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Flattened fauna and mitigation: Traffic victims related to road, traffic, vehicle, and species characteristics

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Abstract

A model is developed to look at the probability of successful road traversing by mammals, based on Poisson-distributed arrivals of cars. It is a double 'blind' model presuming that a collision occurs when the animal and the car are on the same part of the road at the same time. When a car and an animal impact, two types of collisions can occur: 'car hits animal' and 'animal hits car'. The probability of these events, and thus the probability of successful road traversing by animals, is determined by road, traffic, vehicle, and species characteristics. Use of the model shows that, for the parameter ranges, traffic volume and the animals' traversing speed have the largest effects on whether a collision occurs. This model is applied to compare alternative network solutions and to evaluate traffic calming measures on a former arterial highway. It is shown that these measures are effective in mitigating traffic mortality among mammals.

Keywords: Habitat fragmentation; Wildlife traffic mortality; Road ecology; Transportation planning

1. Introduction

"Transport's impact on the environment is multifaceted and can be severe" (Button and Nijkamp, 1999). Nature, especially habitat fragmentation for plants and animals, forms one of these facets. 'Flattened fauna' (carcasses on the road) is a macabre illustration of the most visible negative impact of roads and their traffic flows on nature: traffic mortality among animals traversing the road. This is a frequently studied problem from an ecological point of view. However, in transportation planning, this problem has received little attention so far.

The aim here is to combine knowledge on animal movement through the landscape with transportation engineering knowledge on headway distributions on roads in a traversability model. The road's traversability is defined as the probability of an individual successfully crossing that road. This model can be used to

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estimate changes in the number of traffic victims among traversing animals before and after mitigating measures giving the transportation engineer a tool for calculating the impacts on traversability for animal species when considering alternative regional network policies. The model enables ecologists to get an understanding of the factors that influence traversability. Moreover, this model can be used as a basis for a model for animal population dynamics (Van Langevelde and Jaarsma, 2004).

2. Roads and traffic: impacts on wildlife

The ecological literature describes a wide range of direct and indirect effects of transportation infrastructure on nature (Seiler, 2002; Forman et al., 2003). Indirect effects follow the construction of new roads or railways, for example, consequent industrial development or changes in human settlement and land use patterns. We focus on the effects that directly impact wildlife and its habitat, as these effects are usually the most relevant to the transport sector. On the other hand, direct ecological effects are caused by the physical presence of the infrastructure section and its traffic flows. These ecological effects are generally classified into five major categories as presented in Fig. 1: (1) habitat loss (land uptake, habitat transformation); (2) corridor habitats (corridor, conduit); (3) disturbance and edge effects (avoidance, pollution, predation); (4) barrier effects (by unsuitable habitat/disturbances, repelled by traffic or road characteristics, physical hindrances); and (5) traffic mortality. Together, these effects lead to habitat fragmentation, which is the subdivision of natural habitats into small and isolated patches. Habitat fragmentation could result in conditions whereby species, as well as their populations, are endangered and might become extinct. Habitat fragmentation has been recognised as a significant cause for the decline of biodiversity and has become a major concern for society.

2.1. Habitat loss

Habitat loss is an inevitable consequence of infrastructure construction. The total area designed for transport is estimated to be 5–7% of the land surface in rather densely populated West European countries such as the Netherlands, Belgium and Germany (Jedicke, 1994). For Sweden, where the transportation infrastructure is sparser, roads and railways are estimated to cover about 1.5% of the land surface (Seiler and Erikson, 1997). Excluding private roads in sub-urban areas as well as driveways and parking areas, and based on an average road density of about 0.75 km/km^2, the US devotes about 0.45% of its land area to roads (Forman et al., 2003). These authors estimate that adding the right-of-way zone of public roads would roughly double that amount.

2.2. Corridor habitats

Numerous inventories indicate the great potential of verges to support a diverse range of plant and animal species, but verges may also serve as a conduit for species movement of both generalist species that are tolerant

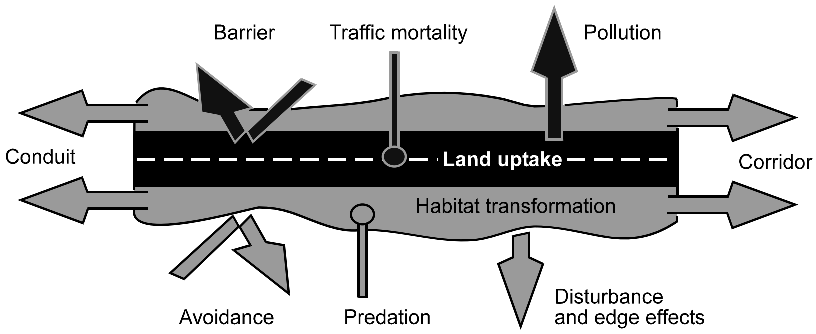


Fig. 1. Schematic representation of the direct ecological effects of infrastructure. Source: Seiler (2002).

of disturbance and 'unwanted' or alien species that spread into the surrounding habitats. "The overall corridor function of infrastructure verges will most likely be influenced by the ecological contrast between the vegetation-structure in the corridor and the surrounding habitat" (Seiler, 2002).

2.3. Disturbance and edge effects

Disturbance and edge effects mainly result from environmental pollution caused by infrastructure construction and use. Physical disturbance appears during construction activities, when soil, landscape relief, surface and groundwater flows change, even on longer distances from the road, and so alter the vegetation. Chemical pollutants through road use, such as road dust, salt, heavy metals, fertiliser nutrients, and toxins, largely contribute to the disturbance and edge effects at distances several hundred metres away from the road (Seiler, 2002).

Traffic noise is one of the major polluting factors in areas where tranquillity is perceived as an increasingly valuable resource. It is questionable whether traffic noise stresses wildlife and humans in a similar way. However, timid species might interpret traffic noise as an indicator of human presence and consequently avoid noisy areas. Birds appear to be especially sensitive to traffic noise. Densities of breeding populations of woodland birds and grassland birds are negatively related to noise burden (Reijnen et al., 1995).

