



Research, part of a Special Feature on [Effects of Roads and Traffic on Wildlife Populations and Landscape Function](#)

Modeling the Effect of Traffic Calming on Local Animal Population Persistence

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ABSTRACT. A steady growth in traffic volumes in industrialized countries with dense human populations is expected, especially on minor roads. As a consequence, the fragmentation of wildlife populations will increase dramatically. In human-dominated landscapes, typically minor roads occur in high densities, and animals encounter them frequently. Traffic calming is a new approach to mitigate negative impacts by reducing traffic volumes and speeds on minor roads at a regional scale. This leads to a distinction between roads with low volumes as being part of the traffic-calmed area, whereas roads with bundled traffic are located around this area. Within the traffic-calmed area, volumes and speeds can be decreased substantially; this is predicted to decrease the disturbance and mortality risk for animals. Thus far, data on the effects of traffic calming on wildlife population persistence remain scarce. Using metapopulation theory, we derived a model to estimate thresholds in the size of traffic-calmed areas and traffic volumes that may allow persistent populations. Our model suggests that traffic calming largely increases the persistence of roe deer in a landscape with a dense road network. Our modeling results show trade-offs between traffic volume on roads within the traffic-calmed area and both the area of habitat available for this species in the traffic-calmed area and the size of the traffic-calmed area. These results suggest ways to mitigate the fragmentation of wildlife habitat by road networks and their expected traffic volumes.

Key Words: *habitat fragmentation; metapopulation theory; mitigation; road ecology; traffic calming; transportation planning*

INTRODUCTION

Roads can impact wildlife in many ways, but mainly they are a source of mortality and habitat fragmentation (Trombulak and Frissell 2000, Spellerberg 2002, Forman et al. 2003). Traffic-related mortality is considered to be among the major causes of mortality for many animals in human-dominated landscapes (Groot Bruinderink and Hazebroek 1996, Trombulak and Frissell 2000); for some species, it is the most likely cause of local extinction (e.g., badger *Meles meles*, Clarke et al. 1998). The expected steady growth of road traffic flows worldwide will further increase these negative impacts (Peden et al. 2004, Kirchner et al. 2005, Vold 2006). We expect that in countries with high human densities, the capacity of the existing road networks will be increased by relatively small adaptations such as building extra lanes or bypasses,

rather than by constructing new roads. Consequently, this will lead to increases in traffic volumes. Currently, motorways are already congested (Bovy 2001), and it is expected that the networks of minor roads, i.e., regional and local roads, will accommodate the expanding flows (Stokes 1991). The environmental impacts of minor roads, which are generally underestimated, will further increase because of increasing volumes on these roads (van Langevelde et al. 2009).

In many industrialized countries, there is a high density of minor roads. For example, road density in The Netherlands is 1.55 km/km², whereas motorways cover 0.07 km/km². To mitigate the negative effects of minor roads on wildlife, a new approach is needed, rather than the traditional one focusing mainly on major roads. We propose the concept of a traffic-calmed area (Jaarsma 1997),

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where minor and major roads are mitigated in conjunction with one another (Jaarsma and Willems 2002, van Langevelde et al. 2007, 2009).

Since the 1970s, traffic calming has been proposed to reduce the accident risk for people and cars in urban areas (Kjemtrup and Herrstedt 1992). Later, this concept was also introduced in rural areas (Jaarsma 1997). Traffic calming aims at reducing vehicle speeds as well as volumes within the traffic-calmed area using speed-reducing measures such as speed bumps and raised level-crossings. The minor road network is restricted to locally bound traffic only. Former diffuse flows of through-traffic are concentrated on a network of major roads around the traffic-calmed area, suited for somewhat higher volumes and speeds. Van Langevelde et al. (2007, 2009) have shown that traffic calming may reduce noise load and traffic mortality for individual animals. However, the effects of traffic calming on wildlife population persistence have not been documented. In transportation planning, the acceptable measures of traffic-calmed areas are clear. The question remains as to what size traffic-calmed areas need to be for animal populations to persist. This will largely depend on many landscape and species-specific factors such as habitat carrying capacity, the biology and demographics of the species, and human disturbance in area, which have not been considered thus far.

Here, we develop a theoretical model to estimate the effect of the size of traffic-calmed areas in relation to traffic volume and habitat area. We use a previous individual-based model that estimates the probability of a successful road crossing for animals based on traffic, road, vehicle, and species characteristics (van Langevelde and Jaarsma 2004, Jaarsma et al. 2006). We implement this model within a metapopulation model to estimate the species persistence in a region. Current metapopulation theory can predict threshold conditions for the persistence of a species in a landscape by deriving the metapopulation capacity (Hanski and Ovaskainen 2000, 2002). A species is predicted to persist in a landscape if the metapopulation capacity of that landscape is greater than a certain threshold determined by the properties of the species relative to the characteristics of the landscape. We focus on the minimal size of traffic-calmed areas and the level of traffic calming required for local population persistence.

