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When road-kill hotspots do not indicate the best sites for road-kill mitigation

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Summary

1. The effectiveness of measures installed to mitigate wildlife road-kill depends on their placement along the road. Road-kill hotspots are frequently used to identify priority locations for mitigation measures. However, in situations where previous road mortality has reduced population size, road-kill hotspots may not indicate the best sites for mitigation.

2. The purpose of this study was to identify circumstances in which road-kill hotspots are not appropriate indicators for the selection of the best road-kill mitigation sites. We predicted that: (i) road-kill hotspots can move in time from high-traffic road segments to low-traffic segments, due to population depression near the high-traffic segment caused by road mortality; (ii) this shift will occur earlier for more mobile species because they should interact more often with the road; (iii) this shift can occur even if the low-traffic segment runs through lower quality habitat than the high-traffic segment. To test these predictions, we simulated population size and road-kill over time for two populations, one exposed to a road segment with high traffic and the other to a road segment with low traffic.

3. Our simulation results supported Predictions 1 and 3, while Prediction 2 was not supported.

4. *Synthesis and applications*. Our results indicate that, for new roads, road-kill hotspots can be useful to indicate appropriate sites for mitigation. On older roads, road-kill hotspots may not indicate the best sites for road mitigation due to population depression caused by road mortality. Direct measures of the road impact on the population, such as per capita mortality, are better indicators of appropriate mitigation sites than road-kill hotspots.

Key-words: animal–vehicle collisions, mitigation measures, mitigation placement, per capita mortality, population depression, population persistence, road ecology, road effects, road mortality, wildlife–vehicle collisions

Introduction

Roads form a ubiquitous network world-wide and are the cause of many negative impacts on wildlife (van der Ree, Smith & Grilo 2015). Due to the awareness generated by road ecology studies, there are legal obligations for mitigating road-kills in many countries. Animal mortality due to wildlife–vehicle collisions is sometimes mitigated by measures such as underpasses, overpasses and fences. However, the effectiveness of these measures depends on their placement along the road (Glista, DeVault & DeWoody 2009).

Choosing priority locations for mitigation measures is a challenge for road planners and ecologists. Many studies and guides of best practices recognize different approaches to prioritize locations, such as places with habitat for target species, stream crossings, places with high animal crossing rates and locations with high road mortality or 'road-kill hotspots' (e.g. Clevenger & Ford 2010; Gunson & Teixeira 2015). Road-kill hotspots are simply road segments of high road-kill relative to other road segments. Different measures are used to identify road-kill hotspots, from simple differences in road-kill counts (e.g. Finder, Roseberry & Woolf 1999) to sites with statistically significantly higher road-kill counts than other sites (e.g. Coelho *et al.* 2012). Using road-kill

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hotspots as priority locations for mitigation (e.g. Bissonette 2007; Huijser *et al.* 2007; Coelho *et al.* 2012; Langen *et al.* 2012; Cramer *et al.* 2014; Gunson & Teixeira 2015) seems logical considering that road mortality is a major impact of roads on wildlife and has stronger effects on population persistence than isolation (Forman & Alexander 1998; Jackson & Fahrig 2011).

However, in situations where road mortality has reduced animal population sizes, road-kill hotspots might not indicate the best sites for mitigation measures. Two empirical studies found more road-killed amphibians ('road-kill hotspots') on road segments with lower traffic than on segments with higher traffic (Fahrig *et al.* 1995; Eberhardt, Mitchell & Fahrig 2013). Amphibian populations are known to be highly susceptible to roads (Rytwinski & Fahrig 2012), and these effects are mainly due to mortality, as amphibians do not avoid roads (Bouchard *et al.* 2009). The authors of these studies (Fahrig *et al.* 1995; Eberhardt, Mitchell & Fahrig 2013) therefore hypothesized that road-kill hotspots were located on low-traffic road segments because populations near the high-traffic segments were depressed due to past road mortality, thus reducing the current numbers of road-killed amphibians on the high-traffic segments. While the number of dead amphibians was higher on the low-traffic segments, the per capita mortality rate was higher on the high-traffic segments (Fahrig *et al.* 1995). The authors therefore suggest that road-kill hotspots might not indicate the best locations for mitigation of road mortality. Instead, mitigation should be most effective where per capita mortality (the chance of an individual in the population being killed by road traffic) is highest; this should be on high-traffic road segments where populations are depressed due to the cumulative effects of past road-kill. If this inference is true, then current expenditures on road mitigation at road-kill hotspots are likely much less effective than they might otherwise be.

