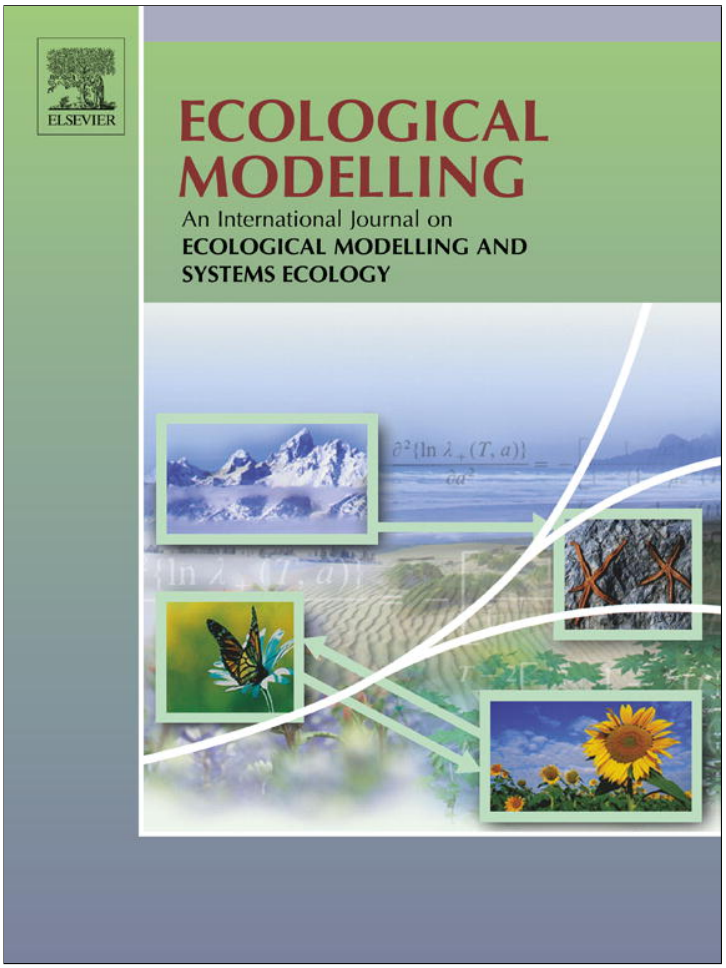

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Wildlife–vehicle collision mitigation: Is partial fencing the answer? An agent-based model approach

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ABSTRACT

Evaluating management options for mitigating the impacts of wildlife–vehicle collisions (WVC) is a major goal for road ecology. Fencing along roads in conjunction with the construction of wildlife road passages has been widely accepted as the most effective way to minimize WVC. However, limited resources often require wildlife managers to focus on a single method of mitigation, yet the relative effectiveness of fences and passages for reducing road mortality and restoring population connectivity is unclear. Using the stone marten (*Martes foina*, Erxleben, 1777) as a model species, we developed an individual-based, spatially explicit simulation model to develop predictions concerning the relative performance of fencing and passage construction under different rates of road mortality. For five levels each, we varied probability of road mortality, fencing extent, and number of passages in a full factorial design, for a total of 125 management scenarios. We then compared the relative impact of these two mitigation approaches on population abundance (N) and genetic differentiation (F_{st}) using linear regression. Our results predict that fences are much more effective than passages at mitigating the effects of road mortality on abundance. Moreover, we show that under most circumstances, fences are also more effective than passages at reducing genetic differentiation. This is likely driven by the ability of fencing to eliminate road mortality, which in turn increases genetic diversity, thereby slowing differentiation across the road. However, partial fencing can reduce road mortality nearly as well as full fencing. Moreover, partial fencing also allows adequate population connectivity across roads. Thus, we argue that partial fencing of roads alone may often be the best and most cost-effective management option for road mitigation.