TRAFFIC CALMING: WHY AND HOW?

There are many measures to mitigate the negative effects of traffic on wildlife. Some are expensive and therefore only realistic for road networks with a limited length such as motorways. The dense network of minor roads offers access to houses, farms, and businesses alongside these roads. Frequent human access prohibits effective low-cost measures on these roads such as fencing. Therefore, another type of intervention must be used for minor roads such as the reduction of traffic volumes, either temporally or permanently, or the reduction of vehicle speed (Jones 2000), which has been shown to dramatically decrease mortality risk (Jaarsma et al. 2006).

To explore opportunities for changing the use of roads, we distinguish between local roads (minor roads) and regional and national roads (major roads; Table 1). Local roads can be divided into local access roads, e.g., to farms and houses, and local collector roads, which connect villages and collect traffic from access roads; these differ in pavement width and traffic volume. The regional road network consists of arterial highways that give access to regions. The national road network consists of motorways, which mainly have a flow function for through-traffic. Motorways are connected with the regional network by a limited number of exit and on ramps.

Urban traffic calming has been shown to improve safety (Elvik 2001). The idea of rural traffic calming was developed in The Netherlands, an industrialized country with a high human density. However, for an application of the concept of traffic calming in areas of other countries, e.g., Australian or United States suburbs, it is essential that the existing minor road network is dense enough to enable a concentration of traffic flows on a limited part of the network. From the perspective of transportation planning, the maximum size of traffic-calmed areas is determined by the time thought to be acceptable for leaving the calmed area to continue on the nearest major road. An acceptable limit of 3 min (Koornstra et al. 1992) allows for a trip length of 3 km on minor roads. This can be achieved in traffic-calmed areas with a maximum mesh size of roughly 4–7 km, covering an area between 20 and 50 km².

Table 1. Characteristics of road networks outside built-up areas in The Netherlands. Source: van Langevelde et al. (2009).

Road type	Scale of road network			
	Minor roads		Major roads	
	Local		Regional	National
	Access road	Collector road	Arterial highway	Motorway
Network characteristics				
Length, paved (km)	47,652 [†]		7508 [‡]	2291
Road density§ (km/km ²)	1.55		0.24	0.07
Mesh width§ (km)	1.3		8.2	26.8
Road characteristics[!]				
Cross-section width (m)	5.5 to 9.5	6.5 to >10	±20	±40 or 60 [¶]
Pavement width (m)	2.5 to 4.5	4.5 to 6.2	±7.5	2 × (12 to 21) [¶]
Number of carriageways	1	1	1	2
Number of traffic lanes	1	1 or 2 [#]	2	4, 6, or 8
Traffic characteristics				
Volume (×10 ³ vehicles/d)	0.1 to 1	0.5 to 5	2 to 25	20 to 200
Legal speed limit (km/h)	60 ^{††}	60 or 80 ^{††}	80 or 100	100 or 120

[†]Road statistics do not allow for specification of the local network by road type.

[‡]Including 868 km of arterial highway belonging to principal national routes (not motorways).

[§]Based on 30,682 km² of land outside built-up areas.

[!]Profiles based on the Dutch concept of sustainable traffic safety.

[¶]Based on a 2 × 2 and a 2 × 4 motorway respectively, total width including two verges of 5 m.

[#]For two lanes, a minimum pavement width of 5.5 m is required.

^{††}Both limits are still in use. The limit has been 80 km/h since 1974; this is still the official limit unless 60 km/h is signposted. Today, the latter is already the case for approximately half of the Dutch network of rural minor roads.

FRAGMENTATION BY ROAD NETWORKS

Several measures can be used to quantify the fragmentation of landscapes by roads. Forman et al. (2003) suggest the use of road density, D , defined as the road length per unit area (units: km/km²). This is a simple but straightforward measure of fragmentation. Forman et al. (2003) cite published examples showing that road density appears to affect many species of larger wildlife (e.g., wolf *Canis lupus*) when it exceeds 0.45–0.6 km/km². Values below this range can be found in some remote areas, but not in industrialized countries such as Western Europe and Japan (Forman et al. 2003). From our data, we estimate paved road density for rural areas in The Netherlands at approximately $D = 1.87$ km/km² ($= [47,652 + 7508 + 2291]/30,682$; Table 1). This density doubles when roads within built-up areas are included.