2.4. Barrier effects

The barrier effect of infrastructure results from a combination of disturbances (such as traffic noise, vehicle movement, pollution, and human activity) and physical hindrances (such as infrastructure surface, ditches, and fences). The clearance of the infrastructure (i.e. the distance from the road to dense vegetation) and the open verge character may also act as a barrier to many species, especially small ones (Oxley et al., 1974). Depending on the species, some animals may not experience any physical or behavioural barrier at all, whereas others may not even approach the road.

Most infrastructure barriers do not completely block animal movements, but they do significantly reduce the number of crossings (Mader, 1984; Merriam et al., 1989). "The fundamental question is this: how many successful crossings are needed to maintain habitat connectivity" (Seiler, 2002). To answer this question, information is needed on the movements of specific species in a fragmented landscape and on the chance of a successful road crossing for those species that actually cross roads.

2.5. Mortality

Traffic mortality is one of the major causes of death for many species in human-dominated landscapes. For the most common species, traffic mortality is not considered a severe threat to population survival (Seiler, 2002). For some species, e.g. badger (*Meles meles*), however, it is most likely responsible for regional extinction (Lankester et al., 1991; Clarke et al., 1998). Moreover, traffic is considered one of the most important sources of mortality for many endangered or rare species. Unlike natural predation, traffic is non-compensatory and kills a constant proportion of the population. Although the number of traffic victims may seriously reduce the population size of a species such as hedgehog (*Erinaceus europaneus*) (Huijser and Bergers, 2000), the effect of traffic mortality on populations is often difficult to measure since other factors, such as area, quality and spatial configuration of the habitat along the road, also play a role.

There are complex relationships between the barrier effect and the mortality effect, which determine mortality during movement (i.e. the movement death rate) and the number of successful crossings (i.e. the crossover rate) (Fig. 2). To quantify these effects, relationships between traffic and road characteristics must be found. For instance, a wider road encourages both higher traffic volumes and speeds. This, in turn, reduces the chance of a successful road crossing. In addition, an increase in traffic volume may lead to a flow of vehicles that prevents individuals from crossing the road. Finally, an increase in traffic volume also determines the noise level, which, in turn, increases the barrier effect. In the next section, we focus on the mortality effect of roads and their traffic since current knowledge on this subject does not allow quantification of the barrier effect of roads.

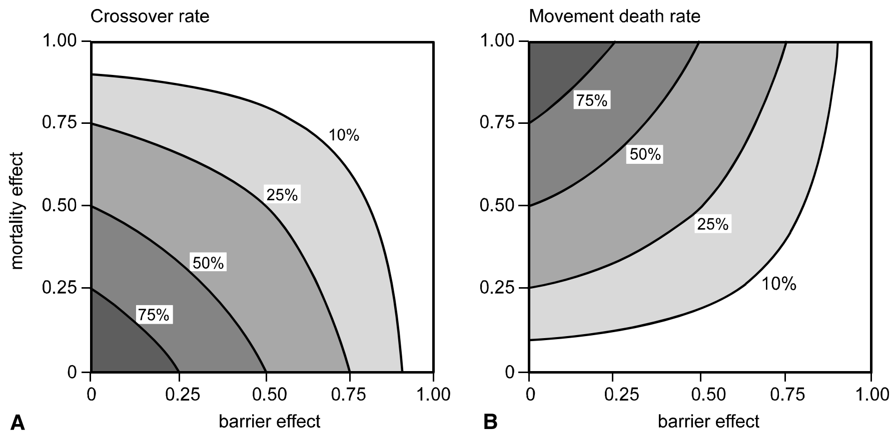


Fig. 2. (A) The crossover rate and (B) the movement death rate as function of the barrier effect and the mortality effect. Source: Verboom (1994).

3. Modeling traversing wildlife: traversability

In traffic engineering, the calculation of headway distributions, i.e. the frequency of the length of gaps between successive vehicles in a traffic flow at a given cross-section is commonly based on the assumption of a Poisson distributed process (Haight, 1963; Daganzo, 1997). The Poisson distribution is a discrete distribution that describes the number of events during a given time period. Here, the event is a vehicle arriving at a given location. In the Poisson distribution, the number of events in sequential time periods of an equal length are independent stochastic drawings. For a given traffic volume, the probability of a certain number of arrivals within a fixed time period depends only on the length of this period and is thus constant for periods of equal length. When the number of arriving vehicles in a sequence of fixed time periods is Poisson distributed, their headways are (negatively) exponentially distributed and independent of each other. To be Poisson distributed, the vehicles must approach a certain location in a so-called undisturbed flow. Therefore, the traffic volumes should not be too high, say 400–1000 vehicles h^{-1} at maximum.

According to the Poisson distribution, the probability $P(x)$ that x vehicles arrive at a given location on a one-way road in time period T (in s) can be described as

$$P(x) = \frac{(\lambda T)^x e^{-\lambda T}}{x!} \tag{1}$$

where λ is the traffic volume in vehicles s^{-1}.

For a successful traversing, x should be equal to 0 at least during the time period T when the animal 'occupies' the road for traversing. For $x = 0$, Eq. (1) changes to

$$P(0) = \Pr\{\text{Headway} > T\} = e^{-\lambda T} \tag{2}$$

In other words, $P(0)$ is the probability that the front of the next car does not arrive within a period of T seconds, given a traffic flow with, on average, λ vehicles s^{-1}. The relevant length of the time period T depends on road, traffic, vehicle and species characteristics, as will be explained further later.

When the road carries traffic in two directions, with flows λ_1 and λ_2, then both flows can be described as a Poisson process. The well-known theory states that the two-way flow on that road, $\lambda = \lambda_1 + \lambda_2$, is also a Poisson process. As a result, Eq. (2) remains the same in this situation, with λ now representing the two-way traffic volume.