1. Introduction

Roads and associated traffic negatively impact a vast number of species (Forman et al., 2003), with mortality due to wildlife–vehicle collisions (WVC) being among the most important effects (Fahrig et al., 1995; Philcox et al., 1999; Mumme et al., 2000; Steen et al., 2006). WVC impact populations beyond the road vicinity (Forman, 2000) and may be responsible for highly reduced population sizes, increased demographic structure, and decreased landscape connectivity (Mumme et al., 2000; Steen and Gibbs, 2004; Nielsen et al., 2006). Reduced population abundance and connectivity can in turn result in inbreeding and loss of genetic variability through genetic drift (Wright, 1931; Miller and Waits, 2003). Taken together, these impacts are expected to reduce individual fitness and the probability of long-term population survival (see Forman and Alexander, 1998; Hanski, 1998; Frair et al., 2008; Balkenhol and Waits, 2009). How to effectively mitigate the effects of WVC on wildlife populations thus merits further study.

The primary aim of WVC mitigation currently is to reduce the access of animals to road pavement while maintaining the permeability of roads to animal movement, in an attempt to retain population connectivity (Clevenger et al., 2001; Mata et al., 2005; Corlatti et al., 2009). Several studies suggest that fencing in combination with wildlife passages is the most effective way to minimize WVC (Clevenger et al., 2001; Bissonette and Cramer, 2008; Huijser et al., 2009). However, given the expense of building these

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mitigating structures, it may not always be possible or desirable to do both, and the question remains as to which of these methods is more effective. That is, what is the relative impact of building fences versus building wildlife passages versus building both on the mitigation of important population impacts due to WVC? Moreover, there is little empirical data concerning whether passages can effectively restore population connectivity and thus decrease genetic differentiation due to roads (Corlatti et al., 2009). Likewise, although complete exclusionary fencing of roads will likely decrease population connectivity (Jaeger and Fahrig, 2004), it is unclear what the impacts of partial fencing of roads will be on population connectivity or on the mitigation of reduced abundance due to road mortality. Thus, road and population managers will benefit from an exploration of the relative impacts of differing amounts of fence and passage construction on the mitigation of populations experiencing varying levels of road mortality.

To investigate this question empirically would be logistically challenging. It would require gathering demographic and genetic data from populations near a large number of roads of similar ages, while controlling for external factors that might be correlated with roads (such as urbanness, habitat structure, or population history). These roads would also need to be furnished with varying levels and combinations of fencing and passages, constructed at similar time periods. Collecting such data would be extremely costly and time consuming (Holderegger and Di Giulio, 2010), and likely impossible for most species. One solution is to use agent-based model simulations (ABM, DeAngelis and Mooij, 2005; Railsback and Grimm, 2011). ABM simulations have several advantages in that they allow for the control of several sources of uncertainty, such as habitat heterogeneity, non-road mortality (e.g., due to disease, competition, or predation), or historical effects (which may particularly affect patterns of genetic structure). In addition, simulations allow for a sufficient number of replicates in order to account for stochastic effects.

In this study, we developed the Road Effects on Population Persistence (REPoP) model, a spatially explicit simulation model that can be adjusted and parameterized to capture the specific life-history and landscape characteristics associated with a variety of species and spatial extents. Previous research throughout Europe has shown high road-kill rates for medium-sized carnivores (Ferreras et al., 1992; Clarke et al., 1998; Philcox et al., 1999; Hauer et al., 2002; Grilo et al., 2009), suggesting that this group will benefit from studies that investigate how to mitigate road-kill effects in natural populations. However, because road-kill events involving medium-sized carnivores rarely represent a threat to human safety, mitigation efforts directed at these species have seldom been implemented or studied (but see Ferreras et al., 2001; Klar et al., 2009). Here we used REPoP to develop predictions concerning the relative performance of fencing and passage construction in mitigating road mortality and restoring population connectivity under different rates of road mortality. We used simulated populations of stone martens (*Martes foina* Erxleben, 1777; hereafter referred to as 'martens'), a territorial mustelid widely distributed throughout Europe (Proulx et al., 2005). Although this species is capable of living in deforested and human-altered environments (Rondinini and Boitani, 2002; Herr et al., 2009), martens are known to be sensitive to the effects of fragmentation due to road presence (Grilo et al., 2009, 2011). Moreover, research on stone marten movement near highways has shown that this species exhibits low highway avoidance (Grilo et al., 2012), and is thus likely very susceptible to mortality due to WVC (Jaeger and Fahrig, 2004). We anticipate that this study will be useful both to road planners interested in mitigation as well to ecologists and conservation biologists who seek to understand the effects of roads on important population processes.