Mesh width, L , is the distance of a road link between two nodes in the road network (units: km). Mesh width is calculated by laying out the total road length in an area in a regular square grid and is related to road density as $L = 2/D$ (Jaarsma and Willems 2002). Mesh width is relevant to habitat fragmentation because it indicates how far an animal can move through the landscape in a straight line before it may encounter a road. The average mesh width in The Netherlands is 1.07 km ($= 2/1.87$). Without the motorway network, mesh width for the network of minor roads and regional roads is 1.11 km.

Mesh size, M , defined as the average size of the polygons enclosed by a road network (units: km²; Jaarsma and Willems 2002), indicates the average size of an area within which an animal can travel through the landscape without encountering a road. The average mesh size for all roads in The Netherlands is 1.14 km² (van Langevelde et al. 2009). The effective mesh size, which denotes the size of the areas when a region is subdivided by roads, seems a more appropriate measure because it includes variability in mesh size (Jaeger 2000). Both road density and (effective) mesh size provide simple measures. However, these measures neglect the effect of traffic volume on animal mortality and habitat fragmentation (Jaeger et al. 2005, van Langevelde et al. 2009).

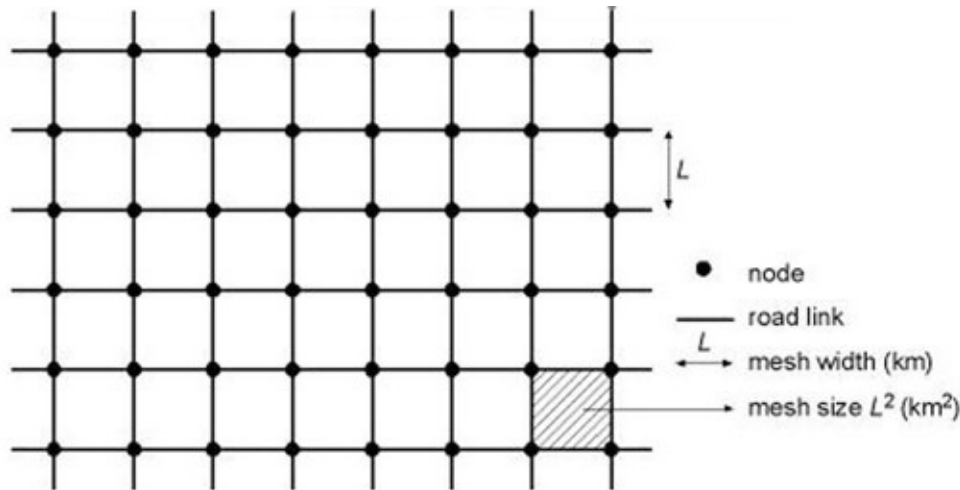
MODELLING TRAFFIC FLOWS IN ROAD NETWORKS

To quantify fragmentation of landscapes by road networks as a function of road density and traffic volume, we first consider an infinite area with a network of minor roads in a regular square grid (Fig. 1). All roads have the same function, namely for local access as well as for traffic that travels somewhat longer distances. The roads have similar road characteristics, e.g., pavement width, and similar traffic volume. The area consists of built areas, agricultural land, and natural areas typical of a human-dominated landscape such as in many parts of western Europe. Larger towns and cities are excluded from our hypothetical rural area. The human population of the rural area lives in both the nodes of the road network and the areas enclosed by this network, here called grid cells. We assume that all traffic flows originate from the nodes. Motorways are not included in our network, and we only consider car traffic. The mesh size in our hypothetical area is $M = L^2$.

Next, we estimate the daily traffic flow on this road network, which is determined by the traffic generation and its distribution over the network. Traffic generation depends on the number of people and the distance travelled daily by car per capita, G (units: km/day). We assume that an equal amount of people start their travel in each node. In an infinite network, every node serves four neighboring grid cells, and every grid cell counts four nodes. The number of people that start their travel in a node can be estimated by multiplying the density of the human population in the region, B , with the mesh size, L^2 . The total amount of daily vehicle travel distance generated in a node is then $F = BL^2G$ (units: km/day). For rural areas in The Netherlands, B is approximately 200 inhabitants/km², G is approximately 16 vehicle km/day-person, and L is 1.11 km. Thus, the total amount of daily vehicle travel distance generated in a node, F , is approximately 4000 vehicle km/day.

