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RESEARCH ARTICLE

Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches

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Abstract Roads can have drastic impacts on wildlife populations. Although there is wide recognition of the negative impacts caused by roads and a wealth of practical studies, there is a lack of theoretical work that can be used to predict the impact of road networks or to implement mitigation measures. Here, using Skellam's diffusion model, we develop analytic and numerical approaches to analyze the impact of road networks on the survival of populations. Our models show that the viability of a population is determined not only by road density but also by the size and shape of patches. Accordingly, we studied the minimum size of a patch to sustain a population with given diffusion and growth parameters. We provide simple formulas to estimate the minimum patch size, and illustrate the importance of shape with square and rectangular patches. Our models also allow the estimation of time to extinction after road construction for a population in a patch smaller than that of the minimum size. Finally, using numerical computations we illustrate how the spatial arrangement of fences strongly affects both the equilibrium density and the spatial distribution of populations, and that not all fence layouts are equally effective. We anticipate that our methods provide a tool to assess the impact of geometrical features of road networks on wildlife and that they can be used to design mitigation measures to prevent the decline and extinction of populations in an anthropogenically disturbed landscape.

Keywords Skellam's model · Reaction–diffusion equations · Dispersal · Road mortality · Mitigation measures · Fences · Spatially explicit model · Minimum patch size · Patch shape

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Introduction

Roads, being associated with human well being and development, tend to occupy a growing percentage of landscapes worldwide. They now cover an average density of 1.2 km/km^2 in the United States (Forman 2000), over 2 km/km^2 in some European countries (Carr et al. 2002), and one can expect that road density will increase in developing countries since there is an inherent relationship between transportation infrastructures and socio-economic development (Wilkie et al. 2000; Laurance et al. 2001).

For the past thirty years many scientists have addressed the issue of roads and their impact on the environment within the framework of "road ecology" (for recent reviews, see Forman 1998; Forman and Alexander 1998; Trombulak and Frissell 2000; Carr et al. 2002; Goosem 2007; Laurance et al. 2009). They have concluded that the main negative consequences of roads on the environment are: pollution (Pratt and Lottermoser 2007), increased human access (Wilkie et al. 2000), exotic species invasions (e.g., Prasad et al. 2010), edge effects, such as, greater wind speed and elevated diurnal ranges of temperature (Pohlman et al. 2009), increased mortality (e.g., Kramer-Schadt et al. 2004) and habitat change, such as, barrier effects, habitat loss and fragmentation (Seiler 2001; Laurance et al. 2004; Ford and Fahrig 2008).

Not surprisingly, the increase in road density raises concerns regarding their impact on biodiversity. Roads affect several taxa, for example, amphibians (Fahrig et al. 1995; Vos and Chardon 1998; Carr and Fahrig 2001), birds (Forman et al. 2002; Laurance et al. 2004), reptiles (Bonnet et al. 1999; Gibbs and Shriver 2002) and mammals (Kramer-Shadt et al. 2004; Dodd et al. 2005; Ford and Fahrig 2008; Grilo et al. 2009). However, most studies remain species and taxonomic group oriented and focus mainly on the aftermaths of road construction or on the impacts of increasing traffic intensity (Fahrig et al. 1995; Bonnet et al. 1999; Saeki and MacDonald 2004). There is a void in the development of theoretical models analyzing the relationship between roads and populations' persistence, as several authors have pointed out (for instance, Carr et al. 2002 and Spellerberg 1998). One exception is the work by Jaeger and Fahrig (2004) and Jaeger et al. (2005), who developed an individual-based spatially explicit model to study the effect of roads and fences on the persistence of populations. Two of their findings served as a starting point for our work. First, Jaeger and Fahrig (2004) showed how dispersal behavior is a determining parameter for survival in a habitat crossed by roads. Specifically, they concluded that, for a population to survive, its individuals had to disperse less to minimize the road-induced mortality, but noticed that such behavioral "adaptation" could be detrimental since it induces population' isolation (Seiler 2001; van der Grift et al. 2003; Ford and Fahrig 2008) and consequent lack of genetic diversity (Epps et al. 2005). Second, Jaeger et al. (2005) studied the impact of different road networks on the persistence of populations and illustrated that the probability of survival was higher for a population in a landscape with perpendicular roads than one with parallel roads. Specifically, in perpendicular networks the level of fragmentation is higher, yet the shape of the patches induces less road encounter hence lower road mortality.

In this paper, we took one step further in the study of perpendicular road networks by investigating which of its characteristics would be compatible with the persistence of populations. Here, instead of an individual-based model, we explore an analytical and computational approach using Skellam (1951) and Kierstead and Slobodkin (1953) model (hereafter only Skellam's model) to predict the impact of a road network on a population characterized by dispersal variance, σ^2, growth rate in its natural habitat, r_1, and survival on roads specified by a (negative) growth rate, r_0. This model has been intensively studied previously (e.g. Pereira et al. 2004; Cosner 2008). One of the advantages of adopting an analytical approach is that it provides a set of simple equations that allows a first approximation to the assessment of a population's persistence in a landscape fragmented by roads.

Our strategy is to study cases of increasing complexity (Table 1). Case 1 considers only the density of roads, without their spatial location, our main purpose being to show its limitations. Case 2 treats the location of the roads explicitly, but its analytical solution is only possible when we assume that animals always die when crossing roads ($r_0 = -\infty$) and that their growth in the natural habitat is exponential. Still, it provides important insights to the following questions: How does the shape and distance between roads influence the population's dynamics, and how long does it take for a road network to impact wild populations? Case 3 relaxes the assumption of infinite r_0 and assumes logistic growth on non-road habitat. The down side of increasing realism is that we have to resort to numerical approximations of Skellam's model of partial differential equations. This numerical approach shows the limitations of case 1 (large dispersal and carrying capacity), replicates the results obtained with case 2 (lethal roads), and allows

Table 1 Summary of the main features of the four cases analyzed in this study

Case	Description	Spatial analysis	Growth (on natural patches)/main parameters	Roads	Survival of the population depends on
1	Very large dispersal and carrying capacity	Analytical and spatially implicit	Exponential/r_1, r_0	Non lethal	Road density (h)
2	Road crossing is always lethal	Analytical and spatially explicit	Exponential/r_1, σ^2	Lethal ($r_0 = -\infty$)	Min distance between roads (L_m)
3	Non-lethal roads	Numerical and spatially explicit	Logistic/r_1, r_0, σ^2	Non lethal	Min distance between roads (L_m)
4	Road mortality mitigation using fences	Numerical and spatially explicit	Logistic/r_1, σ^2	Lethal ($r_0 = -\infty$)	Permeability (f), layout of fences

r_0 and r_1 are growth rates, σ^2 is the dispersal variance

the study of analytically intractable cases. Finally, case 4 builds on case 3 to simulate fences, a mitigation measure widely used due to its low cost and easy implementation. Here we will pay special attention to how different fence layouts, when these only cover a fraction of the roads, affect the survival of a population and the resulting density spatial patterns.

