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Research article

Using traffic flow theory to model traffic mortality in mammals

Frank van Langevelde[1,*] and Catharinus F. Jaarsma[2]
*[1]Resource Ecology Group, Department of Environmental Sciences, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands; [2]Land Use Planning Group, Department of Environmental Sciences, Wageningen University, Gen. Foulkesweg 13, 6703 BJ Wageningen, The Netherlands; *Author for correspondence (email address: frank.vanlangevelde@wur.nl)*

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Abstract

Traffic has a considerable effect on population and community dynamics through the disruption and fragmentation of habitat and traffic mortality. This paper deals with a systematic way to acquire knowledge about the probabilities of successful road crossing by mammals and what characteristics affect this traversability. We derive a model from traffic flow theory to estimate traffic mortality in mammals related to relevant road, traffic and species characteristics. The probability of successful road crossing is determined by the pavement width of the road, traffic volume, traversing speed of the mammals and their body length. We include the traversability model in a simple two-patch population model to explore the effects of these road, traffic and species characteristics on population dynamics. Analysis of the models show that, for our parameter ranges, traffic volume and traversing speed have the largest effect on traffic mortality. The population size is especially negatively affected when roads have to be crossed during the daily movements. These predictions could be useful to determine the expected effectiveness of mitigating measures relative to the current situation. Mitigating measures might alter the road and traffic characteristics. The effects of these changes on traffic mortality and population dynamics could be analysed by calculating the number of traffic victims before and after the mitigating measures.

Introduction

Traffic flows are principal causes of habitat fragmentation (Andrews 1990; Forman and Alexander 1998; Spellerberg 1998; Trombulak and Frissell 2000). There are at least four negative effects of traffic on animals (Van Langevelde and Jaarsma 1997): destruction or alteration of habitat due to construction, disturbance of habitat along the road or railway (noise, vibrations, car visibility, etc.), barriers created by the road or railway (increased resistance for movements), and barriers by traffic (collision risk during crossing). The first two directly affect the habitat of the species. They result in a decline of habitat area or strips along the road with lower quality of habitat. The latter two effects have an impact on individuals. These four effects may have implications for population dynamics and community structure near the road. In this paper, we investigate the mortality due to traffic on roads. We define the traversability of a road as the probability of successfully crossing that road by an individual.

Measures are applied to reduce traffic accidents (Garret and Conway 1999; Singh and Satheesan 2000) and protect biodiversity (Van Bohemen 1998; Trombulak and Frissell 2000). Mitigation measures include keeping wildlife off the road (e.g., fences: Romin and Bissonnette 1996; Putman 1997), providing alternative routes (e.g., fauna passages and ecoducts: Jackson and Griffin 1998; Keller and Pfister 1997) or reducing the risk of collisions (e.g., highway lighting or mirrors: Romin and Bissonette 1996; Putman 1997). Most measures involve technical devices that change the road characteristics. However, also other measures may reduce traffic mortality, such as reduction of traffic volume or speed, and periodic closing of roads (during the night or a specific season). For effectively applying mitigating measures that reduce traffic mortality at locations where no passageways or fences are constructed, insight in the effects of road and traffic characteristics on traffic mortality is needed (Andrews 1990; Kirby 1997; Forman and Alexander 1998).

In this paper, we analyse a model based on the relevant road, traffic and species characteristics to estimate the probability of successfully road crossing. In contrast to other recent studies on traffic mortality (Van Langevelde and Jaarsma 1997; Hels and Buchwald 2001; Clevenger et al. 2003), we explicitly derive the model from traffic flow theory. A sensitivity analysis demonstrates what parameters should be estimated carefully.

Since the number of traffic victims does not directly provide insight in the effects of infrastructure on local population dynamics, we include the traversability model in a simple population model. This model consists of two patches and annual exchange of individuals between the patches. With this two-patch population model, we explore the effects of road, traffic and species characteristics on population dynamics. Therefore, we analyse the population size where traffic mortality affects the daily movements of the animals and the yearly exchange of individuals between the patches. Based on the analysis of the traversability model and the population model, we explore which characteristics make species vulnerable to traffic mortality.

Model for estimating the traversability of roads

Relevant road, traffic and species characteristics

What are the relevant road, traffic and species characteristics that have an effect on the traversability? Regarding the road characteristics, it is clear that as the road is wider, an animal needs more time to cross and the probability of a successful road crossing decreases. Moreover, wider roads carry higher traffic volumes and allow for higher speeds. A small clearance of a road, i.e., a short distance from the road to dense vegetation, has a negative impact on the traversability of the road (Oxley et al. 1974; Adams and Geis 1983; Clevenger et al. 2003). A small clearance can often be found in forested landscapes.

High traffic volumes cause high noise loads and a high collision probability since the intervals to cross between the vehicles are small. An increase of traffic volume may lead to such a flow of vehicles that individuals do not cross the road anymore. The time split of the traffic indicates the seasonal and daily fluctuations of the traffic volume. The traffic volume that largely determines traffic mortality (called the decisive traffic volume) depends on the time split of the daily traffic flow and the activity period of the animals during the day (Figure 1). During these periods, individuals are exposed to traffic mortality when roads are within their activity range. Vehicle speed seems to be important because of the better opportunities for both animal and driver to avoid a collision when the vehicle speed is lower.

Depending on the road and traffic characteristics, different animal species experience differences in traffic mortality, such as in insects (Munguira and Thomas 1992; Vermeulen 1994), reptiles and amphibians (Hels and Buchwald 2001), birds (Clevenger et al. 2003) and mammals (Mader 1984; Lankester et al. 1991; Clarke et al. 1998). Whether these species are vulnerable to traffic mortality depends on characteristics such as their home range size, the period of the day or season during which the animals are active, whether they move large distances during foraging, dispersal or migration, their traversing behaviour (velocity, reaction to approaching vehicles), their body length or the size of the group in which the individuals move.