The hypothesis that road-kill hotspots might be located on low-traffic road segments because of population depression near the high-traffic segments can be expected in some contexts. The first assumption is that there is habitat around the low- and high-traffic road segments to maintain a population without the effect of road mortality. The second assumption is that the road segments should have different traffic volumes, so the road segment with higher traffic has a potential larger impact on population size. The last assumption is that the spatial extent of the road needs to be large relative to the spatial extent of populations that the road-killed animals at different road segments represent individuals from different populations and are independent. All these should be the case for different taxonomic groups in a single road or on road networks, depending on the spatial extent of the study relative to the spatial extent of populations.

The purpose of this study was to determine whether, in these circumstances, road-kill hotspots are appropriate indicators for the selection of the best road-kill mitigation sites. We developed a stochastic, individual-based model representing two road segments, one with higher traffic than the other, and each with a population around it. These road segments may represent segments of different roads in a network (e.g. Sillero 2008, for amphibians; Gomes *et al.* 2009, for owls; Langen *et al.* 2012, for reptiles; Valero, Picos & Álvarez 2015, for ungulates), or segments along the same road but with different traffic volumes (e.g. Coelho, Kindel & Coelho 2008, for mammals, birds and reptiles; Boves & Belthoff 2012, for owls; Garrah *et al.* 2015, for vertebrates; Fig. 1). Our model assumes the spatial extent of road-kill evaluation is large relative to the spatial distribution of populations.

We predicted that: (i) the road-kill hotspot should move in time from a high-traffic road segment to a low-traffic segment due to population depression near the high-traffic segment; (ii) this shift should occur earlier for species with higher mobility because they should interact more often with the road; (iii) this shift can occur even if the low-traffic segment runs through lower quality habitat than the high-traffic segment indicating that high-traffic roads near wildlife habitat would need mitigation. Prediction 1 was supported and Prediction 3 was partially supported by the results of our simulation model, while Prediction 2 was not supported.

Materials and methods

To test the predictions above, we developed a stochastic, individual-based model using NetLogo software (Wilensky 1999). The model was not tailored to a particular species as our goal was to determine whether the predicted patterns are likely to occur in general. The model simulated the dynamics of two hypothetical populations, one living around a high-traffic road segment and the other living around a low-traffic segment. We defined the segment with higher road-kill numbers as the road-kill hotspot, and we calculated per capita road-kill for each population. Note that we did not statistically compare the road-kill numbers, e.g. testing for significant differences, because in a simulation model, significance can be obtained simply by increasing the samples size, making it meaningless. Therefore, we defined hotspots in the simplest way, using the difference in road-kill counts. Note that our simulation implicitly assumes that different road segments evaluated for road-kill are spaced such that the road-kill on them represents individuals from different populations. The model results are not applicable to road-kill hotspot analyses in which hotspots and non-hotspots are identified within the range of a single population (e.g. Ramp *et al.* 2005 for mammals; Snow, Andelt & Gould 2011 for island foxes).

The model description below follows the Overview, Design concepts, Details protocol (Grimm *et al.* 2006, 2010):

PURPOSE

The purpose of the model was to determine whether the location of road-kill hotspots can change over time, and to understand how this change is related to population size.

STATE VARIABLES AND SCALES

The model included two low-level entities: grid units and individuals. Grid units could be habitat or road. Habitat units were