The distribution of the total amount of daily vehicle travel distance, F , starts from each node into four directions. As we assume an infinite network and equal traffic volume on each road link, we may presume that all destinations are found in the four adjacent nodes and not further away, regardless of how far people actually travel. Thus, all road links starting at any node carry $0.25F$ vehicle km/day from that node. However, every road link carries

Fig. 1. Schematic representation of a network of minor roads in a regular square grid. The grid has nodes and road links with a length of L kilometres.



traffic from its two adjacent nodes; therefore, the two-directional flow on every road link is twice this amount: $0.5F$ vehicle km/day. Using this estimation, we can derive the traffic volume, λ , by dividing the vehicle travel distance per day by the length of the road link: $\lambda = 0.5F/L$ (units: vehicles/day). Based on the average statistics for The Netherlands, λ for our hypothetical area (Fig. 1) is estimated as 1800 vehicles/day ($= 0.5 \times 4000/1.11$), with similar roads and an evenly spread human population.

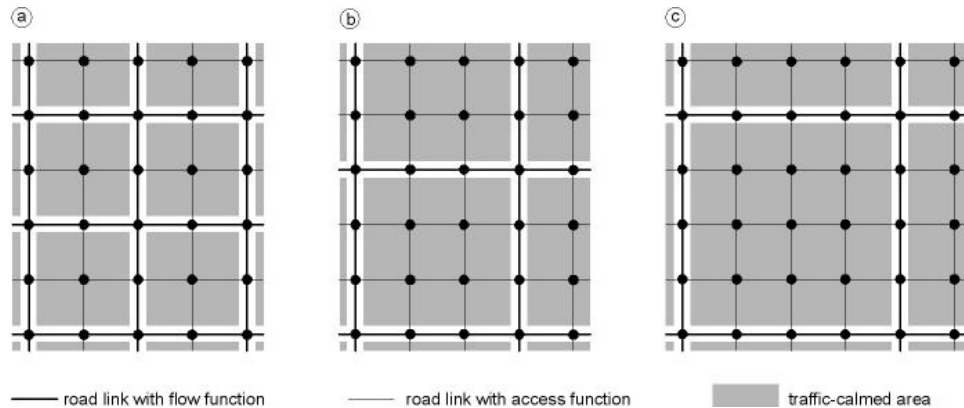
We now consider a road network with a simple distinction between major roads with primarily a traffic flow function and minor roads. This road network is designed so that traffic from minor roads with an access function can quickly flow to roads with a flow function. Roads with an access function will have a much lower traffic volume than roads with a flow function. The effectiveness of this reduction by changing road characteristics is represented by the coefficient γ , indicating the fraction of the original daily volume that is expected to remain on a road with an access function only. This volume, λ_a , can be formulated as $\lambda_a = \gamma\lambda$.

We can now make a distinction between two road types in the road network. The roads with reduced traffic volume are part of traffic-calmed areas, which are enclosed by roads with high traffic

volume; these are, respectively, roads with an access function and roads with a flow function (Fig. 2). The size of traffic-calmed areas can be represented as $(SL)^2$, where S is a scale coefficient for the size of the traffic-calmed area. Different sizes of traffic-calmed areas should have consequences for the distribution of traffic volumes over the roads and the accessibility of the grid cells. In our example, 4, 12, and 24 roads have an access function within a traffic-calmed area and consequently, a reduced volume λ_a (Fig. 2). In general, this number is $2S(S - 1)$, with a total length of $2S(S - 1)L$. Keeping the total amount of daily vehicle travel distance constant, roads surrounding traffic-calmed areas have to carry extra traffic volume because of the bundling of traffic on these roads. In our hypothetical network, the actual number of roads with a flow function per traffic-calmed area is $4S$, with a length of $4SL$. However, because all of these roads also serve the neighboring grid cell, the effective length is only one-half, to avoid double counting of the traffic volume, and so is $2SL$. To calculate the extra volume on roads with a flow function, we first need the ratio of the number of roads with an access function to the number of roads with a flow function $R = [(2S(S - 1))/(2S)] = S - 1$.

The extra traffic volume on roads with a flow function is caused by cars that were using the roads with an access function in the traffic-calmed areas.

Fig. 2. Schematic representation of a rural road network in a regular square grid with two types of roads and different sizes of traffic-calmed areas. The two road types are roads with an access function and roads with a flow function. Road links have a length of L kilometres. The size of the traffic-calmed area is (a) $2L$, (b) $3L$, and (c) $4L$.



This extra daily volume is $(1 - \gamma)\lambda$ for each road that now has an access function in the traffic-calmed area and is added in equal proportions to the existing traffic volume on the roads with a flow function. The extra volume on the latter roads is then $(1 - \gamma)\lambda R$. Daily traffic volume on roads with a flow function becomes $\lambda_f = [1 + (1 - \gamma)R]\lambda$. We have summarized the results for the increasing size of traffic-calmed areas in our hypothetical area (Table 2). These equations allow us to calculate the effect of the size of traffic-calmed areas on the traffic volumes, which depends on human population density, the generated daily vehicle travel distance per capita, and the level of traffic calming.