Traffic flow theory

Central in the traversability model that estimates traffic mortality in animals, is the mathematical description of traffic flows where the probability of a successful road crossing depends on the number of vehicles passing during a certain time period. The traversability model is based on the assumption that the road crossing of an animal is successful if an ‘acceptable’ gap in the traffic flow appears at the start of the crossing. A crossing during a smaller gap results in a collision since an animal and a vehicle will be at the same location at the same moment. The model does not include ‘corrections’ by human or animal when this occurs. In traffic engineering, this gap acceptance approach has already been applied to model traffic flows (e.g., see Haight 1963, 1966; Drew 1968;

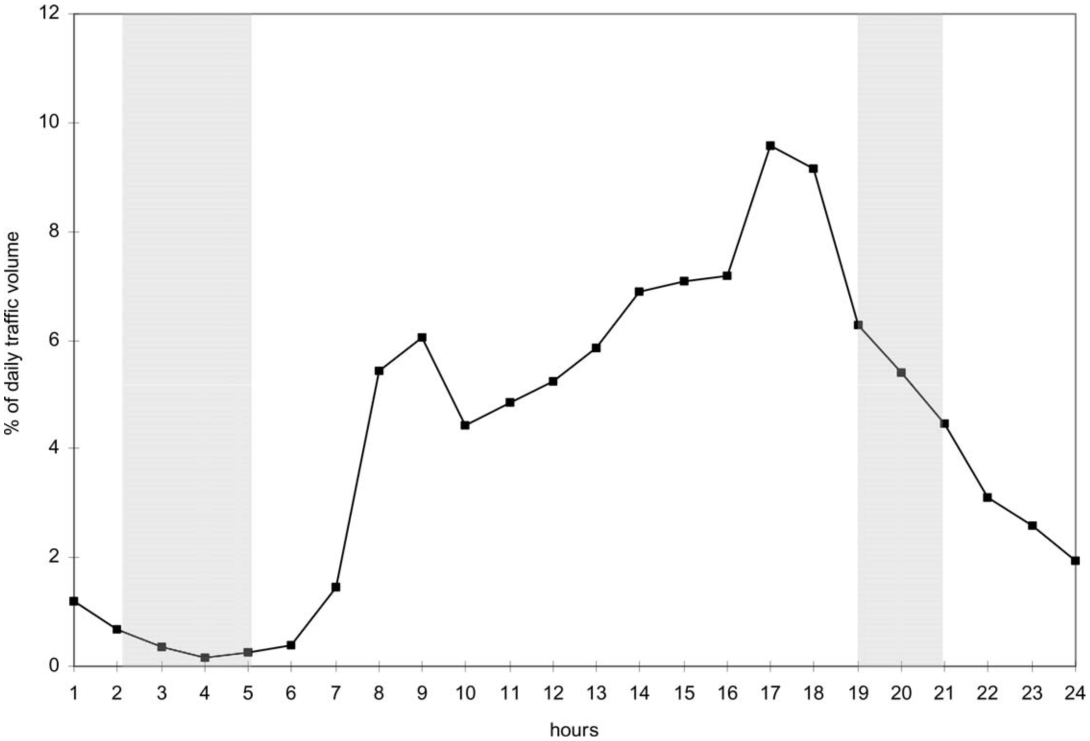

Figure 1. Time split of the hourly traffic volume in % of daily volume. Given is the yearly average distribution of the traffic volume per hour for a two-lane road in The Netherlands. With the grey areas, the daily activity period (sunset and sunrise) is illustrated for mammals such as beech marten *Martes foina*, pine marten *Martes martes* and polecat *Mustela putorius*. The traffic flow that largely determines traffic mortality is the one during these daily activity periods.

Leutzbach 1988). Particular models are derived, e.g., for waiting times of pedestrians for crossing the road as a function of traffic volumes (Hunt and Abduljabbar 1993).

For the application of gap acceptance to animal species, several assumptions are made. The main difference in road crossing by people and animals is that most people can reasonably estimate whether a gap between two successive vehicles is sufficiently large to cross safely. Most animals are assumed to traverse roads without any waiting time, especially in situations with a low clearance. Since the strategies used by animals to traverse roads are often unknown, it is assumed that they cross without any waiting time, in a right angle and with a constant speed. So, the time C_i (in s) needed for a road crossing by an individual of species i can be calculated from

$$C_i = \frac{(B + L_i)}{V_i} \qquad (1)$$

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

In traffic engineering, the calculation of the probability of gaps with certain duration in a traffic flow is commonly based on the assumption of a Poisson distributed process (Haight 1963, 1966; Drew 1968; Leutzbach 1988). The Poisson distribution is a discrete distribution that can describe the number of events during a certain time period. Here, the event is a vehicle arriving at a certain location. 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 vehicles in a sequence of fixed time periods is Poisson distributed, the numbers of gaps between vehicles at a certain place are (negatively) exponentially distributed, and the length of the time periods of these gaps is independent. To be Poisson distributed, it is necessary that the vehicles approach a certain location without any disturbance, due to for example traffic lights. Also, the traffic volumes should be not too high so that the vehicles impede each other.

According to the Poisson distribution, the mean value of the number of arrivals in a certain time period equals the variance. The variance decreases when the traffic volume increases because the probability of more or less constant time intervals between the vehicles increases. It is suggested that the arrivals in a traffic volume until 1000 vehicles h^{-1} can be described by a Poisson distribution (Harders 1968). When this volume appears during the rush hour, it is equivalent to a daily volume of about 10,000 vehicles (conforming to the rule of thumb in traffic engineering that the rush hour carries about 10% of the daily volume). In later studies, the maximum traffic volume that can be described by a Poisson distribution is set lower. Baerwald (1976) suggests validity up to volumes of 500 vehicles h^{-1} and Botma (1986) suggests 400 vehicles h^{-1}. When these volumes are measured during rush hour, the corresponding daily volumes are 5,000 and 4,000 vehicles respectively.