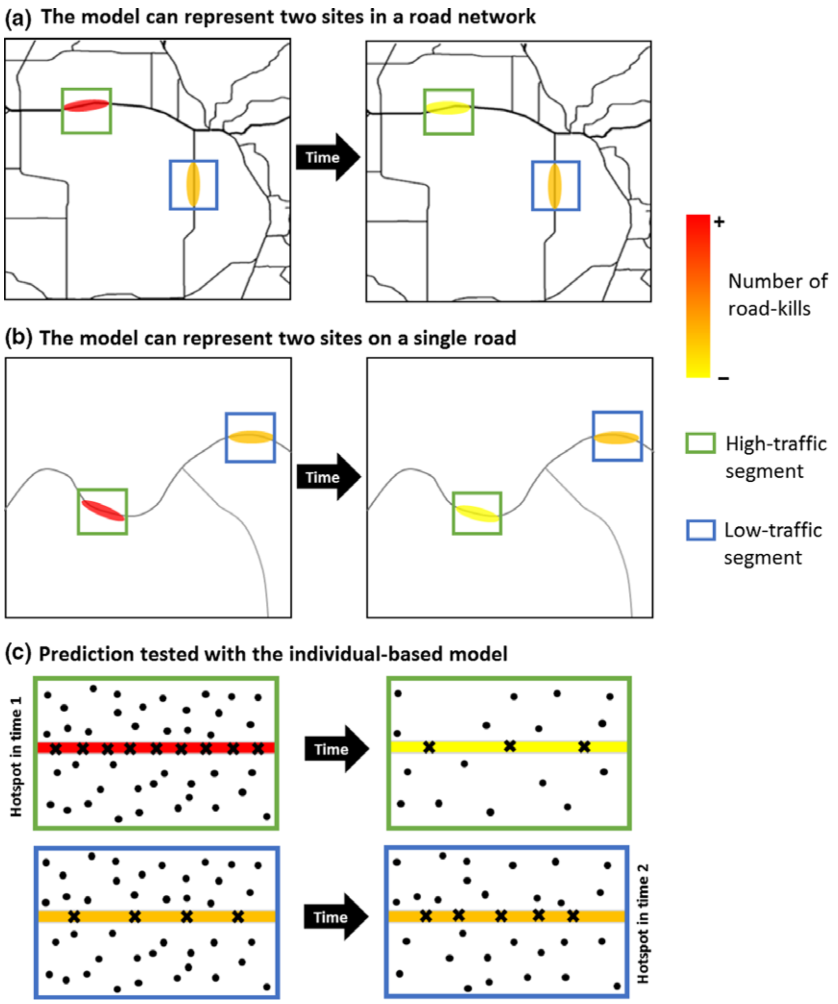

Fig. 1. The simulation model represents populations near two road segments, one a road-kill hotspot and the other a non-hotspot. The two road segments differ in traffic volume, and they can represent (a) locations on two different roads or (b) two road segments on a single road. (c) Illustration of the prediction that road-kill hotspots can move in time due to population depression as tested with the individual-based model. [Colour figure can be viewed at wileyonlinelibrary.com]

characterized by reproduction probability, mortality probability and density dependence. Road units were characterized by road-kill probability. The model comprised two 25 × 25 cell grids with the road segment bisecting the grids in the centre. Two higher level entities were considered: populations of individuals in each grid, and number of road-kills in each road segment. Road mortality began at the 400th time step, representing the time at which the road segments were constructed.

PROCESS OVERVIEW AND SCHEDULING

The model proceeded in time steps. Within each time step, five submodels were processed in the following order: reproduction, mortality, density dependence, movement and road-kill. Within each submodel, individuals were processed in a random order. Each submodel was applied to all individuals in the two grids before the next submodel started.

DESIGN CONCEPTS

Basic principles

The general hypotheses underlying the model's design were related to the relationship between population abundance, probability of an individual being killed on a road segment and the number of road-kills. The model provided insights about where road-kill hotspots can occur (in relation to population abundance) and their usefulness for defining mitigation locations. The two road segments represented in this model can be analogous to two road segments within one road or two road segments in a road network (Fig. 1).

Emergence

Population size emerged from the behaviour of individuals, and an individual's reproduction and mortality were entirely represented by empirical rules as probabilities.

Stochasticity

All parameters were interpreted as probabilities. This was done to include demographic noise and because the focus of the model was on population-level phenomena, not on individual behaviour.

Observation

For model analyses, population size and number of road-kills were observed, and the road segments with higher mortality (road-kill hotspot) and the one with higher per capita road-kill were calculated in each time step.

INITIALIZATION

Each population started with 400 individuals randomly placed in each grid.

INPUT DATA

The model does not use input data from external sources that represent processes that change over time, (e.g. changing traffic volume, changing carrying capacities). Changes over time in the model are the result of internal processes only.