2. Methods

2.1. Model description

Our model description follows the ODD (Overview, Design concepts, Detail) protocol for describing agent-based models (Grimm et al., 2006, 2010) and is based on previous model descriptions (Railsback and Johnson, 2011). The model was implemented in NetLogo (Wilensky, 1999), and therefore we use some of its conventions (e.g., variable names).

2.1.1. Purpose

The purpose of the REPoP model is to investigate the relative effectiveness of two road mitigation measures—fences and passages—under varying degrees of road mortality. The evaluation will be performed through the effects on population size and genetic differentiation. This model is parameterized using basic life history traits of marten.

2.1.2. Entities, state variables and scales

2.1.2.1. Entities. The model is a spatially explicit individual-based system, consisting of a landscape with reflecting borders, not toroidal (individuals at one edge of the space cannot jump to cells on the opposite edge), and occupied solely by marten individuals. There are three types of entities: martens, territories and road passages. Martens are the main entity in the model, and are represented as mobile individuals with *state variables* related to their identity, location and biology (Table 1). Marten identity is used to link juveniles to their mother and to compute the genotype of juveniles. Marten coordinates are used to track the position of martens in respect to the road and road passages, and to link adult males to their territory. The timing of life history events (which we call "life stages") such as mating, birth, dispersal, and death follows the known marten annual cycle.

All territories are considered to have equal habitat quality. Territories are designated as 'left' or 'right' according to their position relatively to the road. When required, the patches adjacent to the road can be furnished with road passages and/or fencing. When encountering a fenced section, simulated martens are not able to cross the road at these patches unless a passage is within it. When the selected management option includes passages, martens always use the nearest passage if one is available (<220 m). Different numbers of road passages and fenced sections are located along the road, according to the simulated management scenario (Fig. 1). Both road passages and fenced sections are randomly assigned to patches along the road. When the number of fence sections and passages differ, the model first assigns a location to the maximum number of patches with both mitigation measures, and then randomly assigns locations to the remaining mitigation measures.

2.1.2.2. Scales. The spatial extent of the model is 20×24 patches ($n = 480$). We considered patches to be 2200 m × 2200 m in size (529 ha), representing territories inhabited by a single individual. This cell size was based on previous research on organisms tracked near highways (Grilo et al., 2012). The total area is therefore over 250,000 ha and is assumed to be large enough to capture large-scale population dynamics. For simplicity, there is no overlap among territories.

Each time step equals one day. Each simulation is first run for 25 years without a road present to allow time for populations to reach a steady state. Then a vertical road is added which evenly bisects the landscape. Thirty additional years of population dynamics are then simulated in the presence of the road. In addition to simulations that include a road ("treatment" scenarios), we simulated a control scenario without roads (which we refer to as the "null" scenario) in order to obtain an expected "baseline" population outcome with

Table 1
Attributes for the entities used in the model: Martens, territories and road passages. Each entity is characterized by different parameters.

Entities	Parameters	Values/range and unit
Marten	Identifier	Unique number
	Sex	M/F
	Location	Spatial coordinates
	Territoriality	Y/N
	Territory	Patch identity (NetLogo convention)
	Life stage (age in days)	Juveniles (0–120), sub-adults (121–510) and adults (>511)
	Pregnancy condition (for females)	Y/N
	Movement steps	150 m each
	Annual death rate	0.26
	Genotype (diploid)	Microsatellite length
Territories	Inhabited	Y/N
	Roadside	Left, right
	Fenced	Y/N
Road passages	Funnel distance	100 m

which to compare outcomes from the treatment simulations. The null scenario was run the same number of generations as the treatments.

2.1.3. Process overview and scheduling

At each daily time step a given list of actions is performed by martens, depending on the life stage and time of the year (Fig. 2). These actions consist of mating, birth, dispersal and death. For each action, the order in which martens are called to execute them is randomly assigned.

Mating: during the mating period (Fig. 2) males try to find non-pregnant adult females in nearby territories (Section 2.1.7.1). Males can mate with more than one female. Interactions with roads, fences, and road passages can occur during mating. *Birth*: on the second day of March pregnant females give birth. Litter size is dependent on population density (Section 2.1.7.2). *Dispersal*: when juveniles reach the sub-adult life stage, May 1st in the model, they disperse from the mother's home range, searching for an empty territory. While dispersing, sub-adults are susceptible to road-kill events and may also interact with fences and road passages (Section 2.1.7.3). *Death*: martens can die by natural death, road-kill events or absence of a vacant territory. Natural death becomes more likely with aging (Section 2.1.7.4).