The model

Consider a population inhabiting an infinite landscape consisting of patches surrounded by roads (Fig. 1). Roads are unfavorable habitats where the population has a negative growth rate, r_0, and patches are natural habitat where the population has positive growth rate, r_1. The dispersal distance of the population is described by its dispersal variance, σ^2. Our starting point is a reaction–diffusion equation (e.g., Skellam 1951) describing the population dynamics and dispersal

$$\frac{\partial N(x,y,t)}{\partial t} = \begin{cases} \frac{\sigma^2}{2}\nabla^2 N(x,y,t) + r_1 N(x,y,t)\left(1 - \frac{N(x,y,t)}{K}\right) & \text{if } (x,y) \notin road \\ \frac{\sigma^2}{2}\nabla^2 N(x,y,t) + r_0 N(x,y,t) & \text{if } (x,y) \in road \end{cases}, \qquad (1)$$

where $N(x,y,t)$ is the population density on location (x,y) at time t, and K the carrying capacity; the symbol ∇^2 stands for $(\partial^2/\partial x^2 + \partial^2/\partial y^2)$. The first term on the right-hand side of Eq. 1 describes the changes in time and space of the density of a population on the basis of its dispersal distance (assuming it to be Gaussian). The second term on the top branch corresponds to logistic growth (outside roads) and in the bottom branch corresponds to exponential decay (on roads) because $r_0 < 0$.

Case 1: very large dispersal and carrying capacity

Here we assume exponential growth, $K \to \infty$, so we ignore the term $(1 - N(x,y,t)/K)$ in the top branch of Eq. 1, and ignore the spatial location of the roads ($\sigma^2 \to \infty$,), considering only road density, h. In Supplemental Information we derive a condition for the critical road density, that is, the maximum road density above which the population goes extinct, which is

$$h_{crit} = \frac{r_1}{r_1 + |r_0|}. \qquad (2)$$

Notice that Eq. 2 assumes that density is calculated as the ratio of two areas and, hence, it is a dimensionless quantity.

Equation 2 offers an easy rule of thumb to estimate the maximum road density on the basis of the population growth rate and mortality on the roads. However, as we discuss in Supplemental Information, Eq. 2 was obtained using a sufficient condition, therefore it is possible that even when $h > h_{crit}$ the population may persist and, therefore, in some cases

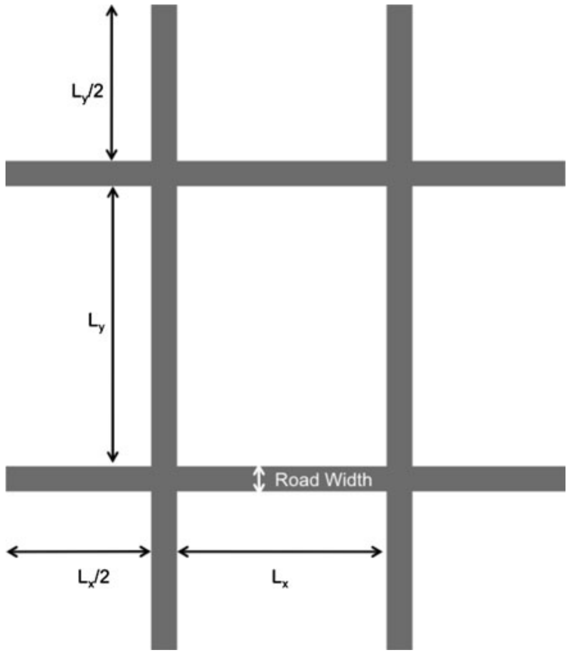


Fig. 1 Location of the roads on the landscape, where L_x and L_y are the distances between roads along the x and y axes, respectively, with $L_y = \alpha L_x$ and $\alpha \geq 1$. We assume periodical boundary conditions, that is, an individual leaving from the left (right) hand side reenters from the right (left) hand side, and one leaving from the top (bottom) reenters at the bottom (top). To guarantee that all patches have the same size when connected, the ones on the border have widths $L_x/2$ and $L_y/2$

h_{crit} may underestimate the maximum possible road density for a population to persist. In addition, anticipating the comparison with the next cases, notice that Eq. 2 was derived assuming that $\sigma^2 = \infty$, whereas next models show that σ^2 is an important parameter for predicting the survival of a population.

Case 2: road crossing is always lethal

Here we consider the location of the roads explicitly, assuming their spatial configuration to be that of a grid, as depicted in Fig. 1, and we explore square and rectangular shapes. For analytical tractability, we assume infinite carrying capacity and that all individuals die when crossing a road, hence $r_0 = -\infty$. The analytical solution can be found in Supplemental Information. Here, the important result is the minimum size of the smallest side of a patch of rectangular shape (i.e., the smallest distance between roads), L_m, such that the population remains constant or increases:

$$L_m = \pi\sqrt{\frac{\sigma^2}{2r_1}\left(1+\frac{1}{\alpha^2}\right)}, \tag{3}$$

where $\alpha \geq 1$ is the ratio of the largest to the smallest side. In the case of a square $\alpha = 1$, and

$$L_m = \pi\sqrt{\frac{\sigma^2}{r_1}}. \tag{4}$$

Equations 3 and 4 show two important features. First, the minimum size L_m required for a population to survive increases with the dispersal variance, σ^2, and, second, L_m decreases with the growth rate, r_1. We can understand the first feature by observing that individuals of a more mobile species, corresponding to larger σ^2, have a higher probability of reaching a road, hence of dying; Fig. 2a shows the dependence of L_m on σ^2, for constant r_1, assuming square patches. We can understand the second feature by realizing that for two species with the same σ^2, the one with the highest growth rate can compensate for higher mortality on the roads; Fig. 2b shows the dependence of L_m on r_1, for constant σ^2, assuming square patches. Notice, however, that both relationships are non-linear: L_m increases slowly when the dispersal distance increases (Fig. 2a) and L_m decreases fast when the growth rate increases (Fig. 2b).