To apply headway distributions of traffic flows to traversing animal species, several assumptions are made. The main difference in road crossing by people and by animals is that most people can reasonably estimate whether a gap between two successive vehicles is sufficiently large to cross safely. In contrast, the strategies animals use to traverse roads are unknown, but it is assumed that they act 'blind', i.e. do not respond to the presence of a car, if any, and maintain a constant speed during their traverse. 'Blind' traversing is a realistic supposition, especially in situations with a low clearance. In addition to the 'blindness' of the animal, we also

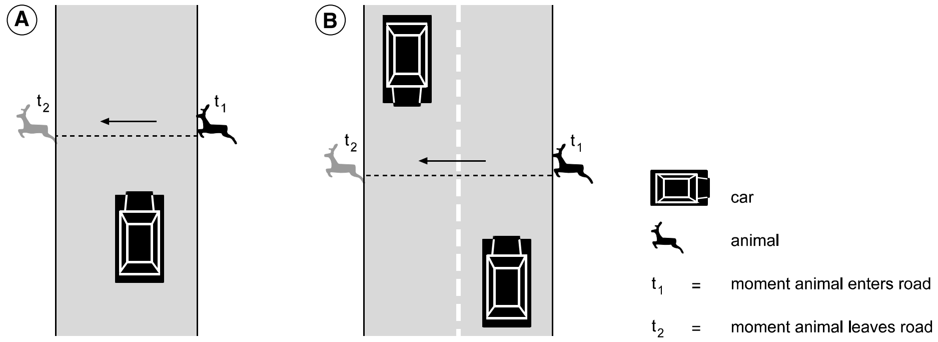


Fig. 3. An animal perpendicular traversing a road in a double blind situation. (A) One-lane road. (B) Two-lane road.

presume that the driver is 'blind' because the time available to avoid a collision with a traversing animal is around 1 s or less. Because of the short reaction time, the traversability model does not include 'corrections' by human and/or animal when their presence coincides. Two further assumptions for modelling are (1) when an animal moving through the landscape finds a road, it will traverse this road promptly, with a constant speed and at an angle ($\pi/2 - \alpha$) with the road axis (the crossing is perpendicular for $\alpha = 0$), and (2) the traversing animal will be killed in a collision if the appearing gap in the traffic flow at the start of its traversing is too small. On the other hand, if the appearing gap is at least as large as the animal needs for its traverse, the traverse will be successful. Fig. 3 illustrates the successful perpendicular traversing: no car arrives on the cross-section between the moment the animal's front enters the road, t_1, and the moment its rear leaves it, t_2.

In the first stage of the development of the traversability model (Jaarsma and van Langevelde, 1997; Van Langevelde and Jaarsma, 1997, 2004), only a perpendicular traversing was included. Further, the car and the animal were considered to collide when the animal was (partly) on the cross-section of the *road* on the moment that the (first) car arrived. Then, the time δ_a (in s) needed for a road traversing by an individual animal of species a can be calculated from

$$\delta_a = \frac{(B + L_a)}{V_a} \tag{3}$$

where B is the pavement width of the road (in m, measured as the width of roads between bordering pavement or verges), L_a is the average body length of the species (in m, measured from snout to tail tip) and V_a is the traversing speed of the species (in m s^{-1}).

For a successful traversing, T (Eq. (2)) should be at least equal to δ_a. Consequently, the probability P_a to successfully traverse a one-lane road for an individual animal a is

$$P_a = e^{-\lambda_1 \frac{B_1 + L_a}{V_a}} \tag{4}$$

where λ_1 is the traffic volume on that lane and B_1 its pavement width.

In the case of two directional traffic, both flows λ_1 and λ_2 can be separately described by a Poisson process. Subsequently, the probability of successfully traversing can be calculated as a function of the characteristics in both directions, formulated as

$$P_a = e^{-\lambda_1 \frac{B_1 + L_a}{V_a}} \cdot e^{-\lambda_2 \frac{B_2 + L_a}{V_a}} \tag{5}$$

where B_1 and B_2 are the pavement widths of these two lanes. When $B_1 = B_2$, Eq. (5) can be rewritten:

$$P_a = e^{-(\lambda_1 + \lambda_2)\frac{B_1 + L_a}{V_a}} = e^{-\lambda \frac{B_1 + L_a}{V_a}} = e^{-\lambda \frac{\frac{1}{2}B + L_a}{V_a}} \tag{6}$$

where λ is the decisive two-way volume of the two-lane road ($\lambda = \lambda_1 + \lambda_2$) and B is the total pavement width ($B = B_1 + B_2 = 2B_1$ and so $B_1 = \frac{1}{2}B$).[1]

[1] In the formula presented by Van Langevelde and Jaarsma (2004) the $\frac{1}{2}$ is erroneously omitted.

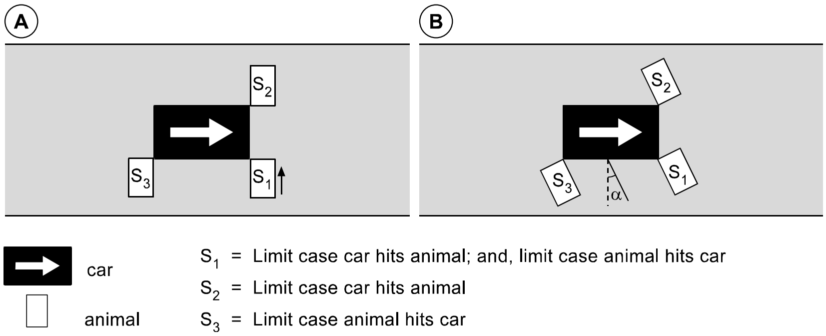


Fig. 4. A road traversing by an animal, considering the dimensions of the car, again in a double blind situation. (A) Perpendicular traversing. (B) Angle traversing.