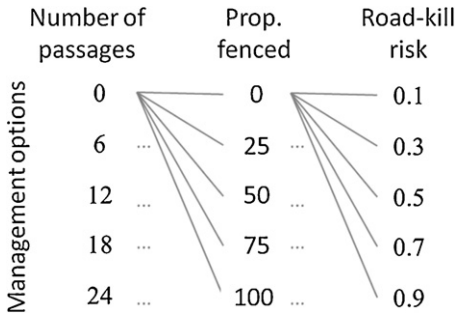

Fig. 1. Simulation experiment treatments using the REPoP model to assess the relative effectiveness of WVC mitigation management options. We simulated 125 scenarios involving a factorial combination of *number of passages*, *proportion of road fenced* and *road-kill risk* (five levels each). All scenarios were run for 1000 replicates. Population size (N) and F_{st} were calculated at the end of each simulation run.

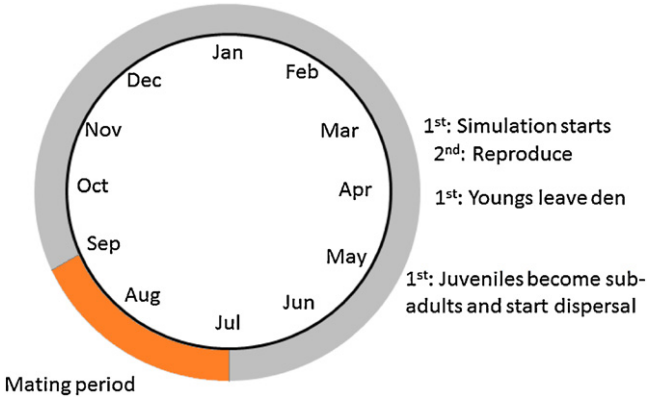

Fig. 2. Annual calendar of all marten life-history events in the model.

2.1.4. Design concepts

This section describes the model at a conceptual level, using the eleven design concepts of the ODD protocol (Grimm et al., 2010).

2.1.4.1. Basic principles. In this section we describe the ecological parameters used when modeling marten life cycle and biology/behavior. These parameters include animal movement, population growth and fecundity, and probability of being killed while crossing a road. Where empirically derived parameter estimates are lacking for martens, we instead use accepted estimates from other carnivores or closely related mammals.

Animal movement: Two types of movement were simulated: (1) males searching for female mates and (2) adults dispersing. For mate search, we used a simple random walk, where searching was constrained to the eight neighboring patches of a male's territory (Section 2.1.7.1). For dispersal events, dispersers follow a highly correlated path, i.e., they make few large turns (see Palmer et al., 2011 and citations therein). We implemented this constraint by limiting the movement directionality to a 60° cone centered in the previous step azimuth (Section 2.1.7.3). Each movement step has a length equal to one tenth of the linear home range size (LHRS, the square root of home range area), which is 220 m in this model. We chose to relate the movement to the LHRS as this approach has been successfully applied previously (Bissonette and Adair, 2008). For each time step (day), martens can perform 20 movement steps, summing 4400 m per night. This conforms to the estimated path length per night that martens patrol territory (Genovesi et al., 1997; Grilo et al., 2012).

Population growth and fecundity: In REPoP, population growth is density dependent, which has been shown in closely related species including *M. americana* (Fryxell et al., 1999) and *M. martes* (Zalewski and Jedrzejewski, 2006). For simplicity, in REPoP, density dependence is imposed on birth rate (where three pups per female is the maximum litter size; Section 2.1.7.2).

Probability of being killed while crossing a four-lane highway: In the real world, the probability of WVC may vary according to traffic volume, species/vehicle speed, animal/driver ability to perceive the car/animal approaching, or road configuration (tortuosity) (e.g.

Malo et al., 2004; Grilo et al., 2011). These different sources of variability are not modeled because they are not relevant to our main question which regards the relative impact of WVC on population size and genetic differentiation, and how to mitigate them, regardless the mechanistic details.