EFFECT OF TRAFFIC CALMING ON POPULATION PERSISTENCE

To estimate the effect of traffic calming on population persistence, we use a simple general metapopulation model, ignoring several parameters that also have an effect such as quality of the habitat, age structure of the population, noise load, and food availability (Hanski and Ovaskainen 2000, 2002). We include a model to estimate the probability of an animal successfully crossing a road (Appendix 1; van Langevelde and Jaarsma 2004, Jaarsma et al. 2006). Using this model, we can derive the

conditions for a species' persistence in a landscape as function of traffic volume and the species' movement ecology. To illustrate the effect of the size of traffic-calmed areas and the level of traffic calming on the equilibrium fraction of occupied patches, we assume a network of roads with $L = 2$ km, which encloses areas with mesh size of 4 km^2 . Road density in our hypothetical landscape is $D = 1 \text{ km/km}^2$. We use a model species with the characteristics of roe deer *Capreolus capreolus*. Roe deer is a common species, and individuals are frequently killed by traffic (Groot Bruinderink and Hazebroek 1996). The region is 100 km^2 in total and divided into 25 grid cells of equal size. Habitat is a certain fraction, a , of that region, and each grid cell contains one habitat patch of $4a \text{ km}^2$, which is located in the center of the grid cell. Based on this simple configuration, we can calculate the distance d_{ij} between each pair of habitat patches and the number of roads that animals have to cross between each pair of patches, assuming that animals do not cross at the nodes. The number of roads crossed is the sum of all roads crossed in the east-west direction (horizontal lines in Fig. 2) and in the north-south direction (vertical lines in Fig. 2) between each pair of patches. We first assume that all roads have similar characteristics and equal traffic volume and analyze the effect of traffic volume on the fraction of occupied patches H^* (Eq. 3 in Appendix 1). The fraction of occupied patches H^* decreases

Table 2. Road and network characteristics for a regular square grid with a length of L kilometres and different levels of traffic calming.

Variable	Original network (Fig. 1)	Level 1 (Fig. 2a)	Level 2 (Fig. 2b)	Level 3 (Fig. 2c)	Level n
Scale factor S	1	2	3	4	n
Length of roads with flow function surrounding traffic-calmed area	L	$2L$	$3L$	$4L$	nL
Number of grid cells in traffic-calmed area		4	9	16	n^2
Length of roads with flow function†	$2L$	$4L$	$6L$	$8L$	$4nL/2 = 2nL$
Length of roads with access function	0	$4L$	$12L$	$24L$	$2n(n-1)L$
Ratio of access roads to flow roads R	0	1	2	3	$n-1$
Volume on access roads λ_a^\ddagger	λ^\S	0.1λ	0.1λ	0.1λ	$\gamma\lambda$
Volume on flow roads λ_f^\P	λ	1.9λ	2.8λ	3.7λ	$[1 + (1 - \gamma)R]\lambda$

†The actual number is divided by two because all roads surrounding the grid cell also serve its adjacent grid cells.

‡Calculated with a value of $\gamma = 0.1$.

§In the original situation, all roads have both a flow and access function.

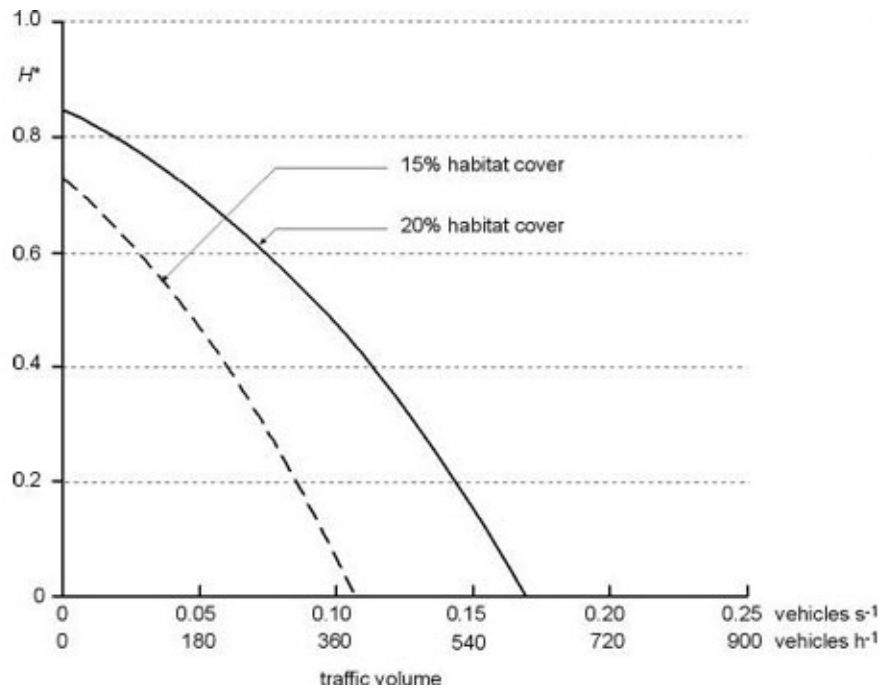
¶Roads with a flow function also serve the local access of adjacent grid cells.