Equations 3 and 4 also show how shape influences minimum patch size. Specifically, they show that for the same area a population inhabiting a rectangle needs to have a smaller ratio σ^2/r_1 than one in a square. One could argue that this happens because for the same area a rectangle has a larger perimeter than a square, hence a larger contact region with roads. However, one should be careful with an explanation based on the perimeter-to-area ratio. In general, what matters is the size of the core area of the patch, with core area roughly defined as the area at a certain distance from the border (e.g., Fagan et al. 1999; Cantrell and Cosner 2003). So, for example, a patch with a very wriggled boundary, and therefore a large perimeter-to-area ratio, would have the same σ^2/r_1 threshold as a patch with a smooth boundary, as long as they have equal core areas (see, for example, Fig. 1 of Fagan et al. 1999). Using the rough definition of core area given above, one can see that the reason why a rectangle requires a smaller σ^2/r_1

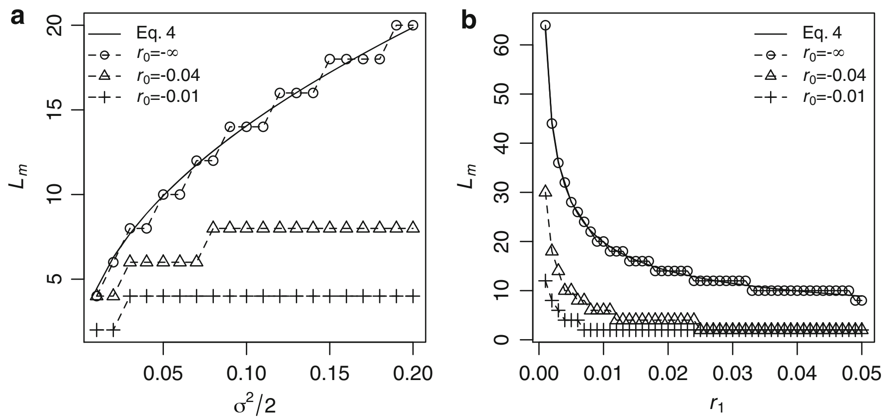


Fig. 2 Minimum distance between roads, L_m, that allows a population to persist, as a function of the dispersal distance, $\sigma^2/2$, plot (a), and as a function of the growth rate, r_1, plot (b), for square patches, $\alpha = 1$. Plot (a) was obtained with $r_1 = 0.01$, plot (b) with $\sigma^2/2 = 0.02$; arbitrary units

than a square of the same area is because the former has a smaller core area.

With the present model we can also determine the time to extinction of a population in a nonviable patch, that is, one with area, A, smaller than that of the minimum patch size, A_m. However, instead of using the total time to extinction, we will use the relaxation time, t_{rel}, defined as the time a population takes to reach $1/e$ of its original size, because it obviates the need to define the density threshold below which the population is extinct, which can be different for different populations. Counting from the moment roads were built, $t = 0$, the time the population takes to reach $1/e$ of its original abundance is (see Supplemental Information)

$$t_{rel} = \frac{1}{\frac{\sigma^2}{2}k^2 - r_1}, \qquad (5)$$

where $k^2 = \pi^2/L^2 + \pi^2/(\alpha L)^2$. t_{rel} is shown in Fig. 3 for different values of $L < L_m$ assuming a square patch.

As expected, the larger the size of the plot the longer it takes for the population to reach $1/e$ of its initial size. We will return to the relaxation time when $r_0 \neq -\infty$ in case 3.

Case 3: Non-lethal roads

We now combine (i) explicit spatial location of the roads, (ii) mortality different from 100% on roads, and (iii) logistic growth outside roads. Under these assumptions the analytical solution of the model is no longer possible, thus we use a numerical approach to obtain its equilibrium solution by transforming the differential equations into difference equations using Euler's explicit method (see Supplemental Information).

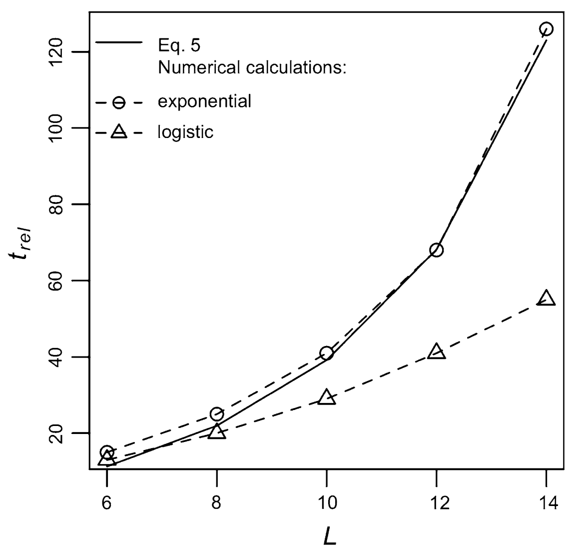


Fig. 3 Relaxation time, t_{rel}, for nonviable populations as a function of the patch size, $L < L_m$, on the basis of Eq. 5, continuous line, and numerical calculations using Eq. 6 assuming exponential and logistic growth. The parameters used were $r_1 = 0.01$, $r_0 = 0.01$ and $\sigma^2/2 = 0.18$; arbitrary units