Traffic flows in practice

The total number of vehicles per day depends, however, on the type of road. Some motorways in industrialised countries carry more than 100,000 cars per day. In rural areas on a somewhat larger distance from the cities, daily volumes on most arterial highways do not exceed 10,000 cars. Generally, traffic volumes on minor roads and even many rural highways are much lower. Minor roads are defined as low-traffic roads (OECD 1986) when their traffic volume is less than or equal to 1,500 vehicles d^{-1}. Of the 13 countries surveyed, with on average 75%, the majority of their total road system exists of low-traffic roads (OECD 1986).

Traffic volumes vary by hour of the day, for example see Figure 1. The daily pattern has characteristic peaks in the rush hours (7% in the morning and 10% in the afternoon) and an intermediate situation during the evening (about 5%). During the night hours only 1 or 2% of daily volumes pass. Figure 1 shows that when animals are active during dusk and night they deal with considerably lower hourly volumes than during day light time. Moreover, most animals only cross a road when traffic volume is rather low, which is the case during dusk and night (Clevenger et al. 2003).

When the Poisson distribution is valid for volumes up to 400 vehicles h^{-1}, the corresponding daily volume is 4,000 vehicles when the rush hour is the decisive time for animal crossing. More often, however, the night hours will be decisive for crossing. During these hours, only a few percents of the daily traffic volume pass. Therefore, even for busy roads of, say, 20,000 vehicles d^{-1}, the hourly volumes during the night are low enough to be Poisson distributed. We therefore conclude that for most roads, traffic flows can be considered to be Poisson distributed, taking into account the periods where most animal species are active.

Formulation of the traversability model

According to the Poisson distribution, the probability *P(x)* that *x* vehicles arrive at a certain location in time period *T* (in s) can be described as

$$P(x) = \frac{(\lambda T)^x e^{-\lambda T}}{x!} \tag{2}$$

where λ is the traffic volume (vehicles s^{-1}). For a successful road crossing, x should be equal to 0 during the time period T when the animal crosses the road. For $x = 0$, Equation (2) changes into

$$P(0) = e^{-\lambda T} \tag{3}$$

For a successful crossing, T should be at least equal to C_i . Then, the probability P_i to successfully cross a one-lane road for an individual of species i is

$$P_i = e^{-\lambda_1 \frac{B_1 + L_i}{V_i}} \tag{4}$$

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

In practice, most roads carry traffic flows in two directions. Then, both traffic flows separately can be described by a Poisson process and the theory learns that the two-way flow on that road is also a Poisson process. Again the probability of successfully crossing can be calculated as a function of the volumes in both directions. It can be formulated as

$$P_i = e^{-\lambda_1 \frac{B_1 + L_i}{V_i}} e^{-\lambda_2 \frac{B_2 + L_i}{V_i}} \tag{5}$$

where λ_1 and λ_2 are the decisive traffic volumes of both lanes respectively and B_1 and B_2 the pavement widths of the two lanes. When $\lambda_1 = \lambda_2$ and $B_1 = B_2$ Equation (5) can be rewritten as

$$P_i = e^{-\lambda \frac{B+L_i}{V_i}} \tag{6}$$

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 ($B = B_1 + B_2$).

Based on the Equation (4-6), the number of traffic victims D_i during time period τ can be estimated by

$$D_i = (1 - P_i)K_{i,\tau} \tag{7}$$

where $K_{i,\tau}$ is the number of attempts to cross the road by individuals of species i during the time period τ. The parameter $K_{i,\tau}$ is difficult to measure 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.

For what species?

Which characteristics make species vulnerable for traffic mortality? Here, we distinguish between characteristics that affect directly and indirectly the traffic mortality. The traversability model assumes that two species characteristics are directly influencing traffic mortality: traversing speed and body length. To investigate the traffic mortality for a range of species, we estimate the traversing speed of animals by using the allometric description of the maximum velocity. Peters (1983) relates the maximum (non-sustained) speed of running to body mass. These estimates serve to set an upper bound on velocity. As expected, maximum speed (in m s^{-1}) increases with body weight, as larger animals can usually outrun smaller ones, according to (Peters 1983)

$$V_{i,\max} = 10.4\, W_i^{0.38} \tag{8}$$

where W_i is the body weight of species i (in kg). For the speed of crossing roads, we assume 25% of the maximum running speed since individuals usually do not cross the road with maximum speed (but also move faster in unsuitable environments as roads than the average velocity observed in their habitat, see Peters 1983).

The body length of most common mammal species is often known, for example for The Netherlands see Lange et al. (1994) who also give the average body weight of the mammals. The data on body length and the allometric relationship for velocity can be used to parameterise the two species characteristics in the traversability model. As can be expected, larger animals and animals that traverse the road fast are less vulnerable for traffic mortality. The effect of both velocity and body length is further investigated in the sensitivity analysis of the traversability model (see below).

Also other species characteristics determine traffic mortality, such as habitat characteristics, behaviour during seasonal or dispersal movement and home-range size. These factors do however not directly affect the probability that an individual successfully crosses a road, but have their influence via parameter $K_{i,\tau}$ in Equation (7). Species of closed and half-open landscapes with a large home range that move large distances are relatively sensitive to traffic mortality since they frequently cross roads that have a low clearance (e.g., Oxley et al. 1974; Adams and Geis 1983; Groot Bruinderink and Hazebroek 1996; Clarke et al. 1998). Fast moving mammals (often large animals) are less vulnerable for traffic mortality. However, these animals often have relatively large home ranges or move large distances. For these animals, the effect of traffic mortality on population dynamics can only be assessed when their daily and seasonal road crossings are considered.