2.1.4.2. Interaction. There are several interactions occurring in the model among agents. Female adults reproduce if their territory is visited by an adult male during mating period. Otherwise, females will not give birth. Offspring inherit half of their diploid genotype from each parent. Sub-adults can only settle in vacant territories. When a road is present, individuals interact with the road, fences and passages.

2.1.4.3. Stochasticity. Stochasticity is used in initializing the model, to randomly assign territories, sex and genotypes to adult martens. During simulations, stochasticity is also used to (1) assign directionality to animal movements (during both mating and dispersal); (2) determine whether martens die when crossing the road; (3) assign number of offspring to each female; (4) assign parental alleles to offspring; and (5) determine whether martens succumb to natural death.

2.1.4.4. Observation. For each simulated scenario, the population size, genetic differentiation between roadside 'populations' (settled individuals) using F_{st} (Weir and Cockerham, 1984) and total number of road-kills are recorded every year for each replicate for use in analysis (see Section 2.2).

2.1.4.5. Emergence. Population dynamics emerge from the life cycle of individuals and, in cases where a road is present, from the interaction of individuals with roads, fences, and passages.

2.1.4.6. Sensing. When crossing a road, marten are able to perceive any passages within 220 m.

Adaptation, objectives, Learning, Prediction and Collectives do not apply to REPoP model.

2.1.5. Initialization

The model is initialized by randomly assigning age, sex, and territory to martens. Simulations start on March 1st, where adult males are set to search for a mate (Section 2.1.7.1); all simulations initialize without a road, and hence there is no mitigation. All individuals possess 20 diploid unlinked microsatellite loci (30 possible alleles per locus), which evolve under a strict stepwise mutation model (mutation probability = 10^{-4}) without recombination (Bhargava and Fuentes, 2010).

2.1.6. Input data

The model does not use input data to represent time-varying processes.

2.1.7. Sub-models

The following subsections provide full detail on how model processes are simulated according to marten life cycle.

2.1.7.1. Mating. During the mating period (July–August, Fig. 2), males search for mating females (procedure '*find-a-female*'). Within this period, males search within the eight neighboring cells. If a male steps into the territory of a non-pregnant female, they mate. One male can mate with several females but not vice versa. Each male is allowed to perform ten movement steps per day, after which the procedure '*go-home*' is invoked, which sends males back to their territory. In both '*find-a-female*' and '*go-home*' procedures, road-kills can occur if a male crosses the road without using a passage. When an adult male encounters a fence, it changes its direction toward a randomly chosen patch on the same 'roadside'. An exception to this is when a fence is approached while responding to the '*go-home*' command. In this case, if a fence is approached, a marten will attempt to return to its territory using the nearest road passage or unfenced patch.

2.1.7.2. Birth. Pregnant females give birth to between one and three pups, depending on animal density: for each roadside, if there are available territories during mating, then litter size is set to three. Otherwise, it decreases randomly to one or two pups. This litter size estimate is based on marten body size (see Buskirk and Ruggiero, 1994). Note that although martens normally produce two to four pups (Reig, 2007) we restrain the number to a maximum of three to accommodate other causes of death that likely occur at or near birth in natural populations.

Births occur at March 2nd (marten females undergo winter embryonic diapause, Fig. 2). For each of the 20 diploid microsatellite loci, offspring randomly inherit one allele from each parent. Offspring remain in the mother's territory until the age of four months. We do not assume male parental care.

2.1.7.3. Dispersal. Juveniles become sub-adults at two months and initiate dispersal. Every unsettled sub-adult searches the landscape for an empty territory. At each movement-step, if an individual enters into an unoccupied territory, it occupies it (and stops moving). Dispersal lasts for four months, after which unsettled sub-adults die. All settled sub-adults become adults on the last day of August the following year, at the age of one year.

2.1.7.4. Death. Animals may die from natural death or from WVC. Natural death becomes more likely as animals age. There are two exceptions: (1) if a mother dies, her juveniles also die; (2) unsettled sub-adults die at the end of the dispersal period (Section 2.1.7.3). To parameterize natural death rates, we used annual death rate estimates based on American martens from Bull and Heater (2001; 37%) and McCann et al. (2010; 19%), and on pine martens from Zalewski and Jedrzejewski (2006; 38%). We fixed the daily probability of natural death for all individuals at 0.07% (based on an annual probability of 26%) as this yielded optimum stability in population dynamics. Thus, the probability of any individual reaching the sub-adult stage, adult stage, or maximum life span is 90%, 74% and 22%, respectively. WVC may kill dispersing sub-adults or male adults searching for a mate.