We now consider the population density in a finite number of cells in a two dimensional grid. It is worth presenting Eq. 1 in the difference equations form under the new assumptions because it will give us further insights on the processes that it describes. We have

$$n_{i,j,t+1} = \begin{cases} n_{i,j,t} + \frac{\sigma^2}{2}(n_{i-1,j,t} + n_{i+1,j,t} + n_{i,j-1,t} + n_{i,j+1,t}) - 4\frac{\sigma^2}{2}n_{i,j,t} + r_1 n_{i,j,t}(1 - n_{i,j,t}/K) & \text{if} \quad (i,j) \notin road \\ n_{i,j,t} + \frac{\sigma^2}{2}(n_{i-1,j,t} + n_{i+1,j,t} + n_{i,j-1,t} + n_{i,j+1,t}) - 4\frac{\sigma^2}{2}n_{i,j,t} + r_0 n_{i,j,t} & \text{if} \quad (i,j) \in road \end{cases} \tag{6}$$

where $n_{i,j,t}$ is the density of the population in cell (i, j) at time t, with $i = 1,\ldots,I$, $j = 1,\ldots,J$, and $t = 1,\ldots,T$. Equation 6 can be interpreted as follows (and see Fig. 4 for a schematic representation): The density at time $t + 1$, $n_{i,j,t+1}$, is equal to the density at time t, $n_{i,j,t}$, plus the term $\frac{\sigma^2}{2}(n_{i-1,j,t} + n_{i+1,j,t} + n_{i,j-1,t} + n_{i,j+1,t})$, which is the contribution from the four adjacent cells (since the population has the same dispersal variance independently of the cell, $\frac{\sigma^2}{2}$ is the same for all), minus the term $4\frac{\sigma^2}{2}n_{i,j,t}$, which is the fraction lost to the four adjacent cells, plus the term $r_1 n_{i,j,t}(1 - n_{i,j,t}/K)$, which corresponds to the logistic growth in the cells, or the term $r_0 n_{i,j,t}$, which corresponds to the mortality on roads.

The computation region consists of a grid with $I \times J$ cells with the road configuration of Fig. 1. We assume periodic boundary conditions; hence, to ensure that all patches have the same shape and size in the (infinite) periodic landscape, the roads are located at ¼ and ¾ of the sides of the plot. For the population density initial condition we choose it to be uniformly distributed on the grid; in the majority of the cases we used $n_{i,j,0} = 1$, but when studying time to extinction we used $n_{i,j,0} = K$, the carrying capacity. In Supplemental Information we discuss the domain of stability of the solutions of Eq. 6.

We now use numerical solutions of Eq. 6 to replicate the previous results and extend the analyses to situations where analytic results are unattainable. We start by comparing the critical road density, h_{crit}, obtained with Eq. 2 and numerical calculations when we change the road mortality, r_0. Figure 5 shows examples of good and poor agreement between the results of numerical calculations and those of Eq. 2, the former occurring for larger σ^2 and the latter for smaller σ^2, revealing that when individuals are not very mobile, not only road density is important but

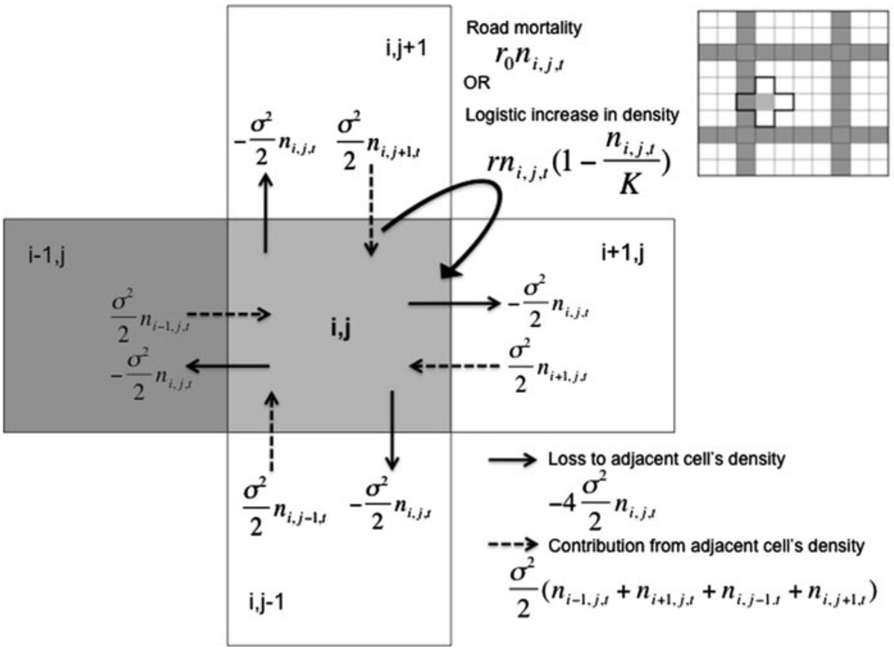


Fig. 4 The plot on the top right of the figure shows the landscape from where 5 cells were highlighted to illustrate the geometrical interpretation of Eq. 6. This scheme represents the dynamics of the population in the cell (i,j) for each time step. The part of Eq. 6 representing the temporal dynamics depends on whether the cell is a road ($r_0 n_{t,i,j}$) or not ($r_1 n_{t,i,j}(1 - n_{t,i,j}/K)$)

also their layout. Our conclusion is that, although Eq. 2 provides an easy rule of thumb to assess the viability of a population on the basis of growth rates and road density, it is only a first approximation (see also the "Discussion" section and Supplemental Information).

Figure 5 also illustrates two important aspects determining the persistence of a population. First, a decrease in the mean dispersal distance leads to an increase in critical road density, because contact with roads is reduced, as discussed previously. Second, as expected, when road mortality increases (r_0 decreases) the critical road density decreases, that is, for a population to survive an increase in road mortality requires a decrease in the road area.

Comparing now the results for non-lethal roads with those of lethal roads (case 2), we return to the question of the minimum patch size. Figure 2 shows, in addition to full mortality, $r_0 = -\infty$, the results obtained for finite r_0, which are not possible with case 2. The curves obtained with numerical calculations are stepwise because of the discrete nature of the possible values of L_m. Nevertheless, there is an excellent agreement between the results of the calculations when $r_0 = -\infty$ and the predictions of Eq. 4. The results obtained with numerical solutions for finite r_0 show, as expected, that a decrease in the mortality on the roads (smaller $|r_0|$) reduces the value of the minimum patch size, L_m.