Sensitivity analysis of the traversability model

To assess the relative influence of each parameter in the traversability model as formulated in Equation (6), a sensitivity analysis is conducted. Therefore, we calculate the relative sensitivity S of the probability P_i to relative changes in parameters according to

$$S = \left| \frac{\theta}{P_i} \frac{\partial P_i}{\partial \theta} \right| \tag{9}$$

where θ represents a parameter that affects the value of P_i . Here, the relative sensitivity S should be interpreted as the percentage that the probability P_i changes when the parameter θ changes 1%.

The relative sensitivity S of the probability P_i to relative changes in the parameters is illustrated in Figure 2. The ranges of the parameters for the

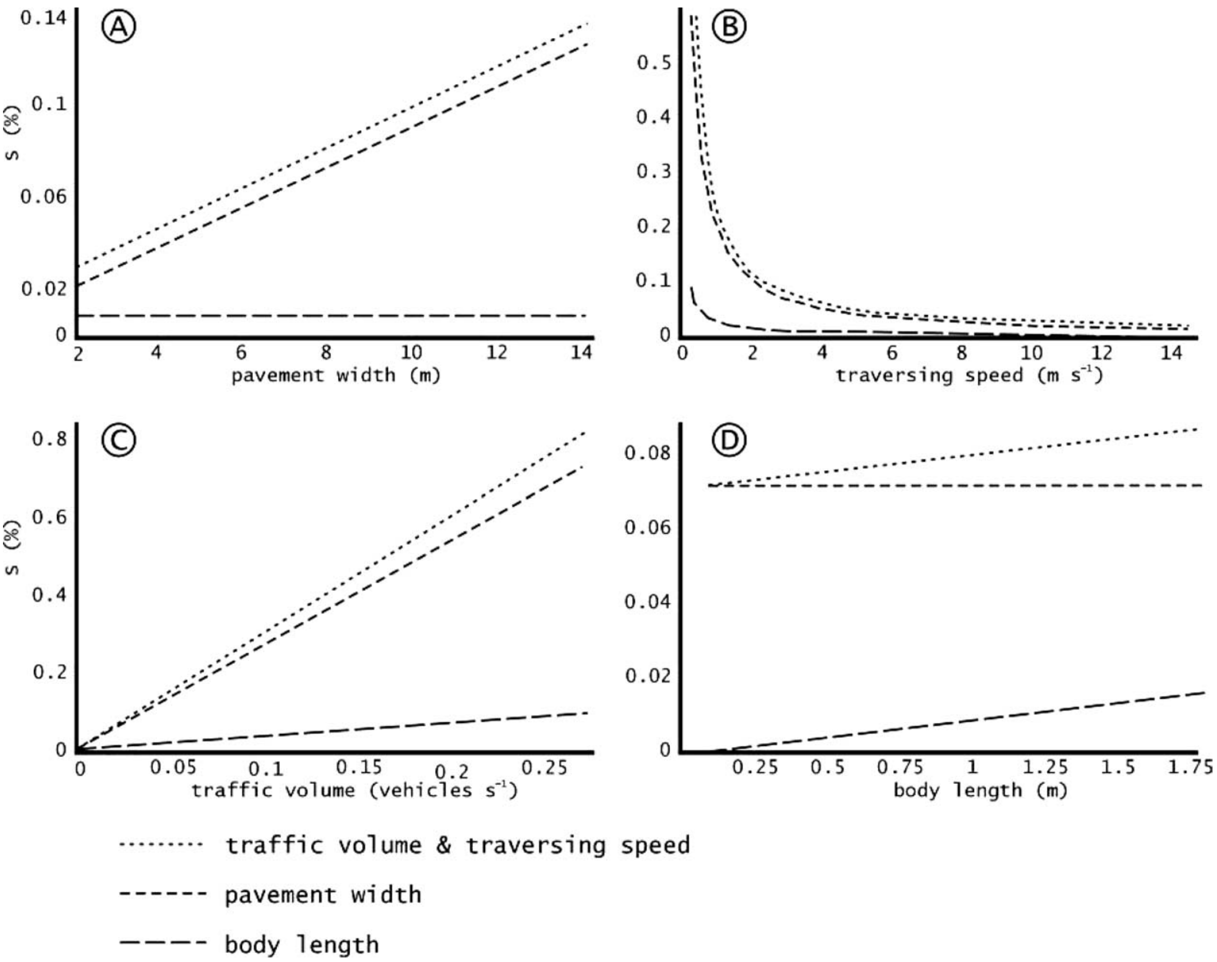

Figure 2. The relative sensitivity S in % (Equation 9) of the probability of successfully road crossing P_i (Equation 6) to changes of 1% in each parameter (pavement width B, traversing speed V_i and the body length L_i of animal species i, the traffic volume λ). In figure (a), for each value of the pavement width B, the effect on the relative sensitivity S of a 1% change in all 4 parameters is given, including a 1% change in the pavement width B. In figure (b), the same is done for the traversing speed V_i of animal species i, in figure (c) for the traffic volume λ, and in figure (d) for the body length L_i of species i. It appears that a 1% change in the traffic volume and traversing speed give the same effect on the relative sensitivity. Note that the scales of the y-axes differ greatly among the figures. Parameter values: (a) $\lambda = 0.027$, $L_i = 1.0$, $V_i = 3.0$, (b) $\lambda = 0.027$, $L_i = 1.0$, $B = 8.0$, (c) $L_i = 1.0$, $V_i = 3.0$, $B = 8.0$, (d) $\lambda = 0.027$, $V_i = 3.0$, $B = 8.0$

traversing speed V_i (by using Equation (8)) and body length L_i are based on data of the most common terrestrial mammal species found in The Netherlands (Lange et al. 1994). For the traffic volume and pavement width, we consider the values found on low-traffic roads ($\lambda = 0$–5,000 vehicles d^{-1}, $B = 2.5$-5.5 m) and motorways ($\lambda = 5{,}000$–50,000 vehicles d^{-1}, $B = 7.5$–14 m). For the decisive traffic volume during the period that most of the animal species are active, we follow rules of thumb in traffic engineering. Therefore, we assume that on average 75% of the daily traffic volume appears during daylight hours (between 7 and 19 h) and the other 25% during the evening and night. This means that during the 12 evening and night hours (between 19 and 7 h) per hour on average 2% of the daily traffic volume passes (these figures are confirmed by Figure 1).