2.2. Data analysis

We first ran REPoP for 1000 iterations under "null" conditions (i.e., with no road present) which allowed us to obtain a "baseline" distribution of expected population outcomes (population size and genetic differentiation) with which to compare outcomes emerging from the various road and mitigation treatments. We then simulated five levels each of WVC probabilities (ranging from 0.1 to 0.9), fencing proportions (ranging from 0 to 100% road fencing), and passage numbers (ranging from 0 to 24 passages) in a full factorial design (for a total of 125 treatment scenarios; Fig. 1). Each scenario was performed for 1000 replicates. The maximum number of passages was chosen based on Bissonette and Adair (2008), who used allometric methods to infer optimal spacing between wildlife crossings such that population connectivity is maintained. They found that setting the distance between passages to the linear home range distance (LHRD, square root of home range area) could provide adequate road permeability. At the end of each simulation run (at year 55), we calculated population size (N) and genetic differentiation (F_{st}) (Weir and Cockerham, 1984). F_{st} was calculated between groups of individuals bisected by the road (this same grouping was done for the "null" condition, despite no road being present).

To determine the relative effectiveness of passages and fences for mitigating WVC effects, we performed multiple regressions where response variables were population size and F_{st} (in separate analyses) and predictor variables were numbers of passages (*Pass*) and proportions of fencing (*Fenc*), both treated as categorical data. For each response, we repeated three regressions where *Pass* and *Fenc* were included separately and jointly in the model. This was repeated for the five levels of road-kill risk. Akaike information criterion (AIC) values were calculated to determine the information value of each variable (*Pass* and *Fenc*) when predicting population size and F_{st} outcomes. R^2 values were calculated to compare model fit. Variable coefficients from the full model were used to determine the influence of road passages and fences at each mortality level. We carried out analyses using the R package R 2.13.1 (R Core Team, 2011).

3. Results

As expected, 'Null' conditions led to stable population sizes (N) over time and a lack of genetic differentiation (F_{st}) throughout all simulations (Fig. 3). These outcomes were similar to those from treatment scenarios with no mitigation (e.g., number of passages = 0 and proportion of fencing = 0%) and low probability of road mortality (0.1). This is evidenced by a large proportion of outcomes from this treatment (from >90% of replicates) falling within the 99% confidence intervals of the "null" model outcomes (Fig. 4).

Regarding the relative effectiveness of the mitigation measures, the majority of variation in N was governed by the proportion of road fenced (*Fenc*) rather than the number of passages (*Pass*) (Table 2). Except for the lowest road-kill level (RK = 0.1; in which case neither fences nor passages improved abundance), *Fenc* explained nearly all of the non-random variation in N (*Fenc*: $R^2 = 0.33–0.80$; *Pass*: $R^2 = 0.01–0.02$), as expected. In fact,

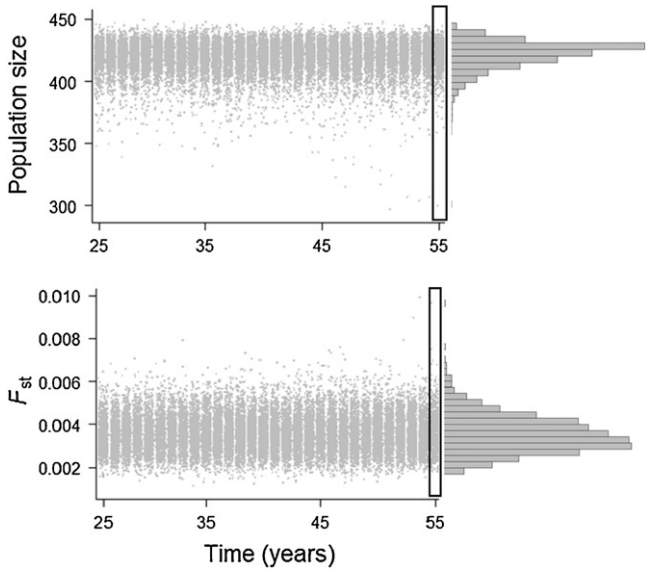

Fig. 3. Population size (N) and F_{st} for roadless simulations (scenario 'Null', 1000 replicates). For year = 55 (highlighted) the histograms with the distributions of N and F_{st} are shown.