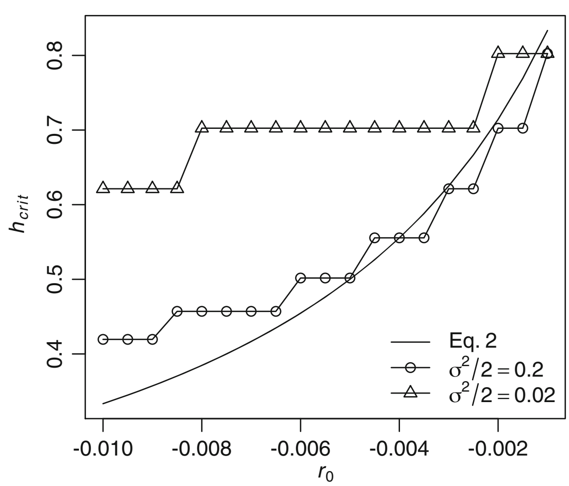


Fig. 5 Comparison of the results obtained with numerical calculations (case 3) and those predicted by Eq. 2 (case 1). Notice the reasonable fit for the largest $\sigma^2/2 = 0.2$ and the poor fit for the smallest $\sigma^2/2 = 0.02$. We used $r_1 = 0.005$; arbitrary units

Continuing the comparison with lethal roads, case 2, we consider now the decaying times for non-viable populations. Starting with exponential decay, Fig. 3 shows an excellent agreement between the results of the simulations with those of Eq. 5. When we consider logistic growth, which is not possible with case 2, the time it takes to reach $1/e$ depends on the original size of the population, contrarily to what happens to exponential decay. Here we assume that the population has initial size equal to its carrying capacity, K. Observe from Fig. 3 that the relaxation time is now much shorter, as expected, because logistic growth, being smaller than exponential growth, leads to a faster decay of the population. Notice that if the original size of the population had been small, in the regime where logistic growth (or decay) is almost exponential, the results would have been similar to those predicted by Eq. 5.

Before proceeding, we would like to compare the prediction obtained from cases 2 and 3 with the estimates for maximum road density for wolves of Mech et al. (1988), Mladenoff et al. (1999) and Whittington et al. (2005). These authors estimated that the critical road density for wolves is between 0.36 and 1 km/km^2. We do not have estimates for σ^2 or r_1 for wolves, so we used the values listed for coyotes by Pereira and Daily (2006): $\sigma^2 = 133$ km^2/year and $r_1 = 0.88$/year. If we assume square patches, application of Eq. 4 gives $L_m = 38.62$ km. If we use road density, as it is usually expressed in km/km^2, then we obtain for a portion of the landscape like that of Fig. 1, $8L_m/(4L_m^2) = 0.051$ km/km^2. This value is much smaller than the estimates given above, but it is not unexpected, because Eq. 4 assumes that all animals die on roads, a clearly unrealistic assumption for wolves. In order to use the more realistic case 3 (non-lethal roads) we need a value for r_0. Again we use the value listed in Pereira and Daily (2006) for coyotes in an entire region of unfavorable habitat, $r_0 = -0.1$/year, based on natural mortality and zero birth rates. In roads the assumption of zero birth is reasonable, but mortality is likely to be much larger, hence we assume it to be one order of magnitude larger, $r_0 = -1.0$/year. If we use the values provided by Pereira and Daily (2006), $\sigma^2/r_1 = 133/0.88$ km, then we obtain $L_m = 4$ km, or a road density of ~ 0.36 km/km^2. We recognize that our calculations are crude, but their similarity to that of the estimates on the basis of empirical studies is nevertheless remarkable.

Case 4: road mortality mitigation using fences

We now use the theoretical results of case 2 (lethal roads) and the framework provided by case 3 (nonlethal roads) to explore how fences can allow a population to survive in an otherwise nonviable patch.

Equations 1 and 6 were derived under the assumption that individuals have equal probability of moving in all directions with a specified average speed (unbiased Brownian motion). The presence of a fence reduces, or eliminates, movement along one or more directions, therefore, we have a biased random walk. Biased movement across a boundary has been studied by several authors (e.g., Cantrell and Cosner 1999; Ovaskainen and Cornell 2003; Pereira et al. 2004). If a fence is permeable, that is, if it allows some animals to go through, the value of σ^2 between the road cell and the habitat cell is reduced by a factor $f < 1$, $\sigma^{2*} = (1 - f)\sigma^2$. In the extreme case of $f = 0$, the fences are nonexistent, and in the extreme case of $f = 1$ fences completely block access to roads, and $\sigma^{2*} = 0$. In addition to varying the permeability of the fences, we also consider how much of the perimeter of a patch must be fenced so that a population can persist. When fences cover only part of the road we study the effectiveness of different fence layouts; the inset plots in Fig. 6 show the different fence layouts studied, that we called “alternate”, Fig 6b, and “geometries 1,2,3, and 4”, plots Fig. 6c–f. This choice of different layouts is not meant to be exhaustive, but simply to illustrate that they have different consequences for a population’s persistence.