This sensitivity analysis demonstrates which parameters should be determined exactly. It appears that for high values of traffic volume λ (Figure 2c) and low values of the traversing speed V_i (Figure 2b), small changes in traffic volume λ, pavement width B and traversing speed V_i have relatively high impact on the probability of successful road crossing P_i , whereas small changes in body length L_i have a relatively small impact. For all values of pavement width

B (Figure 2a) and body length L_i (Figure 2d), small changes in traffic volume λ, traversing speed V_i, pavement width B and especially body length L_i have a relatively small impact on P_i. Exact determination is thus necessary for pavement width B, traversing speed V_i and traffic volume λ for animals that move relatively slow or when roads with a high traffic volume are crossed. The effects of the traversing speed and body length of larger mammal species are minor, especially for roads with low traffic volume or pavement width (Figure 2a, Figure 2c): an exact estimate of traversing speed V_i and body length L_i is then not necessary.

Mortality effect on population dynamics

Two-patch population model

Next, we include the traversability model in a simple population model. Consider a single species occupying a spatially heterogeneous landscape. This can be represented by modelling the growth and movement of individuals in two patches (cf. Amarasekare 1998). The change in the number of individuals in patch 1 is given by

$$\frac{dN_1}{dt} = f(N_1) - e(N_1) + c(N_2) \tag{10}$$

where the function $f(N_1)$ describes the local dynamics within patch 1, $e(N_1)$ is the number of individuals emigrating from patch 1 and $c(N_2)$ is the number immigrating from patch 2. We take time steps of 1 year during which dispersing individuals only once move between the two patches. Similar equations can be formulated for patch 2. For mammals, we assume logistic population growth with

$$f(N_1) = (r_1 - m_1 N_1) N_1 \tag{11}$$

where r_1 is the per capita growth rate and m_1 the per capita mortality rate in patch 1. The maximum local population size or ‘carrying capacity’ of patch 1 is equal to r_1/m_1. We assume that the two patches are similar ($r_1 = r_2 = r$ and $m_1 = m_2 = m$). The number of individuals emigrating from patch 1 is given by

$$e(N_1) = a_1 N_1^s \tag{12}$$

where a_1 is the per capita emigration rate from the population in patch 1 and s measures the strength of density dependence in emigration. When $s = 0$, emigration is density-independent and occurs at rate a_1. When $s = 1$, emigration increases linearly with increasing density. When $s > 1$, per capita emigration rate increases at an accelerating rate (Amarasekare 1998). We consider symmetric dispersal ($a_1 = a_2 = a$) and assume that $s = 1$. The immigration from patch 2 to patch 1 is defined as

$$c(N_2) = d'\ e(N_2) \tag{13}$$

where d' denotes the fraction of the emigrants that successfully reaches patch 1. For both patches, the fraction d' is similar.

We explore the effect of traffic mortality during movements between the two patches on the population dynamics. Therefore, we decrease the migration success due to traffic mortality assuming that there is a two-lane road between the two patches that reduces the number of individuals that safely reach the other population. The fraction of the emigrants that successfully reaches the other patch is then denoted as

$$d' = P_i\, d \tag{14}$$

where d is the fraction of the emigrants that during 1 time step successfully reaches patch 1 excluding the effect of traffic mortality. We assume that individuals cross the road only once in each time step, i.e., during dispersal. Moreover, the effect of the road is assumed to be equal for the dispersers from both local populations. Then based on Equation (10) – (14), the model can be denoted as

$$\frac{dN_1}{dt} = (r - m\,N_1)\,N_1 + a\,(P_i\, d\, N_2 - N_1) \tag{15a}$$

$$\frac{dN_2}{dt} = (r - m\,N_2)\,N_2 + a\,(P_i\, d\, N_1 - N_2) \tag{15b}$$

Then, we include traffic mortality on two roads: the road between the patches that affect the yearly exchange (now called road 1) as well as another road (road 2) that intersects patch 2. Road 2 affects the