This approach, however, overestimates the probability of a collision because the coincidence of a car's arrival and an animal's presence on a road does not automatically cause a collision. A collision only occurs when the animal and the car are on the same part of the road at the same time. Therefore, the width of a car is preferable to the width of the road as an explanatory factor of the collision. Following the idea of a double blind situation (animal as well as driver), there is a second chance for a collision, not included so far, namely when the animal hits the side of a car. Assuming that car and animal can be represented by a rectangle, the limit cases of both situations for a perpendicular traversing are schematically presented in Fig. 4A and those for the angle traversing in Fig. 4B. In these schemes, the traversing is considered to be successful if neither the situation "car hits animal" nor the situation "animal hits car" appears. This is the case when no car arrives during the δ_1 seconds between the limit cases S_1 and S_2 and the δ_2 seconds between the limit cases S_1 and S_3.

Distinguishing these two chances for a collision, the period δ_1 (in s), during which the car hits the animal, is (Fig. 4B)

$$\delta_1 = \frac{\frac{W_c}{\cos(\alpha)} + L_a}{V_a} \tag{7}$$

where W_c is the car's width[2] (in m), and L_a and V_a are the animal's length (in m) and speed (in m s^{-1}), respectively. For $\alpha = 0$, i.e. perpendicular traversing, Eq. (7) reduces to (Fig. 4A)

$$\delta_1 = \frac{W_c + L_a}{V_a} \tag{8}$$

As a result, if the animal traverses the road at an arbitrary moment, it can survive if the front of the next car does not arrive within a period of δ_1 seconds. The probability of this event, P_1, is

$$P_1 = \Pr\{\text{Headway} > \delta_1\} = e^{-\lambda\delta_1} \tag{9}$$

The period δ_2 (in s) during which the animal can hit the car is

$$\delta_2 = \frac{L_c + W_a\cos(\alpha)}{V_c} \tag{10}$$

where W_a is the animal's width (in m) and L_c and V_c are the car's length (in m) and speed (in m s^{-1}), respectively. In contrast to the former model of Eq. (6), vehicle speed is included. However, it acts only on the "animal hits car" situation. If the animal traverses the road at an arbitrary moment, it will not hit a car and can survive if the front of the last car has passed at least a period of δ_2 seconds ago. The probability of this event, P_2, is

$$P_2 = \Pr\{\text{Headway} > \delta_2\} = e^{-\lambda\delta_2} \tag{11}$$

[2] Hels and Buchwald (2001) argue that a collision only occurs when the animal is hit by a *wheel*. However, they only deal with amphibians. However, most mammals are too big to survive between the wheels, while birds and insects are hit by the front of the car. Amphibians are indeed flattened by wheels, but this may also be caused by a second car, after they were upset by a first car's wind speed.

Combining both events, the animal can traverse without a collision with probability P_a that equals the product of Eqs. (9) and (11)

$$P = e^{-\lambda\delta_1} e^{-\lambda\delta_2} = e^{-\lambda(\delta_1+\delta_2)} \quad (12)$$

Expressed in the characteristics of animal and car, this equation transfers into

$$P_a = e^{-\lambda\left(\frac{\frac{W_c}{\cos(\alpha)}+L_a}{V_a} + \frac{L_c+W_a\cos(\alpha)}{V_c}\right)} \quad (13)$$

For the perpendicular traversing, $\alpha = 0$ and Eq. (13) becomes

$$P_a = e^{-\lambda\left(\frac{W_c+L_a}{V_a} + \frac{L_c+W_a}{V_c}\right)} \quad (14)$$

Based on Eqs. (6) or (14), the number of traffic victims of species a, D_a, during time period τ can be estimated by

$$D_a = (1 - P_a)K_{a,\tau} \quad (15)$$

where $K_{a,\tau}$ is the number of attempts to traverse the road by individuals of species a during the time period τ. The parameter $K_{a,\tau}$ is difficult to measure, however, and depends on several species and landscape characteristics such as home-range size, movement behaviour during foraging or dispersal, road density and the location of the road with respect to, for example, the foraging areas. We therefore suggest that the model not be used to calculate the absolute number of traffic kills of species a during a season but to use it in an indirect way. Consequently, traffic mortality (Eq. (15)) is estimated for two situations with the same number of attempts to traverse the road. The present situation (or the autonomous development) is compared with the planned situation with new road and traffic characteristics and the difference between both is considered to be the impact.

To illustrate the probability of animals traversing a road, we present some results of the traversability model for the animals in Table 1. The calculations are made for both the former model (Eq. (6) and Table 2) and the model considering the car's dimensions (Eq. (14) and Table 3). The calculations are based on a

Table 1
Animal characteristics applied

Animal	Length (m)	Width (m)	Speed (m s^{-1})
Red deer (*Cervus elaphus*)	2.1	0.6	15.5
Roe deer (*Capreolus capreolus*)	1.4	0.4	5.2
Badger (*Meles meles*)	1.0	0.4	6.5
Otter (*Lutra lutra*)	1.2	0.25	5.6
Rabbit (*Oryctolagus cuniculus*)	0.4	0.15	5
Hedgehog (*Erinaceus europaeus*)	0.3	0.25	1

Table 2
Animal victims by species as a function of traffic volumes (relative to a volume of 400 vehicles h^{-1})

Animal species	Kills per 10^4 traverses and 400 vehicles h^{-1}	Relative kills (%) per 10^4 traverses and 200...4 vehicles h^{-1} (theoretical number of kills for 400 vehicles h^{-1} = 100)					
		200	100	40	20	10	4
Red deer	290	50	25	10	5	3	1
Roe deer	701	51	26	10	5	3	1
Badger	500	51	25	10	5	3	1
Otter	615	51	26	10	5	3	1
Rabbit	519	51	26	10	5	3	1
Hedgehog	2255	53	27	11	6	3	1

Note: Road characteristics used: pavement width 4 m.
Source: Van Langevelde and Jaarsma (2004).