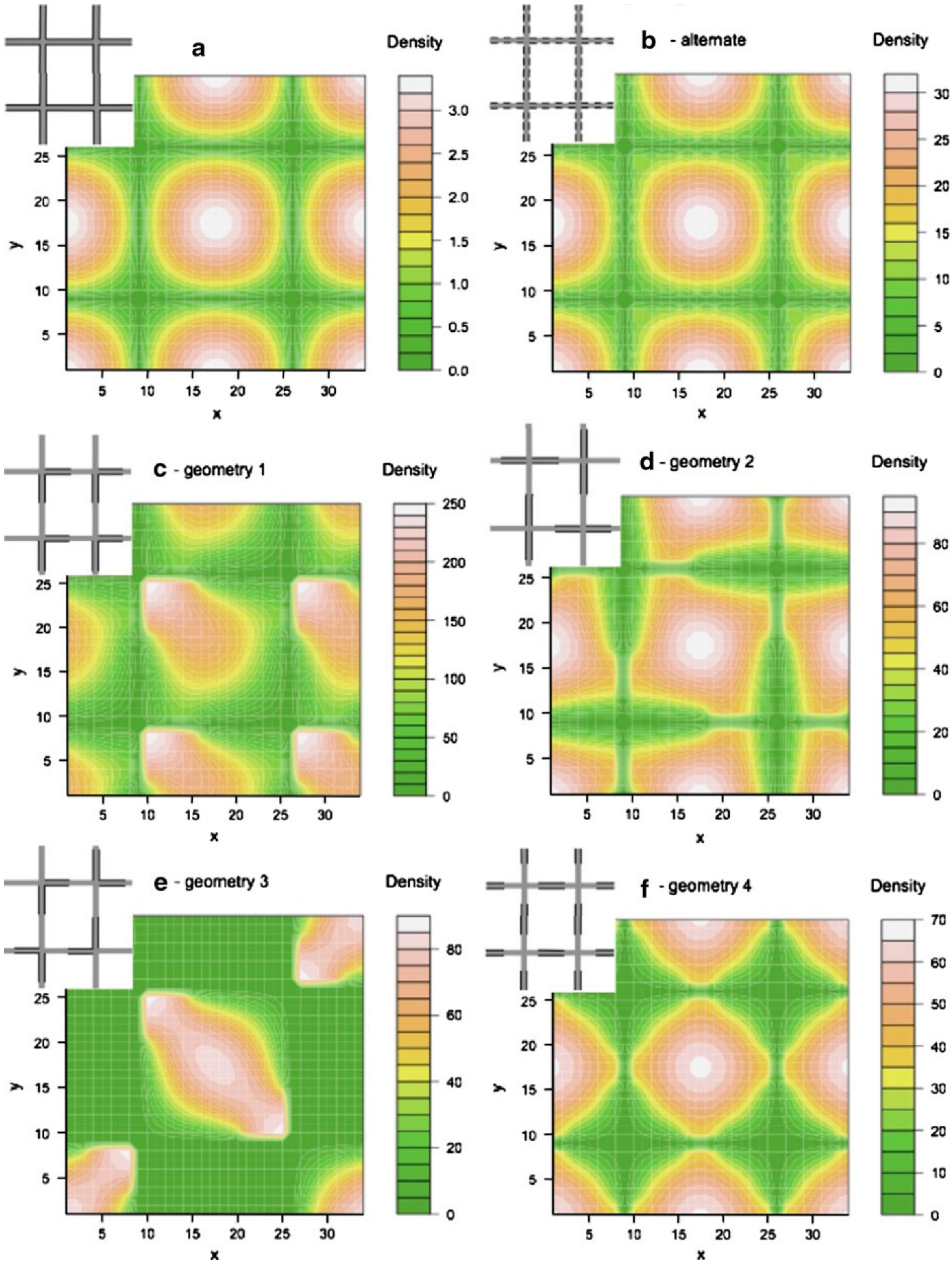
To study how fences may rescue a population in a nonviable fragment we calculated, first, the minimum patch size, L_m, for given values of σ^2 and r_1 using Eq. 4 (assuming square patches) and, then, we simulated the presence of fences in patches with $L < L_m$. When fences have permeability, f, different from 1 we assume that the roads are completely fenced, and the question is: what is the value of f above which the population survives? When we study different layouts, we assume $f = 1$, that is, no animals can go through the fences, and the question

Fig. 6 Population density for different fences’ layouts; the ▶ inset plots show the spatial arrangement of the fences. These plots correspond to the minimum fences permeability, plot (a), or minimum perimeter fenced required for a population to survive in an otherwise square patch of nonviable size $L = 16$ when $L_m \sim 19$; the parameters used in the simulation were $r_1 = 0.01$, $r_0 = -\infty$ and $\sigma^2/2 = 0.19$; arbitrary units. Notice that the different fences’ geometries lead to very different densities. Interestingly, one fence layout, plot (e), leads to the extinction of the population in some patches but not in others

is: what percentage of the roads’ perimeter should be fenced so that the population survives? Not having the perimeter fully fenced is important for, at least, two reasons. First, it reduces costs and, second, and more importantly, it allows the movement of animals between patches, eventually rescuing the population in regions where it has become extinct, and, reducing genetic isolation.

Figures 6 and 7 show the results of the simulations, where the darkest regions correspond to low densities and the lightest ones to high densities. Notice that, not unexpectedly, the alternate layout, plot 6 (b), leads to a spatial pattern of the population density very similar to that of a permeable fence, plot 6 (a). This result was expected because we can interpret a permeable fence as limiting case of an alternate layout. The similarities between these two cases can also be seen in Fig. 7, where the curves for the fraction of fenced perimeter and the value of the permeability, f, are almost identical. However, as plots 6 (a) and 6 (b) show, the alternate layout allows for much larger population densities.

Observe from Fig. 7 that different layouts require different fractions of fenced perimeter. Among the layouts studied the most efficient is the one labeled “geometry 4”, plot 6 (f), where fences are located at equal distance from road intersections. “Geometry 1”, plot 6 (c), leads to a spatial pattern similar to that of “geometry 3”, but without population extinction in some patches. In fact, plot 6 (e), geometry 3, shows that the population can go extinct in some patches and survive in others. What happens in this case is that fences are connected on some corners, forming a larger contiguous fence for some patches, but not for others. Recall that this result was obtained assuming that roads are lethal ($r_0 = -\infty$). If a percentage of animals survives when crossing roads, then for some finite values of r_0 the population will be present in all patches, but with lower density in the patches where it previously went extinct. What is happening now is


a
Density
b - alternate
c - geometry 1
d - geometry 2
e - geometry 3
f - geometry 4
x
y

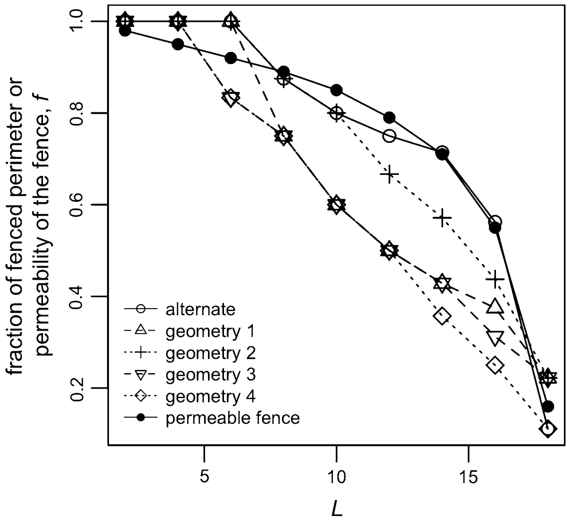


Fig. 7 Minimum fraction of fenced perimeter or maximum permeability, f, of the fence such that a population can survive in a square patch of size L smaller than the minimum viable size $L_m \sim 19$ of an unfenced patch (arbitrary units). When fences are permeable we assume that roads are completely fenced. The geometries are those depicted in the insets in Fig. 6. As expected, the smaller the size of the patch, the larger f or the percentage of fenced perimeter required. Notice, however, that some geometries require less fenced area for the same patch size L. The parameters used in the numerical calculations were $r_1 = 0.01$, $r_0 = -\infty$ and $\sigma^2/2 = 0.19$; arbitrary units

that growth in the previously non-viable patches compensates for the mortality in the roads, and some individuals can disperse from the viable to the non-viable patches.