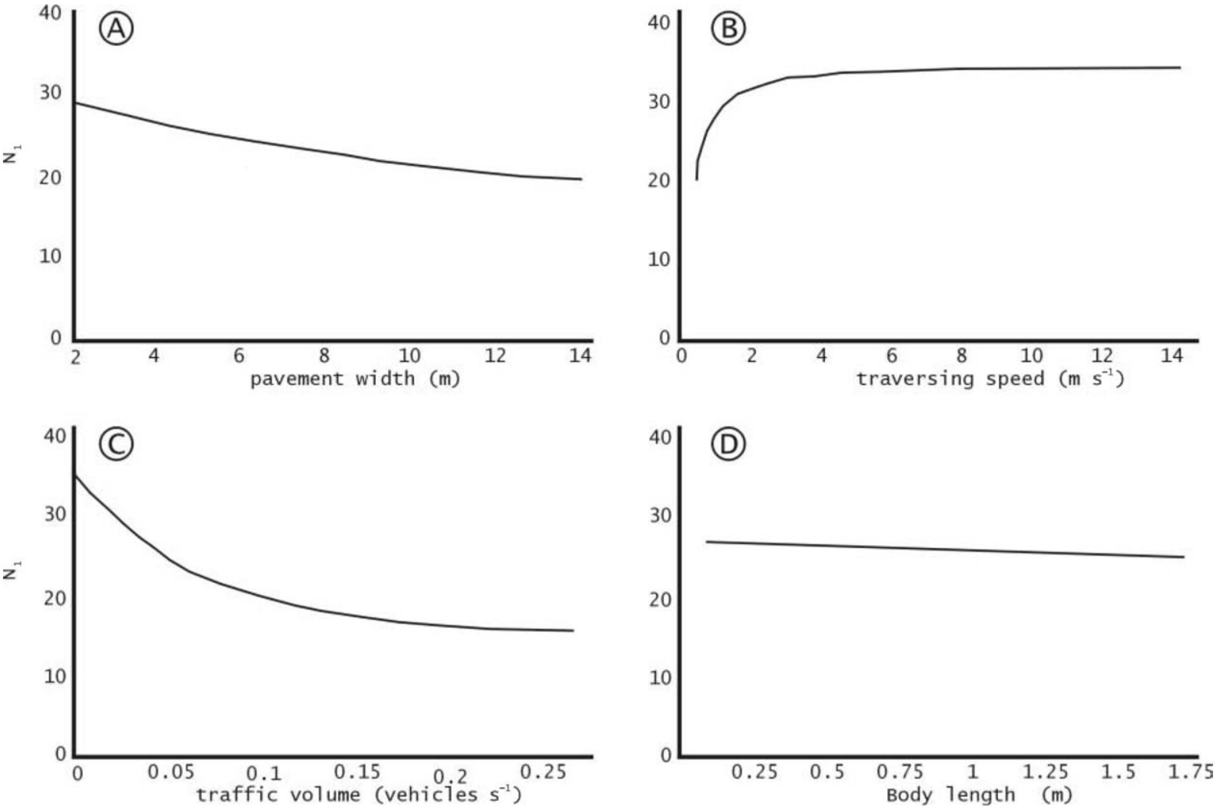

Figure 3. Effect of (a) pavement width, (b) traversing speed, (c) traffic volume and (d) body length on the equilibrium size of population 1. Parameter values: $r = 0.8$, $m = 0.02$, $a = 0.5$, $s = 1$, $d = 0.8$, (a) $L_i = 1.0$, $V_i = 0.5$, $\lambda = 0.05$, (b) $L_i = 1.0$, $B = 6$, $\lambda = 0.05$, (c) $L_i = 1.0$, $V_i = 0.5$, $B = 6$, (d) $V_i = 0.5$, $\lambda = 0.05$, $B = 6$

daily activities of the individuals in this patch. Now, we use $P1_i$ as the traversing probability of road 1 and $P2_i$ for road 2. When looking at the effects over 1 year (the time step of the model), then the increase in mortality due to traffic kills on road 2 equals the probability being killed per crossing times the number of crossings in a year. Road 2 will then increase the mortality rate of individuals in population 2 with $K_{i,t}$ $(1 - P2_i)$, where $K_{i,t}$ is the number of times that an individual crosses road 2 during 1 year. Now, the change in population 2 is denoted as

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = \left(r - \left(m\,N_2 + K_{i,t}(1 - P2_i)\right)\right) N_2 + a\,(P1_i\,d\,N_1 - N_2) \qquad (16)$$

Analysis of the two-patch population model

In Figure 3, the effects of traffic volume, pavement width, body length and traversing speed on the equilibrium size of population 1 are given based on the road between the two patches that affects the dispersal of individuals. The size of population 2 is the same as population 1. As can be expected, the population size decreases with increasing pavement width (Figure 3a) and traffic volume (Figure 3c) since these effects cause a decrease in the probability that an individual successfully crosses the road during dispersal. When animals move faster, a higher population size can be expected (Figure 3b). Body length seems to have hardly any effect when all the other parameters are kept constant for the given parameter ranges (Figure 3d). This is also predicted by the sensitivity analysis (Figure 2d). The formal stability analysis of these equilibria is given in the Appendix.

In Figure 4, the size of both the populations 1 and 2 is presented. There is still a road between the two populations (road 1) and patch 2 is intersected by road 2. For both slow and fast moving species, it appears that the size of population 2 is largely determined by the road and traffic characteristics of road 2, even