SUBMODELS

Reproduction

Asexual reproduction was used for model simplification since the objectives of this study did not include understanding gender-specific responses or genetic responses. When an individual was alone in a habitat cell, a random number from 0 to 1 was chosen and, if that number was lower than the reproduction probability, that individual produced another individual. The probability that an individual reproduced during each step was set to 0·02 for both grids in all runs, except in the grid with low habitat quality near the low-traffic road segment for model runs used to test Prediction 3 (see below).

Mortality

For each individual in any cell in the grids, a random number from 0 to 1 was chosen and, if that number was lower than the mortality probability in the model, that individual died. The probability that an individual died during each time step was set to 0·013 for both grids in all runs. Calibration was carried out to choose reproduction and mortality parameters that permitted populations to persist to the 400th time step (when road construction occurred) without growing or declining exponentially.

Density dependence

If there were more than the maximum number of individuals in a given cell at a given time step, this submodel randomly killed the excess individuals. The model included a density limit of five individuals per cell for both grids in all runs.

Movement

For each individual, a direction and distance for movement were chosen in each time step. Individuals moved in a correlated random walk and each angle of movement was randomly chosen between 270° and 90°. The maximum number of cells for movement was defined *a priori* in each run as a movement range, and varied between runs from 1 to 9 cells.

Road-kill

When an individual's movement path intersected the road segment, it suffered road-kill with a given probability. The probability of an animal being killed *once it is on the road* was 1 for the high-traffic segment and 0·5 for the low-traffic segment.

Full model code in NetLogo language is available in Appendix S1, Supporting Information.

We ran 200 replicate runs for each combination of parameters, and each replicate run had 900 time steps (Table 1). In testing Prediction 1, the maximum number of cells moved per individual per time step was 4, and per capita reproduction probability was 0·02, in both grids in all runs. For testing Prediction 2, we used the same reproduction probability value of 0·02, and we varied the maximum number of cells moved per individual per time step between runs, from 1 to 9 cells. For testing Prediction 3, reproduction probability was 0·02 in the grid with the high-traffic road segment and 0·015 in the grid with the low-traffic segment, to represent lower habitat quality (see below).

SENSITIVITY ANALYSES

We conducted sensitivity analyses to determine whether our conclusions were sensitive to the particular parameter values used. We varied probability of road-kill at high- and low-traffic segments and the difference in road-kill probability between the high-traffic and low-traffic roads, and we varied the maximum number of cells moved per individual per time step. We also varied probability of reproduction and mortality, and we compared the effects on our conclusions of varying overall density by changing the maximum occupancy per cell vs. by changing the mean reproductive rate.

TESTING THE PREDICTIONS

To test our first prediction, we determined whether the location of the hotspot (the road segment with higher road-kill) shifted

Table 1. Parameters combinations used for testing each prediction. Each combination of parameters had 200 replicate runs

Parameter	Reference value Testing of prediction 1	 Testing of prediction 2	 Testing of prediction 3
Road-kill probability at high-traffic road	1	1	1
Road-kill probability at low-traffic road	0·5	0·5	0·5
Reproduction probability in the grid with the high-traffic road segment	0·02	0·02	0·02
Reproduction probability in the grid with the low-traffic road segment	0·02	0·02	0·015
Mortality probability	0·013	0·013	0·013
Density limit	5	5	5
Movement	4	1–9	1–9