with increasing traffic volume on these roads (Fig. 3). When patches are larger (i.e., larger value of a), the traffic volume where $H^* = 0$ is higher. We can now also plot traffic volumes where $H^* = 0$ as a function of the size of the habitat patches (Fig. 4). When a smaller fraction of each grid cell is covered by habitat, the traffic volume on the roads in the traffic-calmed areas should be lower to guarantee the persistence of the species in the region. For parameter combinations below the line (shaded area in Fig. 4), the species is able to persist in the landscape.

After establishing traffic-calmed areas, we can recalculate the hypothetical conditions for a persistent population. We therefore systematically increase the size of the traffic-calmed area so that its size increases from 1 grid cell ($S = 1$; Fig. 1) through 4, 9, and 16 ($S = 2, 3, 4$; Fig. 2) to 25 grid cells ($S = 5$). Using the equations (Table 2), we

determine the traffic volume of the roads in the traffic-calmed area and the roads surrounding this area so that the total daily vehicle distance traveled is constant. The average traffic volume for all road links is constant, λ , but there is a clear separation between roads with an access function, λ_a , and roads with a flow function, λ_f . Because we no longer consider an infinite road network, but rather a region surrounded by roads with a flow function, we calculate the distribution of traffic over both the access roads and roads with a flow function using the equations (Table 2), and correct this distribution for the expected traffic flow on these surrounding roads. We find that for different values of γ , the predicted fraction of occupied patches H^* increases with the increasing size of the traffic-calmed area (Fig. 5). When traffic-calmed roads receive only 10% of the original traffic volume, the species is predicted to persist, even when the average traffic volume increases up to 0.25 vehicles/s in large

Fig. 3. The predicted fraction of occupied patches as function of traffic volume on the roads surrounding traffic-calmed areas for different sizes of habitat patches. The total number of patches is 25, with one per grid cell in a given road network. The solid line is for patches covering 20% of each grid cell; the broken line is for patches covering 15% of each grid cell. Parameter values (see Appendix 1 for definitions): $\alpha = 1$, $\delta = 0.3$, $w_c = 2$, $l_c = 5$, $v_c = 20$, $l_a = 1.4$, $v_a = 5.2$, $w_a = 0.4$ (roe deer as model species), and $K = 5$. Dimensions of region: $L = 2$, $M = 4$, region is 10 km².



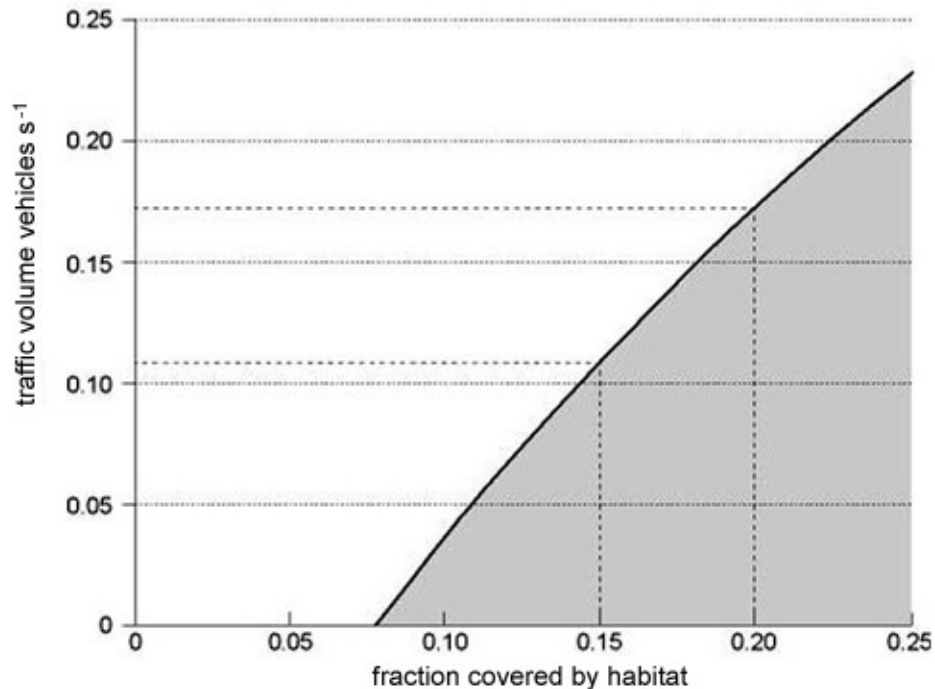
traffic-calmed areas ($\gamma = 0.1$, upper panel in Fig. 5). The results show positive effects of traffic calming on the predicted persistence of the species, even when traffic-calmed roads still receive 50% of the original volume ($\gamma = 0.5$, lower panel in Fig. 5).

