Sciences*, 270, 417-423.
- Kenney, J., Allendorf, F. W., Mcdougal, C. & Smith, J. L., 2014. How much gene flow is needed to avoid inbreeding depression in wild tiger populations? *Proc Biol Sci*, 281, 20133337.
- Kernighan, B. W. & Ritchie, D. M., 1978. *The C Programming Language*, Prentice-Hall.

- Kociolek, A., Grilo, C. & Jacobson, S., 2015. Flight Doesn't Solve Everything. *Handbook of Road Ecology*. John Wiley & Sons, Ltd.
- Lankester, K., Van Apeldoorn, R. C., Meelis, E. & Verboom, J., 1991. Management perspectives for populations of the Eurasian badger (*Meles meles*) in a fragmented landscape. *Journal of Applied Ecology*, 28, 561-573.
- Liberg, O., Andren, H., Pedersen, H. C., Sand, H., Sejberg, D., Wabakken, P., Kesson, M. & Bensch, S., 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biol Lett*, 1, 17-20.
- Lima, S. L., Blackwell, B. F., Devault, T. L. & Fernandez-Juricic, E., 2015. Animal reactions to oncoming vehicles: a conceptual review. *Biol Rev Camb Philos Soc*, 90, 60-76.
- Mcgregor, R. L., Bender, D. J. & Fahrig, L., 2007. Do small mammals avoid roads because of the traffic? *Journal of Applied Ecology*, 45, 117-123.
- Müller, S. & Berthoud, G., 1997. *Fauna/Traffic Safety - Manual for civil engineers*, Lausanne, Switzerland, LAVOC.
- Pianka, E. R., 1970. On r- and K-Selection. *The American Naturalist*, 104, 592-597.
- Putman, R. J., Langbein, J. & Staines, B. W., 2004. Deer and road traffic accidents: A review of mitigation measures: costs and cost-effectiveness. *Report for the Deer Commission for Scotland*, papers2://publication/uuid/F77B33A6-04B3-4BC3-B62C-C1CACBA8BD07.
- R Core Team, 2015. R: A language and environment for statistical computing. Vienna, Austria; 2014. URL <http://www.R-project.org>.
- Rea, R., 2004. Investigating methods to reduce urban moose-related vehicular collisions within the city of Prince George, British Columbia.
- Rea, R. V., Johnson, C. J. & Emmons, S., 2014. Characterizing Moose–Vehicle Collision Hotspots in Northern British Columbia. *Journal of Fish and Wildlife Management*, 5, 46-58.
- Reh, W. & Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog (*Rana temporaria*). *Biological Conservation*, 54, 239-249.
- Rolandsen, C. M., Solberg, E. J., Herfindal, I., Van Moorter, B. & Sæther, B.-E., 2011. Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density? *Ecosphere*, 2, art113.
- Rytwinski, T. & Fahrig, L., 2011. Reproductive rate and body size predict road impacts on mammal abundance. *Ecological Applications*, 21, 589-600.
- Rytwinski, T. & Fahrig, L., 2015. The Impacts of Roads and Traffic on Terrestrial Animal Populations. *Handbook of Road Ecology*. John Wiley & Sons, Ltd.
- Schippers, P., Verboom, J., Knaapen, J. & Van Apeldoorn, R., 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography*, papers://59F6652F-E3FF-4FF7-BE89-9A861C9AA38C/Paper/p2722, 97-106.
- Seiler, A., 2004. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology*, 10, 301-313.
- Seiler, A., 2005. Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology*, 42, 371-382.