Table 3
Animal victims by species as a function of traffic volumes (relative to a volume of 400 vehicles h^{-1}) using the model considering car dimensions

Animal species	Kills per 10^4 traverses and 400 vehicles h^{-1}	Relative kills (%) per 10^4 traverses and 200...4 vehicles h^{-1} (theoretical number of kills for 400 vehicles h^{-1} = 100)					
		200	100	40	20	10	4
Red deer	587	51	26	10	5	3	1
Roe deer	976	51	26	10	5	3	1
Badger	781	51	26	10	5	3	1
Otter	885	51	26	10	5	3	1
Rabbit	787	51	26	10	5	3	1
Hedgehog	2478	54	28	11	6	3	1

Note: Vehicle characteristics used: length, width and speed 5 m, 2 m and 72 km h^{-1}, respectively.

volume of 400 vehicles h^{-1} and 10^4 traverses. We compared this with changing volumes in a range between 200 and 4 vehicles h^{-1}.

Comparing the number of kills in Tables 2 and 3, systematically higher results are found in Table 3. Excluding the red deer (twice the number of kills) and for the hedgehog (only 10% more kills), the model taking into account car dimensions suggests about 50% more kills. This is surprising at first because we expected an overestimation by the former model. However, taking into account road and vehicle characteristics (a rural road width of 4 m and a car width of 2 m), the results using Eq. (6) resembles those of Eq. (8), representing the outcome of a collision between car and animal. The model considering car dimensions further includes a second type of collision, namely between animal and car, which increases the number of kills. This effect hardly depends on species characteristics (Eq. (10)). Given the car characteristics, the second type has a relatively large impact for fast moving animals with only a small chance for a vehicle-animal collision (as the red deer). In contrast, its impact is only small for slow moving animals (as the hedgehog).

Furthermore, the number of traffic kills is approximately proportional to the traffic volumes, as can be seen in the relative number of kills in Tables 2 and 3. This proportionality can be explained by the property of the exponential function that $(1 - x)$ is a good approximation of $\mathrm{EXP}[-x]$ if x is small compared to 1. As such, the outcome becomes proportional to x. The traffic volumes applied are indeed small enough to fulfil this condition for both models (Eqs. (6) and (14)). As a consequence, the conclusions based on the former model as presented by Jaarsma and van Langevelde (1997) and Van Langevelde and Jaarsma (1997, 2004) will not change drastically when this model is replaced by that based on car dimensions.

From this point, we will only use the model based on car dimensions, as formulated in Eq. (14) because the width of the car as applied in this model is, from a theoretical viewpoint, preferable to the width of the road as an explaining factor. Following the idea of a double blind situation, this model includes a second chance for a collision, i.e. where an animal hits the side of a car.

4. Sensitivity of the model to relevant road, traffic, vehicle, and species characteristics

To assess the relative influence of the different parameters in the traversability model as formulated in Eq. (14), a sensitivity analysis has been conducted. This sensitivity analysis demonstrates the necessity of exact determination of these parameters. Moreover, it gives insight into the possible effects of changing road and traffic characteristics, e.g., due to mitigating measures. Therefore, we will first discuss the relevant road, traffic, vehicle, and species characteristics.

The barrier and mortality effects of narrow roads for traversing animals are assumed to be lower than for wide roads. However, the low clearance often found on narrow roads has a negative impact on their traversability (Clevenger et al., 2003). The width of roads determines traffic volumes and vehicle speed; both are included in the model.

The decisive traffic volume that largely determines traffic mortality depends on both the time split of the daily traffic flow and the activity period of a species during the day. In Van Langevelde and Jaarsma (2004) it was concluded that headways in traffic flows on most roads can be considered to be exponentially distributed, taking into account that most animal species are active during dusk and night and only traverse a road when traffic volume is rather low (Clevenger et al., 2003), which is the case during dusk and night.

Looking at the speed of the car, we see that it acts only on the ‘animal hits car’ situation, as the probability of a safe traversing slightly increases if the speed of the car increases (Eq. (10)). At first glance, this might be surprising, but if the speed of the car is higher, it is obvious that the probability that an animal will hit the car reduces. One may argue that lower vehicle speeds give better opportunities for both driver and animal to react to each other, but it is a basic assumption of the double blind model that this is negligible. Besides vehicle speed, car length and car width also determine the probability of successful road crossing by an animal. In short, the wider or longer the car, the lower the probability is for successfully crossing the road.

The traversability model assumes that three species characteristics directly influence traffic mortality: body length, body width and traversing speed of animals. The body length and width of most common mammal species is often known (Lange et al., 1994). In Van Langevelde and Jaarsma (2004) it is estimated the traversing speed of animals by using the relationship between the maximum (non-sustained) speed of running and body mass. To calculate animal speed for traversing roads, we assumed 25% of the maximum running speed because individuals usually do not traverse the road with maximum speed (but also move faster in unsuitable environments on roads than the average velocity observed in their habitat). The model for traversing animals has some other assumptions, such as traversing with a constant speed and without waiting (‘blind’). Data for these assumptions is, however, lacking. Moreover, individual animals or specific species will react in another way, i.e. by resting on the warm asphalt or by fleeing when a car approaches. Some of these divergences from the basic assumptions lead to underestimations, while others lead to an overestimation of the chance for successfully traversing. These divergences become less important, however, when the model compares two situations for the same species.

To assess the relative influence of these road, traffic, vehicle, and species characteristics, we calculate the relative sensitivity S of the probability P_a to relative changes in parameters according to

$$S = \left| \frac{\theta}{P_a} \frac{\partial P_a}{\partial \theta} \right| \tag{16}$$

where θ represents each parameter that affects the value of P_a. Here, the relative sensitivity S should be interpreted as the percentage that the probability P_a changes for each percentage of change in the parameter θ. The relative sensitivity S of the probability P_a to relative changes in the most sensitive parameters is illustrated in Fig. 5.