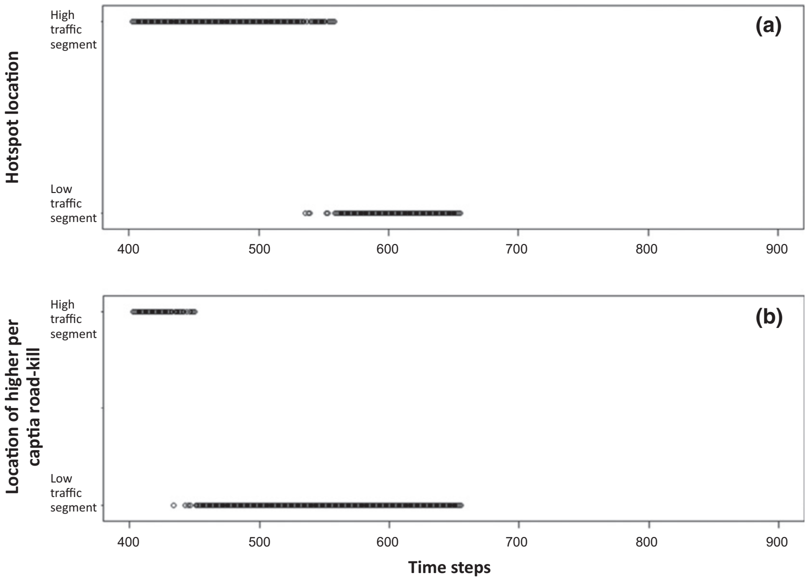

Fig. 2. The road-kill hotspot was located on the high-traffic segment in the first time steps and shifted to the low-traffic segment with time due to population depression near the high-traffic segment. Mean results obtained from 200 replicate runs for reproduction probability, 0·02; mortality probability, 0·013; and maximum movement range, four cells. Road mortality occurred beginning at the 400th time step (road construction). (a) Black circles indicate the location of the road-kill hotspot. (b) Black circles indicate the location with higher per capita road-kill.

over time from the high-traffic to the low-traffic road segment. To test our second prediction, for each movement range, we identified the time step in each replicate run when the hotspot shifted from the high-traffic road segment to the low-traffic segment. To test our third prediction, we reduced the habitat quality around the low-traffic segment by reducing reproductive probability there. We then determined whether the location of the hotspot shifted over time from the high-traffic to the low-traffic segment.

Results

While the sensitivity analyses indicated quantitative shifts in responses, they did not change any of the qualitative conclusions of the study reported below. The sensitivity analysis results are described in Table S1 and Figs. S1–S4.

Consistent with our first prediction, the road-kill hotspot was initially located on the high-traffic road segment but over time it shifted to the low-traffic segment (Fig. 2a). Per capita road-kill was higher for the population near the high-traffic segment for some time after the road-kill hotspot had shifted to the low-traffic segment and then it fluctuated between the two segments (Fig. 2b).

Our second prediction was not supported. The shift of the road-kill hotspot from the high-traffic segment to the low-traffic segment did not occur earlier for populations with higher mobility (Fig. 3).

Our third prediction was partially supported. The road-kill hotspot shifted from the high-traffic segment to the low-traffic segment even when the low-traffic segment ran through lower quality habitat than the high-traffic segment (Fig. 4), but this did not occur for the lower movement ranges. The population persistence was also lower for populations with higher mobility for the simulation runs where habitat quality was reduced near the low-traffic segment (Fig. 4).

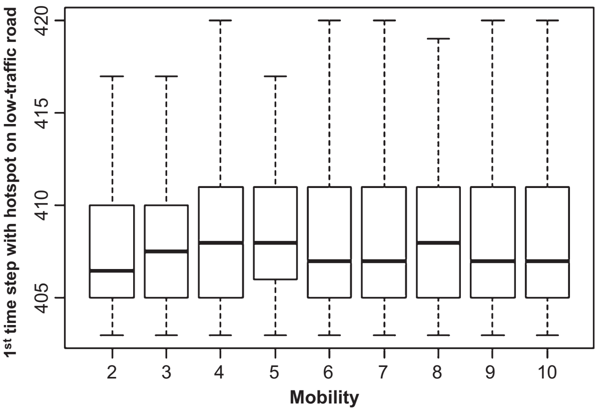

Fig. 3. First time step with the road-kill hotspot on the low-traffic segment for each mobility (maximum number of steps). The median of 200 replicate runs is represented by the black bold line, 25th and 75th percentiles are represented by the bottom and the top of the box, and the quartile deviations are represented by whiskers. Based on Prediction 2, we expected a negative relationship between the time at which the hotspot shifted to the low-traffic segment and mobility.