- Seiler, A. & Helldin, J. O., 2006. Mortality in wildlife due to transportation. In: Davenport, J. & Davenport, J. L. (eds.) *The ecology of transportation: managing mobility for the environment*. Amsterdam: Kluwer.
- Seiler, A., Helldin, J. O. & Eckersten, T., 2003. Road mortality in Swedish Badgers (*Meles meles*). Effect on population. *The toll of the automobile: Wildlife and roads in Sweden*. Uppsala: Ph.D. thesis at the Department for Conservation Biology, SLU.
- Seiler, A. & Jägerbrand, A. K., 2016. *Hidden statistics in wildlife-vehicle accident statistics - interpretation of drivers surveys and database comparisons*. (In Swedish: *Mörketal i viltolycksstatistik – tolkning av viltolycksenkät och databasanalyser*), Borlänge, Trafikverket Publikation 2016 in press.
- Seiler, A. & Olsson, M., 2015. *Viltstängsel - en lönsamhetsbedömning*, Uppsala, Triekol rapport, CBM:s skriftserie.
- Seiler, A., Olsson, M. & Helldin, J. O., 2011. *Klövvtolyckor på järnväg - kunskapsläge, problemanalys och åtgärdsförslag*, Borlänge, Trafikverket Publikation 2011:058.
- Seiler, A., Olsson, M. & Lindqvist, M., 2015. *Analys av infrastrukturens permeabilitet för klövdjur*, Trafikverket Publikation 2015:254.
- Seiler, A., Rosell, C., Torellas Arnedo, M. & Sjölund, M., 2016. *Case studies on the effect of local road and verge features on ungulate-vehicle collisions*. *SAFEROAD Technical report 8*, Brussels, Conference of European Directors of Roads (CEDR).
- Sunnucks, P. & Balkenhol, N., 2015. Incorporating Landscape Genetics into Road Ecology. *Handbook of Road Ecology*. John Wiley & Sons, Ltd.
- Trafikverket, 2012a. *Krav för vägars och gators utformning*, Borlänge, Trafikverket Publikation.
- Trafikverket, 2012b. *Socio-economic principles and calculations for the transport sector* (In Swedish: *Samhällsekonomiska principer och kalkylvärden för transportsektorn: ASEK 5*), Borlänge, Swedish Transport Administration (Trafikverket Publikation) 2012:085.
- Trafikverket, 2014. Guideline on wildlife exclusion fences (In Swedish: *Viltstängsel*). *Swedish Transport Administration (Trafikverket)*, TDOK 2014-0115.
- Trafikverket, 2015. Guideline landscape (In Swedish: *Riktlinje landskap*) *Swedish Transport Administration (Trafikverket)*, TDOK 2015-0323.
- Van Apeldoorn, R., Vink, J. & Matyáščík, T., 2006. Dynamics of a local badger (*Meles meles*) population in the Netherlands over the years 1983–2001. *Mammalian Biology*, 71, 25-38.
- Van Apeldoorn, R. C., Knaapen, J. P., Schippers, P., Verboom, J., Van Engen, H. & Meeuwsen, H., 1998. Applying ecological knowledge in landscape planning: a simulation model as a tool to evaluate scenarios for the badger in the Netherlands. *Landscape and Urban Planning*, 41, 57-69.
- Van Der Grift, E. A., Seiler, A. & Helldin, J. O., 2016. *Guidelines for outcome-based specifications in road mitigation*. *SAFEROAD Technical report 2*, Brussels, Conference of European Directors of Roads (CEDR).
- Van Der Grift, E. A., Verboom, J. & Pouwels, R., 2003. Assessing the Impact of Roads on Animal Population Viability. In: Irwin, L. C., Garrett, P. & Mcdermott, K. P. (eds.) *International Conference on Ecology and Transportation (ICOET)*. Raleigh, NC: Center for Transportation and the Environment, North Carolina State University.
- Van Der Ree, R., Smith, D. J. & Grilo, C., 2015. The Ecological Effects of Linear Infrastructure and Traffic. *Handbook of Road Ecology*. John Wiley & Sons, Ltd.

- Van Langevelde, F. & Jaarsma, C. F., 2004. Using traffic flow theory to model traffic mortality in mammals. *Landscape Ecology*, 19, 895-907.
- Van Langevelde, F. & Jaarsma, C. F., 2009. Modeling the Effect of Traffic Calming on Local Animal Population Persistence. 14, 39.
- Van Langevelde, F., Vandooremalen, C. & Jaarsma, C., 2009. Traffic mortality and the role of minor roads. 90, 660-667.
- Wilmet, S., 2014. The GLib/GTK+ Development Platform.
- Wilson, R. E., Farley, S. D., McDonough, T. J., Talbot, S. L. & Barboza, P. S., 2015. A genetic discontinuity in moose (*Alces alces*) in Alaska corresponds with fenced transportation infrastructure. *Conservation Genetics*, 10.1007/s10592-015-0700-x, 1-10.

Annex A: Calculation of Encounter rate E

Patch size (A), moving distance (M) and borderline length (L) define the probability that a dispersing individual will encounter (E) and attempt to cross a given borderline.

The calculation of the probability (E) of meeting a given borderline derives from the following considerations. Assume the population patch is circular and all animals are uniformly distributed across this circle with radius R . Let r be the radius of a circle with the same central point with $r < R$. There exists a distance $x = R - r$ at which all animals have the same probability of being on the outside or inside of the circle with radius r . The probability of animals meeting the edge of the population patch is thus:

$$E = \frac{M}{x}$$

$$R^2 * \pi = 2 * (R - x)^2 * \pi \quad | \quad x = (1 - \sqrt{0.5}) * R$$

$$E = \frac{M}{(1 - \sqrt{0.5}) * R}$$

Or:

$$E = \frac{M}{(1 - \sqrt{0.5}) * \sqrt{\frac{A}{\pi}}}$$

Or:

$$E = \frac{M}{K * \sqrt{A}}$$

With:

$$K = \sqrt{\frac{(1 - \sqrt{0.5})^2}{\pi}} \cong 0.16525$$

The formula is the same for both a circle and a regular hexagon: if a regular hexagon and a circle have the same area, then the hexagon's area included and excluded by the radius of the circle are equal.



Saferoad office

Wageningen University & Research
Environmental Research
Droevendaalsesteeg 3
Building 101
6708 PB Wageningen
T +31 317 48 16 00

Project coordinator

Edgar van der Grift
E edgar.vandergrift@wur.nl

Contact person

Vanya Simeonova
E vanya.simeonova@wur.nl

www.saferoad-cedr.org

Partners