In Fig. 5A, for each value of the traffic volume λ, the effect on the relative sensitivity S of changes in all parameters is given. In Fig. 5B, the same is done for the traversing speed V_a of animal species a. The sensitivity analysis demonstrates that for high values of traffic volume λ (Fig. 5A) and low values of the traversing speed of animals V_a (Fig. 5B), small changes in traffic volume λ, animal traversing speed V_a and car width W_c have a

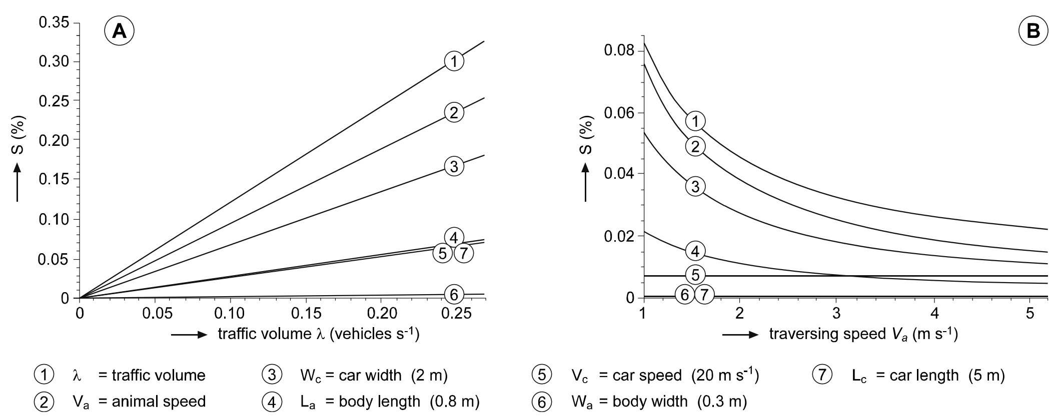


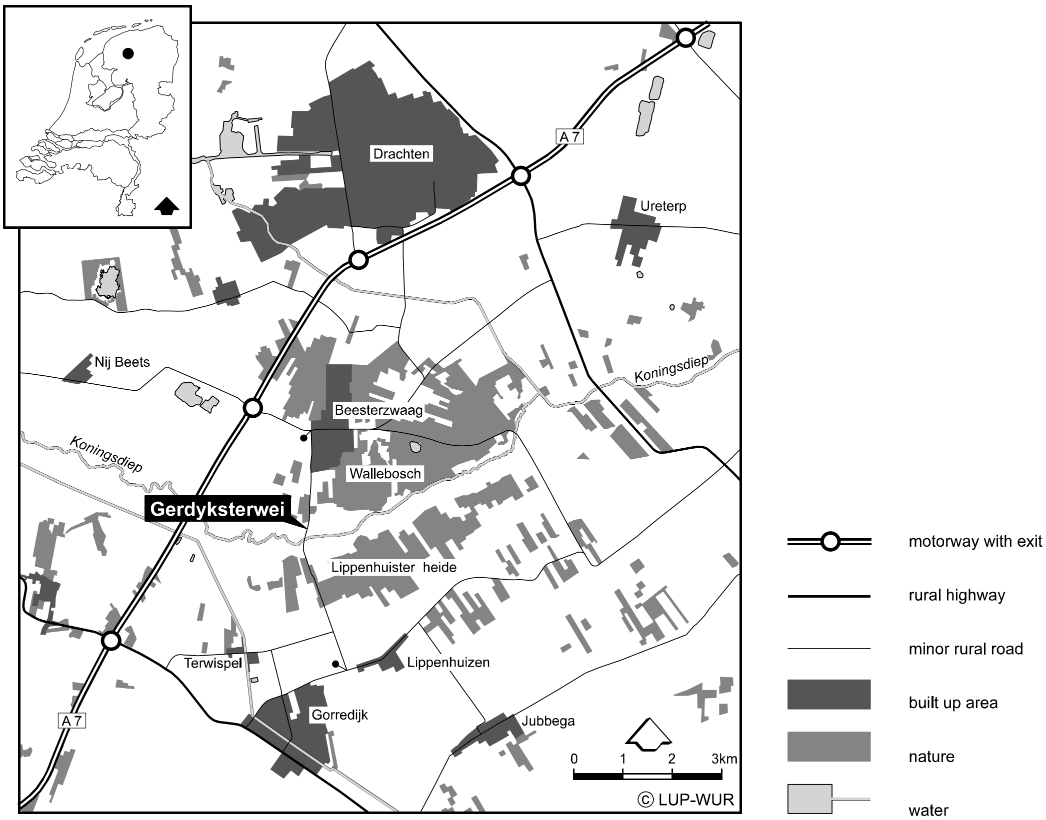
Fig. 5. Relative sensitivity S of the probability of successfully road crossing P_a to changes in each parameter for (A) traffic volume and (B) traversing speed. Parameter values: (A) $V_a = 3\ \mathrm{m\ s^{-1}}$, and (B) $\lambda = 0.027$ vehicles $\mathrm{s^{-1}}$(97 vehicles $\mathrm{h^{-1}}$).

relatively large impact on the probability of successful road traversing P_a. Changes in the body length, L_a, and width of animals, W_a, and in the car length, L_c, car width, W_c, and car speed, V_c, lead to only small changes in the predicted relative sensitivity of all parameters (less than 0.04, and therefore not presented in a figure). Exact determination is thus necessary for traffic volume λ, animal traversing speed V_a and car width W_c when animals that move relatively slow are considered or roads with a high traffic volume are traversed.

5. The traversability model in practice

The traversability model was applied in contexts to compare alternative network solutions and their impacts on traversability for wildlife (Jaarsma and van Langevelde, 1997; Jaarsma and Willems, 2002). Here, we present the example of a former section of the Dutch national road network, the Gerdyksterwei between the Frisian villages Gorredijk and Beetsterzwaag, that is bypassed by the A7 motorway (Fig. 6).

Since the A7 motorway has been in service, carrying daily about 30,000 motor vehicles, the Gerdyksterwei has been meant to serve as a minor rural road with modest traffic flows. However, many drivers between Gorredijk and the nearby town of Drachten and further to the north still prefer the former route above the functional route along the A7. Therefore, daily volumes on the Gerdyksterwei (4100) and in the centre of the village of Beetsterzwaag (5300) are too high for a minor road. By autonomous developments, these volumes are expected to increase by 1000 vehicles per day over the next ten years. Although the technical capacity of the Gerdyksterwei is large enough to handle these volumes (the road still has its traditional layout, with a wide pavement, based on its former function in the national network), the present volume creates two problems. First, within the village of Beetsterzwaag, the existence of the inhabitants is threatened. Furthermore, in the rural area, the Gerdyksterwei intersects core areas within the dry and wet National Ecological



Source: Jaarsma and Van Langevelde (1997)

Fig. 6. The Gerdyksterwei in its regional context.