Discussion

Our objective was to identify circumstances in which road-kill hotspots are not appropriate indicators for the selection of the best road-kill mitigation sites. The results of our simulation models supported the prediction that road-kill hotspots can occur on road segments with low per capita road mortality risk, i.e. low-traffic road segments, due to population depression near high-traffic segments. The impact of road-kill on population size is much higher near the high-traffic segment than near the low-traffic segment. Over time, the number of road-killed animals on the high-traffic segment therefore declines to the point that there are more road-kills on the low-traffic

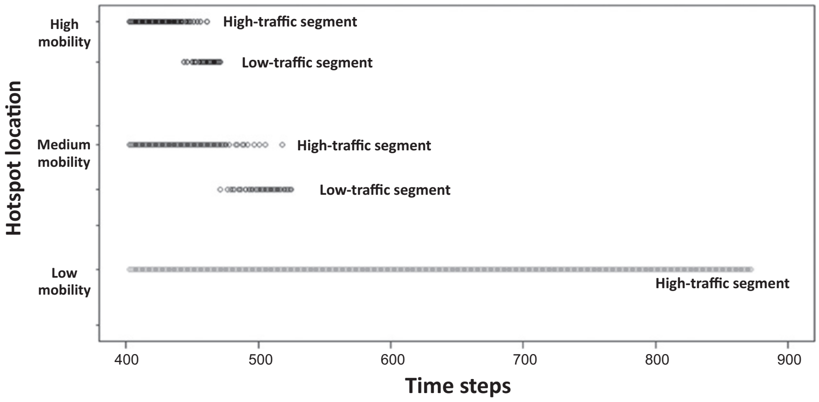

Fig. 4. Road-kill hotspot location vs. time for different movement ranges for the simulation model with two different habitat qualities. Mean results obtained from 200 replicate runs for reproduction probability 0·02 in the high-traffic grid and 0·015 in the low-traffic grid, and mortality probability 0·013. Road mortality occurs only after 400th time step. Light grey circles = low mobility (maximum number of cells crossed = 2), dark grey circles = medium mobility (maximum number of cells crossed = 6) and black circles = high mobility (maximum number of cells crossed = 9). The road-kill hotspot was located on the high-traffic segment in the earlier time steps and shifted to the low-traffic segment with time due to population depression near the high-traffic segment for medium and high mobility (dark grey and black circles), but for low mobility, the hotspot (light grey circles) remained the whole time in the high-traffic segment.

than on the high-traffic road segment. At this point, the road-kill hotspot on the low-traffic segment is a poor indicator of the best location for road-kill mitigation. The best location for mitigation would be on the high-traffic segment where per capita road mortality is higher (as shown in Fig. 2b) when the possibility of population recovery through appropriate mitigation still exists. This result indicates that the use of road-kill hotspots to decide where to put mitigation may be misleading when road-kill hotspots are located on low-traffic segments if non-hotspot segments with high traffic are intersected by wildlife habitat. Our results are valid for situations where spatial extent of road-kill evaluation represents road-kill from different populations.

Our result is in accordance with the hypothesis proposed by Fahrig *et al.* (1995) and by Eberhardt, Mitchell & Fahrig (2013) to explain the occurrence of road-kill hotspots for amphibians on low-traffic road segments, despite the availability of high-quality habitat near the high-traffic road segments. In agreement with our results, Borda-de-Água, Grilo & Pereira (2014) using an age-structured model of the barn owl, predicted a small number of individuals killed in cases of high road-kill probability, due to population depletion. On the other hand, their model simulates a single population subjected to different probabilities of road mortality, while our model compares the difference in the number of road-kills in two populations.

Our results did not support our prediction that the shift in road-kill hotspot location from the high-traffic to the low-traffic road segment should occur earlier for species with higher movement ranges. Although the first time step with the hotspot at the low-traffic road segment was similar for populations with different movement ranges, populations with higher mobility went extinct earlier than populations with lower mobility. This is consistent with studies showing that species with higher mobility (or larger home ranges, as an indicator of movement range) are more negatively impacted by roads (Fahrig & Rytwinski 2009; Rytwinski & Fahrig 2011, 2012), suggesting that mobile species should have priority for road-kill mitigation.

Our results partially supported the prediction that, even when habitat quality is lower near a low-traffic road segment than near a high-traffic segment, hotspots can still occur on the low-traffic segment due to population depression near the high-traffic segment. However, we did not see this shift in scenarios with low mobility. In these cases, the population near the low-traffic segment decreased very quickly and remained smaller than the populations near a high-traffic road segment, resulting in continued higher road-kill near the high-traffic segment.

Our results indicate that, for new roads, road-kill hotspots can be useful to indicate appropriate sites for mitigation. However, this quickly changes such that, on older roads, road-kill hotspots may not be reliable indicators of the best sites for road-kill mitigation. Direct measures of road impacts on populations, such as per capita mortality (as shown in Fig. 2b), are better indicators of appropriate mitigation sites than road-kill hotspots (e.g. Fahrig *et al.* 1995; Hels & Buchwald 2001).