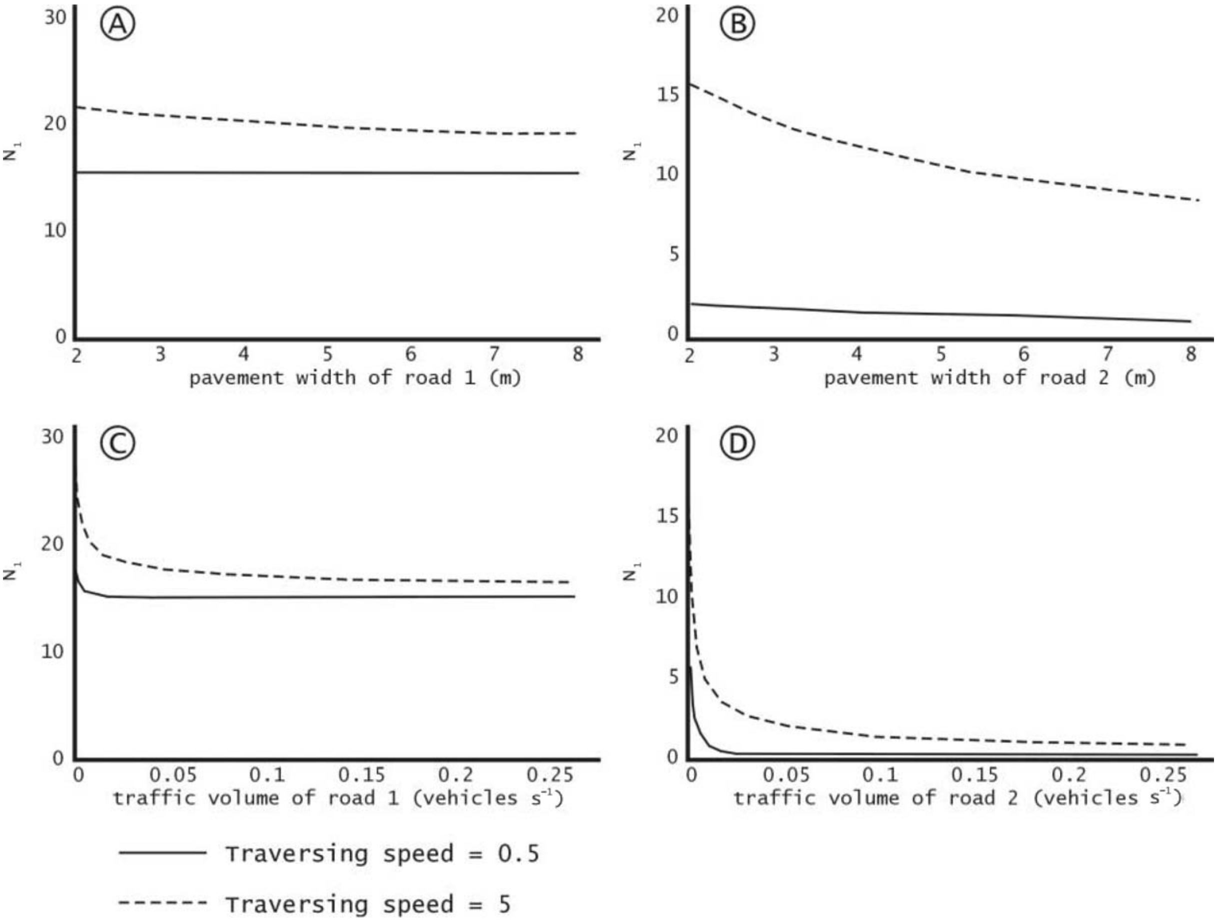

Figure 4. Effects of traffic volume and pavement width on the equilibrium sizes in population 1 and 2 for a slow moving (solid line) and fast (dashed line) moving animal. In between the two populations, the wide and busy road 1 is located that affects dispersal movements. The small and quiet road 2 that affects daily movements intersects population 2. Parameter values: $r = 0.8$, $m = 0.02$, $a = 0.5$, s = 1, $d = 0.8$, $L_i = 1.0$, $K_{i,t} = 120$, (a) $\lambda_1 = 0.1$, $\lambda_2 = 0.03$, $B_2 = 5$, (b) $\lambda_1 = 0.1$, $\lambda_2 = 0.03$, $B_1 = 14$, (c) $\lambda_2 = 0.03$, $B_1 = 14$, $B_2 = 5$, (d) $\lambda_1 = 0.1$, $B_1 = 14$, $B_2 = 5$

when it has the characteristics of a low-traffic road. A reduction in traffic volume and pavement width may largely increase the size of population 2 and thus its persistence time. This may enhance the population size and thus the persistence of the two local populations.

Discussion

In this paper, we derive a model from traffic flow theory to determine the probability that an animal crosses a road successfully based on the relevant road, traffic and species characteristics. The probability of successful road crossing is determined by the pavement width of the road, traffic volume, traversing speed of the animal and its body length. Analysis of the model shows that, for our parameter ranges, traffic volume and traversing speed have the largest effect on this probability. An increase in traffic volume has especially dramatic effects on animals that move slowly, regardless their body length. On wider roads, small animals are especially vulnerable. The sensitivity analysis of the traversability model shows that exact determination of traversing speed appears to be necessary for animals that move slowly. The analysis of the two-patch population model demonstrates also the large impact of traffic volume and traversing speed. One lesson is that mitigation measures to reduce the negative effects of roads should consider reduction in traffic volumes (Jaarsma and Van Langevelde 1997). Additional information is, however, necessary about the expected road clearance, the movement behaviour, dispersal distances and home-range size.

Although the relevant road, traffic and species characteristics determining traffic mortality are included in the traversability model, several aspects are not explicitly included in the model. First, traffic speeds intuitively determine traffic mortality. Lower vehicle speeds will increase the probability of successful road crossing, through the better opportunities for both driver and animal to react on each other and avoid a collision. Vehicle speed is, however, not explicitly included in our formulations since the distribution of time intervals between the vehicles is only related to the traffic volume and does not depend on vehicle speeds.

Second, we consider pavement width as the main road characteristic. Other characteristics also influence the road crossing, such as road lights since some animals avoid roads with road light, whereas others are attracted. Third, some species will flee or stay when a vehicle is approaching: for example, the traversing speed will be underestimated when individuals flee. Moreover, some animals restrain from roads when traffic volume increases. Fourth, it is also assumed that animals cross roads without any waiting time. This may be valid for landscapes where the clearance is low, but otherwise it is plausible that animals are restrained to cross when a vehicle is approaching. They may also be restrained when traffic volume is high due to the constant noise and visibility of vehicles. Fifth, we assume that when an animal and a vehicle are at the same location at the same moment, a collision occurs. This might not be true since corrections by humans and animals and also mis-hits where the animal survives a collision (for example because they are small enough to survive between the tires of a vehicle) also affect traffic mortality. Finally, we assume that the animals cross in a right angle, whereas this may be an underestimation of the time needed to cross.