Discussion

Roads represent a permanent modification of the landscape that threatens the existing habitat and the populations depending on it. In this study, we used an analytical model to assess the impact of a road network on a population and possible mitigation measures using fences. Our model is part of a larger class of models dealing with edge-mediated effects, where the focus is on how edges alter ecological processes and not so much on edge related patterns themselves (Fagan et al. 1999). In our study roads were the edges, and we were particularly interested in how roads interact with the dispersal ability of a population. In our models we assumed that individuals disperse equally in all directions, except when we considered fences, which acted as reflecting boundaries. However, we know, thanks to empirical studies, that some species exhibit preferential directions, for example, by avoiding roads (e.g. Shepard et al. 2008). Incorporation of bias movement, that is, preferential movement in some directions, at a boundary, is, in principle, possible using the framework provided by Eq. 6. There have also been analytic approaches dealing with biased movement (Cantrell and Cosner 1999; Ovaskainen and Cornell 2003; Pereira et al. 2004) and these can in the future be incorporated in studies assessing the impact of roads in populations. One of us, Navarro (unpublished data), performed computer simulations of biased and non-biased movement in a highly fragmented landscape and showed that populations exhibiting preferential movement towards a better habitat attain higher population densities. We expect a similar trend if we apply the same techniques to a landscape with a road network, but it is outside the scope of this work.

Table 1 summarizes the 4 variations of the model studied. Case 1, though simple because it depends only on road density, without requiring knowledge of the spatial layout of the roads, gave very different results from those obtained with the more realistic case 3. Specifically, we found that case 1 only gave good results when dispersal variance, σ^2, was large. This is not to say that road density is not an important aspect to take into consideration. For instance, Vos and Chardon (1998) found a negative correlation between road density and pond occupancy of a moor frog (*Rana arvalis*) population. What our work highlights is that the spatial arrangement of the roads and the shape of the patches are also important.

Cases 2 and 3 considered explicitly the spatial layout of the roads. We emphasize two results from case 2 (lethal roads). The first is that there is a negative relationship between diffusion and population persistence (Eqs. 3 and 4). This supports Jaeger and Fahrig (2004)'s simulation results that increased mobility is detrimental and agrees with empirical studies that showed that road mortality affects primarily those species that show the highest mobility patterns (Bonnet et al. 1999; Carr and Fahrig 2001; Gibbs and Shriver 2002), or those individuals at life stages that require larger mobility such as when dispersing or breeding (Seiler 2001; Clevenger et al.

2003; Saeki and MacDonald 2004; Dodd et al. 2005; Grilo et al. 2009). The second result is that the total patch area is not enough to determine the impact of roads on the survival of the population: the shape of a patch also plays an important role. We exemplified the importance of shape using square and rectangular patches and showed that the former are to be preferred. When we extended this analysis to finite values of r_0, we observed that decreasing road mortality leads to smaller minimum patch sizes, which, from a practical perspective, means that taking measures to reduce road-kills, such as, traffic or speed limitation, can be the first step towards efficient mitigation strategies (van Langevelde and Jaarsma 2004).

We expect a time lag between the construction of roads and observable effects on local populations (e.g., Findlay and Bourdages 2000; Freitas et al. 2010). Using case 2 (lethal roads) we derived an expression, Eq. 5, that estimates the relaxation time for a population in a patch smaller than the required minimum area for survival.

In case 4 we studied the use of fences. Fences are a cost-effective mitigation measure provided that the wild population does not show any systematic road avoidance behavior and that traffic mortality is high enough to jeopardize the population's persistence (Jaeger and Fahrig 2004). However, the role of fences may be detrimental because they increase a population's isolation, and we know from the studies by Casagrandi and Gatto (1999) and Gavinho (2008) that some dispersal is better than no dispersal in a metapopulation; notice, however, for the majority of the parameter space the deterministic disadvantages of dispersal dominate, and the probability of extinction increases with dispersal. Therefore, a fully fenced road network is not the best approach and we studied the fraction of a patch perimeter that should be fenced so that the population can persist.

From a practical perspective, probably the most important result of our models is that some spatial arrangements of fences are more efficient (measured by the total fenced perimeter required) at maintaining a population in an otherwise non-viable patch (Fig. 6). For example, we found that an alternate layout for fences is less efficient than a continuous one (Fig. 7). This result concurs with an empirical study of spatial patterns of road kills conducted by Malo et al. (2004) who found that collision rates were higher when guardrails were intermittent in comparison to areas with continuous guardrails. Importantly, as well, we found that some fence layouts (geometries 1 and 3, Fig. 6c, e) create regions characterized by high population densities, and one configuration (geometry 3, Fig. 6e) may lead to the extinction of the population in some patches. An important message is that the layout of the fences, and not only the total of the fenced perimeter, has implications for the spatial patterns of the populations.

In this study we considered the use of fences to rescue populations that, otherwise, would have become extinct. This is not to say that there are no negative effects associated with fences, such as, for example, increased population isolation. There are also other mitigation measures, such as, underpasses, tunnels and culverts, that do not lead to the isolation of populations and that can be used together with, or instead of, fences. Our model can be extended to study the implementation of these mitigation measures, such as their best locations and geometries. We intend to address these matters in future work.