Our results are valid for situations where different road segments have differences in traffic intensity, and where the segments are independent, in that road-killed animals on the different segments represent individuals from different populations. The sites can be from different roads or different segments within a road. In addition, there must be suitable habitat near the high-traffic road segments. Our conclusion that hotspots may not be the best location for implementing mitigation measures only makes sense in a context where there is available habitat next to non-hotspot segments.

Our model does not consider the case where the high-traffic road segment causes lower habitat quality there due to, for example, pollution or noise from the traffic. However, this would only strengthen our conclusion. Lower habitat quality caused by higher traffic would further decrease the population around the high-traffic road segment relative to the population near the low-traffic road segment. This would increase the intensity of the change in hotspot location from the high-traffic segment to the low-traffic segment, strengthening our conclusion that the road-kill hotspot does not indicate the best location for road mitigation.

In the situation represented in our model, prioritizing road-kill hotspots for mitigation would lead to implementation of measures on the low-traffic road segments and not on the high-traffic segments. This would be a poor choice as it may lead to the local extinction of the population near the high-risk road segment. Per capita road mortality, the chance of an individual in the population being killed by road traffic, would be a better indication of locations with a higher need of road-kill mitigation (as shown in Fig. 2b). Road segments with higher per capita mortality risk can be detected using road-kill only if road-kill monitoring is performed immediately after road construction. Otherwise, road-kill information must be combined with population data to estimate per capita mortality. If not, road-kill data may be meaningless for ranking road segments to prioritize mitigation.

We are not suggesting that mitigation at road-kill hotspots is pointless, but rather that these hotspots might not indicate the most effective sites for mitigation in some cases, particularly on older roads and when there are non-hotspot road segments with suitable habitat. Of course, mitigation in areas with severely decreased populations or where extinction has already occurred only makes sense if the nearby habitat is still suitable and if recolonization of the site is possible. In a study of the impacts of a road widening and paving, Jones (2000) observed that an increase in the number of road-kills occurred in the first year, followed by a decrease and local extinction of two mammal species, in accordance with what is expected according to the results of our simulation model. However, after the installation of mitigation measures, only one of the species monitored by Jones (2000) was able to recolonize the area.

A situation in which our model results may not apply is for species that avoid entering a road in response to traffic. For example, Clarke, White & Harris (1998) and Seiler (2005) found maximum number of road-kills for intermediate traffic volumes. In this case, road-kill may decrease as road traffic increases, because animals will be less likely to attempt to cross the road (Fahrig & Rytwinski 2009). Hypothetically, the presence of hotspots on low-traffic road segments when there is a threshold of traffic avoidance could indicate that mitigation should be implemented at hotspot locations, because road segments with high traffic would have lower mortality due to road avoidance and not due to population depletion.

Probably our finding that sites with higher mortality might not indicate the sites with the largest effect on population persistence may also be valid for other anthropogenic structures that cause direct wildlife mortality due to collisions, such as railroads and power lines. In these cases, higher mortality may be found where populations are not yet depressed by past mortality.

Conclusions

Our model shows that plausible situations exist where hotspots may not be reliable indicators of the best sites for mitigation, and that looking at the populations behind the road-kill numbers will improve selection of sites for mitigating the effects of road mortality. Estimating road mortality in relation to population abundance in the surroundings instead of identifying road-kill hotspots alone is preferable for informing mitigation priorities on older roads, due to the effects of past mortality.

Authors' contributions

All authors were involved in discussions concerning the predictions of this study, and related to the purpose and structure of the individual-based model. A.K., F.Z.T. and L.F. were involved in defining model parameters; F.Z.T. built the model code, ran the analyses and led the writing of the manuscript. All authors discussed the results and implications of this study, and contributed to writing this manuscript.

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Data accessibility

Full model code in NetLogo language is available as online supporting information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Results of sensitivity analyses.

Fig. S2. Results of sensitivity analyses.

Fig. S3. Results of sensitivity analyses.

Fig. S4. Results of sensitivity analyses.

Table S1. Combinations of parameter values tested in sensitivity analyses.

Appendix S1. Model code in NetLogo language.