Network (the Wallebosch and Lippenhuisterheide and the low land brook Koningsdiep, respectively). Here, small and larger mammal species such as hedgehogs (*Erinaceus europaeus)*, rabbits (*Oryctolagus cuniculus*), roe deer (*Capreolus capreolus*), and (when re-introduced) otters (*Lutra lutra*), are exposed to a considerable collision chance when traversing the Gerdyksterwei. Therefore, the local government has investigated the impacts of rural traffic calming for livability and wildlife movement. Within this context, 'traffic calming' means priority being given to nature (in the rural area) and to people (in the village), but not to through traffic (Jaarsma, 1997). The latter finds a high quality alternative via the A7 motorway. Wildlife can traverse the A7 safely through underpasses. As a consequence of traffic calming, speeds and/or volumes on the Gerdyksterwei decrease.

Four levels of traffic calming are examined (i) mainly legal measures, including a rigid enforcement of the present speed limit of 80 km h^{-1}; (ii) implementation of a so-called traffic-calmed area with a legal speed limit of 60 km h^{-1} and with a few speed bumps; (iii) implementation of a stricter traffic-calmed area, with more measures to reduce speed and a narrowed pavement; and (iv) implementation of a traffic-calmed area, with limited access: access for local residents only between 7 pm and 7 am. With these measures, the estimated effective speed on the Gerdyksterwei should decrease. As a result, an increasing part of the through traffic will take the A7 because it offers a faster or at least more comfortable route than the traffic calmed Gerdyksterwei. Based on travel times between Gorredijk and Drachten, it is estimated that the first level of traffic calming will only slightly reduce the future flows while the implementation of a traffic-calmed area will be more effective in avoiding through traffic. The level with limited access reduces the volumes in the time frame from 400 to about 100; on average only 8 vehicles h^{-1}. This extra reduction during the night is relevant considering that the mammals mentioned above are nocturnal. Nightly volumes for the other situations are estimated by the assumption that one quarter of the daily flow appears between 7 pm and 7 am, which is equally spread over these 12 h. Table 4 presents an overview of the road and traffic characteristics used in our calculations. The decisive traffic volumes are the average hourly volumes during the night.

The impacts of traffic calming on wildlife traversability for the Gerdyksterwei are presented in Table 5, showing the relative changes compared to the present situation in traffic mortality per 10^4 traversings for roe deer, otters, rabbits, and hedgehogs.

Table 5, shows traffic calming as an effective method in improving traversability for wildlife. Differences between the four species are small; however, the small and slow moving hedgehog has a somewhat higher victim reduction. The table also clearly shows that if traversability is already considered an ecological problem in the present situation, measures must be taken to improve this situation since it will worsen in the autonomous development.

Compared to the autonomous situation, the first level of traffic calming shows a slight improvement in the traversability, but this is still worse than in the present situation. A further development of measures allows for a considerable improvement: the second and the third calming levels show a reduction of traffic kills of about one third and more than 50%, respectively. In this situation, with wildlife movements during the night as a decisive period, a total closure of the road for through traffic during the night is very effective. It reduces the number of traffic kills to about 10% of the current level.

Table 4
Road and traffic characteristics for the Gerdyksterwei; present situation and estimated for the autonomous development and four levels of traffic calming

Characteristic	Present situation	Autonomous development	Levels of rural traffic calming			
			Level 1	Level 2	Level 3	Level 4
Pavement width (m)[a]	7	7	7	7	5	5
Legal speed limit (km h^{-1})	80	80	80	60	60	60
Estimated effective speed (km h^{-1})	85	80	72	60	50	50
Average annual daily volume (vehicles d^{-1})	4200	5200	4500	2500	1600	1300
Decisive volume (vehicles h^{-1})	84	104	90	50	32	8

[a] Pavement width is not included in formula (14), but it affects both effective speed and traffic volume.

Table 5
Calculated kills by species for the Gerdyksterwei; present situation and relative kills for the autonomous development and four levels of traffic calming

Animal species	Calculated kills per 10^4 traverses in present situation with 84 vehicles h^{-1} (=100%)	Relative kills per 10^4 traverses (%)				
		Autonomous development	Level 1	Level 2	Level 3	Level 4
Roe deer	204	125	112	66	45	11
Otter	184	126	112	66	46	11
Rabbit	162	126	113	67	46	12
Hedgehog	572	124	109	62	41	10

Note: Animal characteristics as in Table 1; vehicle length 5 m and width 2 m (as in Table 3); other characteristics as in Table 4.

6. Discussion

Models are based on assumptions. In this case, one may ask whether it is realistic to approximate animal behaviour by the blind assumption. Some animals may behave as a pedestrian and scan the terrain (the road) before approaching (traversing) it. For roads with a small clearance, however, as in forested areas and along roads with plantings, the blind assumption seems realistic for most animals (Oxley et al., 1974; Clevenger et al., 2003). Differences between species will appear, but these are difficult to observe. The traversability model has not been tested in empirical experiments. For such an experiment, reliable numbers of road crossings by individual animals as well as numbers of traffic kills per road section must be gathered. To our knowledge, there are no studies on the former. Some studies provide the number of victims, but due to scavengers or identification problems, especially for small animals, the actual numbers are difficult to measure. This has held true for 70 years (Stoner, 1936; Hels and Buchwald, 2001; Slater, 2002). It is, therefore, questionable whether an empirical experiment can provide reliable data for the validation of the absolute numbers of traffic kills as calculated by the model. When the model is used to calculate the relative difference between network designs with different road and/or traffic characteristics, systematic errors in the model by animal behaviour, if any, will mainly disappear in the difference between the estimates for both situations. It is plausible that the diverging factors by unknown animal behaviour, resulting in a systematic under or overestimation, will be of the same order for the compared situations. The model is thus primarily developed to balance alternatives, not to calculate the absolute number of traffic kills any given situation.