DISCUSSION

We modeled the effects of traffic calming, i.e., the size of traffic-calmed areas and reductions in traffic volume, on the persistence of one species in a hypothetical landscape. Our theoretical model suggests that traffic calming should increase the persistence of the chosen model species in a landscape with a dense road network. For the chosen parameter values, our results show that there are trade-offs between traffic volume on roads within the traffic-calmed area and both the size of habitat

patches available for this species in the traffic-calmed area (Fig. 4) and the size of the traffic-calmed area (Fig. 5). With more habitat available, i.e., a larger fraction of area covered by habitat, a higher traffic volume can be allowed and still have a persistent population. When the traffic-calmed areas are small, average traffic volumes on the roads, and therefore traffic volume in the traffic-calmed areas, should be low. It should be noted that our results show the average traffic volume that is separated over roads with a flow function and roads with an access function (Fig. 5). Within larger traffic-calmed areas, these low traffic volumes are not required to maintain local populations of the focal species in the region. The predicted sizes of the traffic-calmed areas are realistic within the ranges calculated on the basis of travel times. One or more such areas fit within the size of 50–100 km² that is used for municipal-level planning in rural areas in industrialized countries (Ortúzar and

Fig. 4. Traffic volume of roads surrounding traffic-calmed areas compared to the size of habitat patches for which the predicted fraction of occupied patches is zero. For parameter combinations below the line (shaded area), the fraction of occupied patches is greater than zero and the population is persistent. Parameter values: $\alpha = 1$, $\delta = 0.3$, $w_c = 2$, $l_c = 5$, $v_c = 20$, $l_a = 1.4$, $v_a = 5.2$, $w_a = 0.4$ (roe deer as model species), and $K = 5$. Dimensions of region: $L = 2$, $M = 4$, region is 10 km².



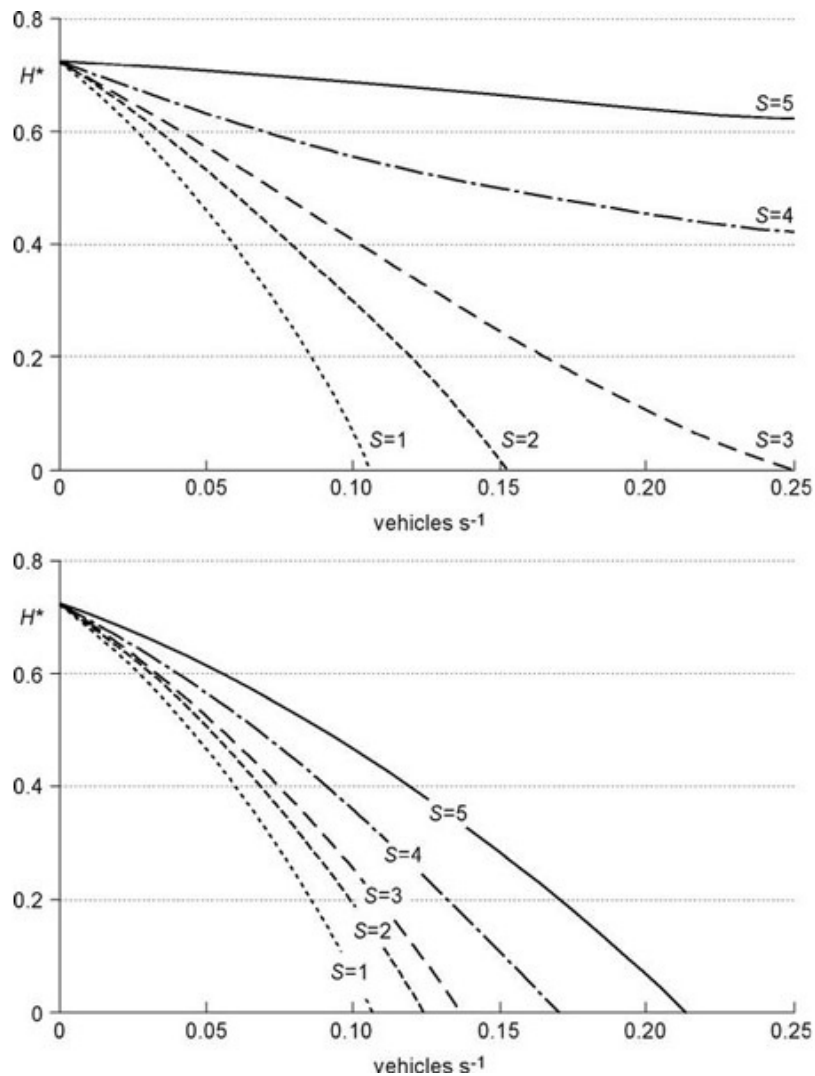
Willumsen 1994, Tolley and Turton 1995). However, the validity and applicability of our findings for management remain uncertain because our model has not yet been validated. We thus report only the results of a theoretical study. We used a model species with the characteristics of roe deer and took only road crossing into account; we ignored other factors that affect movement such as noise and landscape elements. However, the findings may be relevant for other large mammals that are frequently killed by traffic.