So far, the assumptions in the traversability model exclude the above mentioned factors. These factors, however, could be important to determine traffic mortality for specific species. Relaxing these different assumptions does not drastically change the model but have an effect on the predicted traffic mortality, for example by changing the time that an animal needs to cross the road (see Equation 1) or the length of the path to cross the road. Changes in animal velocity, for example due to fleeing, deviations from crossing a road without any waiting time or crossing in a right angle can be easily incorporated in the model by introducing specific formulations for the time C_i (Equation 1) needed for a road crossing by an individual, the traffic volume λ, the pavement width B_i and the traversing speed V_i . Factors such as corrections by humans and animals and mis-hits are difficult to include in the model since hardly any data exist on the probability that drivers or animals prevent a collision by correcting their behaviour or the probability that animals survive collisions.

The analysis of the two-patch population model indicates that especially the road crossings during the daily movements have a large impact on the population size. We analysed the population model by plotting the equilibrium population size as function of parameter values. In reality, one cannot find a population in equilibrium since conditions change over days, seasons and years. However, to properly analyse the effects of changing road and traffic characteristics on species responses, we used this equilibrium approach.

In our population model, the maximum population size was kept constant for differently sized animals. Since small animals, however, have often much larger population sizes, we can expect that especially populations of large animals are vulnerable for traffic mortality. This agrees with studies that argue that traffic mortality is one of the major death causes for many species in human-dominated landscapes (Groot-Bruinderink and Hazebroek 1996; Forman and Alexander 1998; Trombulak and Frissell 2000) and that for some it is most likely responsible for regional extinction (e.g., badger *Meles meles*, Lankester et al. 1991; Clarke et al. 1998). Although, the number of traffic victims may seriously reduce the size of the population (Clarke et al. 1998; 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. The traversability model could be used in population models to estimate effects of traffic mortality on population performance.

Testing the predictions of the traversability model is difficult since it requires both the number of times that individuals successfully cross a road and the number of traffic victims. As far as we know, there are no studies on the fraction of successful road crossings. Some studies provide numbers on traffic victims (e.g., Groot Bruinderink and Hazebroek 1996; Clarke et al. 1998; Hels and Buchwald 2001; Clevenger et al. 2003). However, the actual number of victims is often difficult to measure due to scavengers or identification problems, especially for small animals (Hels and Buchwald 2001).

The relevance of the models discussed in this paper is not to calculate the actual number of traffic victims or the actual effect on population level. Due to the difficulty of testing the predictions and the uncertainty of some parameters in the traversability model, the model should be mainly used to compare the traffic mortality due to changes in road and traffic characteristics, e.g., as result of mitigating measures, see Jaarsma and Van Langevelde (1997) for an example. By comparing changes in road or traffic characteristics or alternatives for road design and traffic volumes, the models can provide insight in the relative effects of these road and traffic characteristics on population dynamics of wildlife. When data on traffic mortality are available (Davies et al. 1987; Groot Bruinderink and Hazebroek 1996; Garrett and Conway 1999), the model could be used to predict changes after applying mitigating measures. When numbers of victims are not available, however, model predictions based on road and traffic characteristics and the distribution and size of the local populations of the species could also be useful to determine the locations where mitigating measures should be applied.

Application of the model could thus predict the expected effectiveness of mitigating measures relative to the current situation. These mitigating measures might affect the road and traffic characteristics. The changes in these road and traffic characteristics could be analysed by calculating the number of traffic victims before and after the mitigating measures. Such a traversability model could be a tool for traffic planners and conservationists to prevent traffic accidents and protect biodiversity.

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Appendix

We analyse the stability of the two-patch population model dN_1/dt and dN_2/dt formulated in Equation (15), where one road is located between the two populations. In order to establish the local stability of an equilibrium (N_1^*, N_2^*), we investigate the Jacobian matrix of this model

$$\mathbf{J} = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix} \tag{A1}$$

The equilibrium (N_1^*, N_2^*) is locally stable if (e.g., Edelstein-Keshet, 1988)

$$\text{trace}(\mathbf{J}) = A_{11} + A_{22} < 0 \tag{A2}$$

$$\det(\mathbf{J}) = A_{11}A_{22} - A_{12}A_{21} > 0 \tag{A3}$$

The algebraic solution for the non-trivial equilibrium is (for $s = 1$ and $i = 1$ and 2)

$$N_i^* = \frac{a(d\,P_i - 1) + r}{m} \tag{A4}$$

Let $F = dN_1/dt$ and $G = dN_2/dt$, the elements of Jacobian matrix are then

$$A_{11} = \left.\frac{\partial F}{\partial N_1}\right|_{N_1^*} = a - 2\,a\,d\,P_i - r \tag{A5a}$$

$$A_{12} = \left.\frac{\partial F}{\partial N_2}\right|_{N_2^*} = a\,d\,P_i \tag{A5b}$$

$$A_{21} = \left.\frac{\partial G}{\partial N_1}\right|_{N_1^*} = a\,d\,P_i \tag{A5c}$$

$$A_{22} = \left.\frac{\partial G}{\partial N_2}\right|_{N_2^*} = a - 2\,a\,d\,P_i - r \tag{A5d}$$

Based on the equations A5a-d, it can be concluded that the trace(**J**) (equation A2) is always negative and the det(**J**) (equation A3) is always positive when $r > a(1 - d\,P_i)$: the per capita growth rate should exceed the loss of individuals due to emigration. Note that r, a, m, d and P_i are all positive and $0 \leq d \leq 1$ and 0

$\leq P_i \leq 1$. In other words, the equilibrium (N_1^*, N_2^*) is locally stable for the used parameter values.

The model formulated in Equation (15a) and (16) is too complex to derive the stability conditions.

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