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References

Bonnet X, Naulleau G, Shine R (1999) The dangers of leaving home: dispersal and mortality in snakes. Biol Conserv 89:39–50

Cantrell RS, Cosner C (1999) Diffusion models for population dynamics incorporating individual behavior at boundaries: applications to refuge design. Theor Popul Biol 55:189–207

Cantrell RS, Cosner C (2003) Spatial ecology via reaction–diffusion equations. Wiley, Chichester, West Sussex, UK

Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of differing vagility. Conserv Biol 15:1071–1078

Carr LW, Fahrig L, Pope SE (2002) Impacts of landscape transformation by roads. In: Gutzwiller KJ (ed) Applying landscape ecology in biological conservation. Springer-Verlag, New York, pp 225–243

Casagrandi R, Gatto M (1999) A mesoscale approach to extinction risk in fragmented habitats. Nature 400:560–562

Clevenger AP, Chruszcz B, Gunson KE (2003) Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. Biol Conserv 109:15–26

Cosner C (2008) Reaction–diffusion equations and ecological modeling. In: Friedman A (ed) Tutorials in mathematical biosciences iv, ecology and evolution. Springer-Verlag, Berlin, pp 77–115

Dodd NL, Gagnon JW, Boe S, Schweinsburg RE (2005) Characteristics of elk-vehicle collisions and comparison to GPS-determined highway crossing patterns. UC Davis: Road Ecology Center. http://www.escholarship.org/uc/item/5r37r5bm

Epps CW, Palsboll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecol Lett 8:1029–1038

Fagan W, Cantrell RS, Cosner C (1999) How habitat edges change species interactions: a synthesis of theory and data. Am Nat 153:165–182

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biol Conserv 73:177–182

Findlay CS, Bourdages J (2000) Response time of wetland biodiversity to road construction on adjacent lands. Conserv Biol 14:86–94

Ford AT, Fahrig L (2008) Movement patterns of eastern chipmunks (*Tamias striatus*) near roads. J Mammal 89:895–903

Forman RT (1998) Road ecology: a solution for the giant embracing us. Landscape Ecol 13:iii–v

Forman RT (2000) Estimate of the area affected ecologically by the road system in the United States. Conserv Biol 14:31–35

Forman RT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Syst 29:207–231

Forman RT, Reineking B, Hersperger AM (2002) Road traffic and nearby grassland bird patterns in a suburbanizing landscape. Environ Manage 29:782–800

Freitas SR, Hawbaker TJ, Metzger JP (2010) Effects of roads, topography, and land use on forest cover dynamics in the Brazilian Atlantic Forest. For Ecol Manag 259:410–417

Gavinho C (2008) Estudos sobre o efeito da fragmentação da paisagem na dimensão de uma população. Dissertation, Instituto Superior Técnico

Gibbs JP, Shriver WG (2002) Estimating the effects of road mortality on turtle populations. Conserv Biol 16:1647–1652

Goosem M (2007) Fragmentation impacts caused by roads through rainforests. Curr Sci 93:1587–1595

Grilo C, Bissonette JA, Santos-Reis M (2009) Spatial–temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. Biol Conserv 142:301–313

Jaeger JA, Fahrig L (2004) Effects of road fencing on population persistence. Conserv Biol 18:1651–1657

Jaeger JA, Fahrig L, Ewald KC (2005) Does the configuration of road networks influence the degree to which roads affect wildlife populations? U. C. Davis: Road Ecology Center. http://www.escholarship.org/uc/item/1783q0kv

Kierstead H, Slobodkin LB (1953) The size of water masses containing plankton bloom. J Mar Res 12:141–147

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. J Appl Ecol 41:711–723

Laurance WF, Cochrane MA, Bergen S, Fearnside PM, Delamônica P, Barber C, D'Angelo S, Fernandes T (2001) The future of the Brazilian Amazon. Science 291:438–439

Laurance SG, Stouffer PC, Laurance WF (2004) Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conserv Biol 18:1099–1109

Laurance WF, Goosem M, Laurance SG (2009) Impacts of roads and linear clearings on tropical forests. Trends Ecol Evol 24:659–669

Malo JE, Suarez F, Diez A (2004) Can we mitigate animal–vehicle accidents using predictive models? J Ecol 41:701–710

Mech LD, Fritts SH, Radde GL, Paul WJ (1988) Wolf distribution and road density in Minnesota. Wildl Soc Bull 16:85–87

Mladenoff DJ, Sickley TA, Wydeven AP (1999) Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. Ecol Appl 9:37–44

Ovaskainen O, Cornell SJ (2003) Biased movement at a boundary and conditional occupancy times for diffusion processes. J Appl Probab 40:557–580

Pereira HM, Daily GC (2006) Modeling biodiversity dynamics in countryside landscapes. Ecology 87:1877–1885

Pereira HM, Daily GC, Roughgarden J (2004) A framework for assessing the relative vulnerability of species to land-use change. Ecol Appl 14:730–742

Pohlman CL, Turton SM, Goosem M (2009) Temporal variation in microclimatic edge effects near powerlines, highways and streams in Australian tropical rainforest. Agric For Meteorol 149:84–95

Prasad AM, Iverson LR, Peters MP, Bossenbroek JM, Matthews SN, Sydnor TD, Schwartz MW (2010) Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landscape Ecol 25:353–369

Pratt C, Lottermoser BG (2007) Mobilisation of traffic-derived trace metals from road corridors into coastal stream and estuarine sediments, Cairns, northern Australia. Environ Geol 52:437–448

Saeki M, Macdonald DW (2004) The effects of traffic on the raccoon dog (*Nyctereutes procyonoides viverrinus*) and other mammals in Japan. Biol Conserv 118:559–571

Seiler A (2001) Ecological effects of roads: a review. Grimso Wildlife Research Station, Department of Conservation Biology, University of Agricultural Sciences, s-730 91 Riddarhyttan, Sweden

Shepard DB, Kuhns AR, Dreslik MJ, Phillips CA (2008) Roads as barriers to animal movement in fragmented landscapes. Anim Conserv 11:288–296

Skellam JG (1951) Random dispersal in theoretical populations. Bull Math Biol 53:135–165

Spellerberg IF (1998) Ecological effects of roads and traffic: a literature review. Glob Ecol Biogeogr Lett 7:317–333

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conserv Biol 14:18–30

van der Grift EA, Verboom J, Pouwels R (2003) Assessing the impact of roads on animal population viability. UC Davis: Road Ecology Center. http://www.escholarship.org/uc/item/4jq850cq van Langevelde F, Jaarsma CF (2004) Using traffic flow theory to model traffic mortality in mammals. Landscape Ecol 19:895–907

Vos CC, Chardon JP (1998) Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. J Appl Ecol 35:44–56

Whittington J, St Clair CC, Mercer G (2005) Spatial responses of wolves to roads and trails in mountain valleys. Ecol Appl 15:543–553

Wilkie D, Shaw E, Rotberg F, Morelli G, Auzel P (2000) Roads, development, and conservation in the Congo Basin. Conserv Biol 14:1614–1622