Contrary the reasoning regarding the role of vehicle speed, some studies (Forman et al., 2003), argue that, besides traffic volumes, traffic speeds affect the number of wildlife collisions. In contrast to our assumption of a double blind traversing model, speed might indeed play a role because of the better opportunities for both animal and driver to avoid a collision when the vehicle speed is lower. For example, lower vehicle speeds give the animal a better opportunity to flee. These opportunities should not be overestimated, however, because during darkness, which is the decisive time period for wildlife movement, drivers have a very limited view. Given the response time of the driver on at least the order of 1 s, 20–30 m will be travelled before the vehicle reacts to a traversing animal when driving with usual speeds on rural roads.

7. Conclusion

A tool has been missing not only to estimate the impacts of infrastructure on wildlife movements but more importantly to estimate the impacts on wildlife of adjustments to a regional road network and/or the layout of specific road sections and the resulting changes in traffic volumes and speeds. The traversability model can fill this gap. In this model, the probability of a collision is determined by traffic volume, traversing speed of the animal, the animal's body length and width, the length and width of a car and its speed.

References

Button, K., Nijkamp, P., 1999. Series preface for environmental analysis and economic policy. In: Hayashi, Y., Button, K., Nijkamp, P. (Eds.), The Environment and Transport. Edward Elgar Publishing, Cheltenham.

Clarke, G.P., White, P.C.L., Harris, S., 1998. Effects of roads on badger *Meles meles* populations in south-west England. Biological Conservation 86, 117–124.

Clevenger, A.P., Chruszcz, B., Gunson, K.E., 2003. Spatial patterns and factors influencing small vertebrate fauna roadkill aggregations. Biological Conservation 109, 15–26.

Daganzo, C.F., 1997. Fundamentals of Transportation and Traffic Operations. Elsevier.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Chutshall, C.D., Dale, V.H., Fahring, L., Goldman, C.R., Heanue, K., Jones, J.A., Swanso, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology. Science and Solutions. Island Press, Washington.

Haight, F.A., 1963. Mathematical Theories of Traffic Flow. Academic Press, London.

Hels, T., Buchwald, E., 2001. The effect of road kills on amphibian populations. Biological Conservation 99, 331–340.

Huijser, M.P., Bergers, P.J.M., 2000. The effect of roads and traffic on hedgehog (*Erinaceus europaneus*) populations. Biological Conservation 95, 111–116.

Jaarsma, C.F., 1997. Approaches for the planning of rural road networks according to sustainable land use planning. Landscape and Urban Planning 39, 47–54.

Jaarsma, C.F., van Langevelde, F., 1997. Right-of-way management and habitat fragmentation: an integral approach with the spatial concept of the traffic calmed rural area. In: Hydro-Quebec Centre de Documentation Environnement, Environmental Concerns in Rights-of-way Management. Proceedings of the 6th International Symposium, New Orleans (LA), 24–26 February, Elsevier Science, pp. 383–392.

Jaarsma, C.F., Willems, G.P.A., 2002. Reducing habitat fragmentation on minor rural roads through traffic calming. Landscape and Urban Planning 58, 125–135.

Jedicke, E., 1994. Biotopverbund – Grundlagen und Massnahmen einer neuen Naturschutzstrategie. Eugen Ulmer Verlag, Stuttgart, Germany (in German).

Lange, R., Twisk, P., van Winden, A., van Diepenveen, A., 1994. Zoogdieren van West-Europa (mammals of western Europa). KNNV, Utrecht (in Dutch).

Lankester, K., van Apeldoorn, R., 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.

Mader, H.J., 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29, 81–96.

Merriam, G., Kozakiewicz, M., Tsuchiya, E., Hawley, K., 1989. Barriers as boundaries for metapopulations and demes of peromyscus leucopus in farm landscapes. Landscape Ecology 2, 227–235.

Oxley, D.J., Fenton, M.B., Carmody, G.R., 1974. The effects of roads on populations of small mammals. Journal of Applied Ecology 11, 51–59.

Reijnen, R., Veenbaas, G., Foppen, R., 1995. Predicting the effects of motorway traffic on breeding bird populations. Road and Hydraulic Engineering Division and DLO-Institute for Forestry and Nature Research, P-DWW-95-736, Delft.

Seiler, A., 2002. Effects of infrastructure on nature. In: Anonymus, 2003. COST 341. Habitat fragmentation due to transportation infrastructure. The European review. European Commission, Directorate-General for Research, Brussel.

Seiler, A., Erikson, I.-M., 1997. New approaches for ecological consideration in Swedish road planning. In: Canters, K.J., Piepers, A., Hendriks-Heersma, D. (Eds.), Habitat fragmentation and infrastructure, Proceedings of the International Conference on Habitat Fragmentation Infrastructure and the Role of Ecological Engineering. The Hague, Maastricht.

Slater, F.M., 2002. An assessment of wildlife road causalities – the potential discrepancy between numbers counted and numbers killed. Web Ecology 3, 33–42.

Stoner, D., 1936. Wildlife casualties on the highways. Wilson Bulletin 48, 276–283.

Van Langevelde, F., Jaarsma, C.F., 1997. Habitat fragmentation, the role of minor rural roads and their traversability. In: Canters, K.J., Piepers, A., Hendriks-Heersma, D. (Eds.), Habitat Fragmentation and Infrastructure, Proceedings of the International Conference on Habitat Fragmentation, Infrastructure and the Role of Ecological Engineering. The Hague, Maastricht.

Van Langevelde, F., Jaarsma, C.F., 2004. Using traffic flow theory to model traffic mortality in mammals. Landscape Ecology 19, 895–907.

Verboom, J., 1994. Een modelstudie naar de effecten van infrastructuur op dispersiebewegingen van dieren (A model study of the effects of infrastructure of fauna dispersal). Rijkswaterstaat/ IBN-DLO, Delft/ Wageningen (in Dutch).