Our analysis provides a measure with which to quantify fragmentation by roads for certain species. So far, few studies have analyzed the mesh size of areas enclosed by roads and derived measures for fragmentation by roads (Jaeger 2000, Forman et al. 2003). The effective mesh size depends not only on road density, but on the traffic volumes of the roads

enclosing the mesh and on a species' biology, as areas with small mesh size may not provide sufficient habitat for local populations of large animals. In addition, there is discussion as to which classes of roads should be taken into account in the calculation of mesh size based on traffic volume and the expected effect on mortality (Jaeger et al. 2008). We include all roads in our approach and calculate the effect of each road link on traffic mortality based on its traffic volume. The next step would be to develop a link between often used measures such as mesh size (Forman et al. 2003) or effective mesh size (Jaeger 2000) and the conditions for population persistence that we have developed.

The effect of traffic calming on the persistence of a species in a landscape not only depends on the size of the traffic-calmed area, but also on the area of available habitat and its carrying capacity for that

Fig. 5. The predicted fraction of occupied patches as a function of the average traffic volume on all roads for different sizes of traffic-calmed area. The size of the traffic-calmed area is represented by a scaling factor S (see text for explanation). The total number of patches is 25, with one per grid cell in a given road network. The average traffic volume is constant, λ , but there is a clear separation between roads with an access function, λ_a , and roads with a flow function, λ_f . The traffic volume on the calmed roads is (a) 0.1 of the original volume ($\gamma = 0.1$), (b) 0.5 of the original volume ($\gamma = 0.5$). Parameter values (see Appendix 1 for definitions): $\alpha = 1$, $\delta = 0.3$, $w_c = 2$, $l_c = 5$, $v_c = 20$, $l_a = 1.4$, $v_a = 5.2$, $w_a = 0.4$ (roe deer as model species), and $K = 5$. Dimensions of region: $L = 2$, $a = 0.15$, $M = 4$, region is 10 km².



species. A species should persist when volumes on traffic-calmed roads are relatively high, as long as the habitat area is sufficient to keep the probability of local population extinction lower than the (re) colonization probability of patches. In addition to habitat area, the habitat quality is important (Hanski 1999); we did not consider it here. In many regions that have high human population density, habitat is highly fragmented and the habitat carrying capacity is low. In landscapes with small habitat patches, our model shows that traffic calming will only be successful if there is a dramatic reduction in traffic volume. The need for such dramatic reduction is especially relevant if traffic volumes indeed increase on minor roads as expected. We argue that species that travel large distances and often cross roads may benefit from traffic calming because it should reduce the risk of mortality during individuals' movement.

Because traffic calming has been applied frequently in urban areas, one would expect that the effects of traffic calming could be validated by data. However, to our best knowledge, the effects of implementing urban traffic calming on changing traffic flows (volumes and speed) have not yet been published. To date, publications of the results of rural traffic calming only focus on improved traffic safety (e.g., Jaarsma and Spaas 2007).

Wildlife biologists, transportation planners, and landscape planners are increasingly concerned about the effects of roads on animal populations (Kanters et al. 1997, Forman et al. 2003, Jaeger et al. 2005). We modeled how traffic calming may reduce the negative effects of traffic on wildlife. Our theoretical study may serve as a tool to estimate the effects of changes in road networks on larger animals, especially changes in volumes as a result of traffic calming. However, the model needs to be validated in terms of animal movements in calmed versus noncalmed areas with diffuse flows. Such validation can only be done by carefully monitoring traffic-calming projects and measuring animal movements, road kills, and population sizes before and after establishing traffic calming.

Responses to this article can be read online at:
<http://www.ecologyandsociety.org/vol14/iss2/art39/responses/>

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Appendix 1. Combining the model for estimating the metapopulation capacity and the model estimating the probability of an animal to successfully cross a road

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