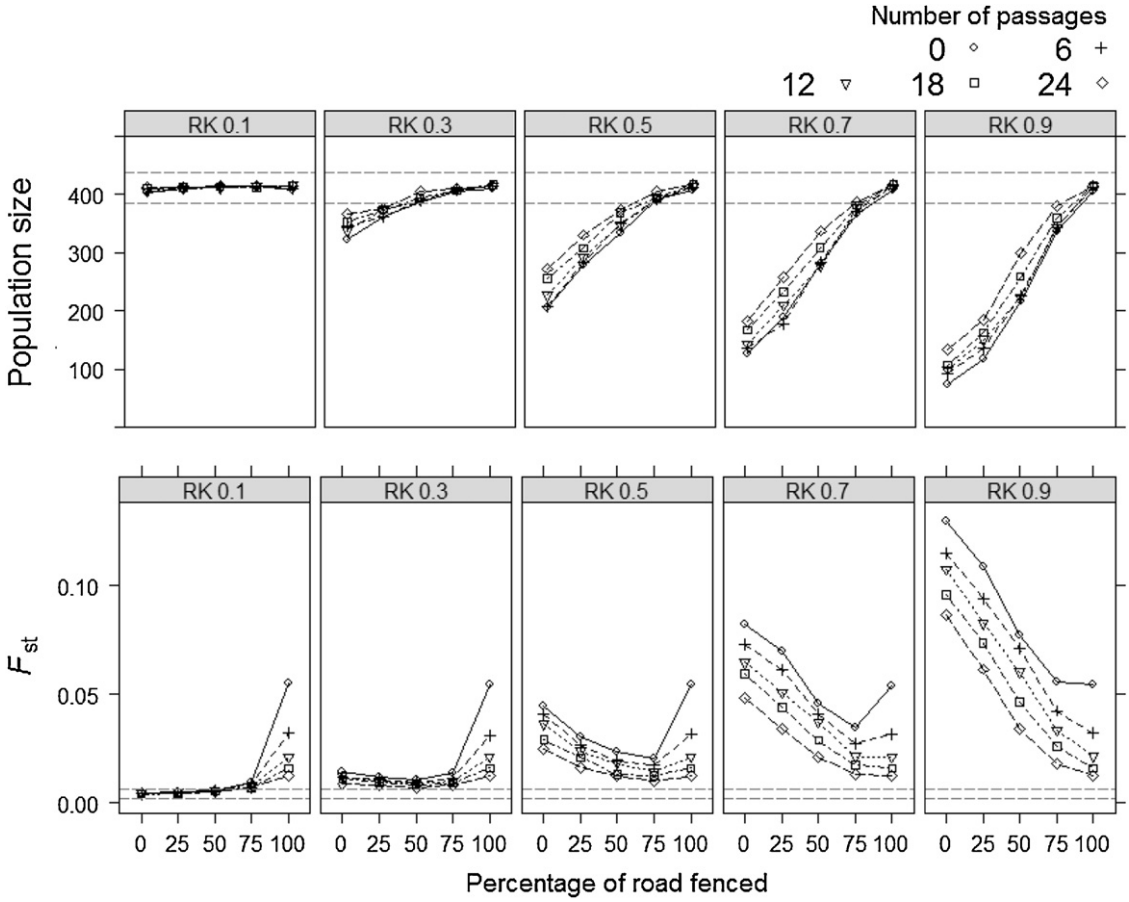

Fig. 4. Results from the simulation of 125 scenarios involving different combinations of road passages (dot symbols), percentage of road fenced (*xx* axis) and road-kill risk (RK, panels from left to right). Outcomes shown are the mean population size (top) and mean F_{st} (bottom). Dotted gray lines represent the 99 percentile envelope from the 1000 replicates of the 'Null' scenario (no road involved).

Table 2
Changes in AIC score and R^2 values for all linear regression models relating population size (N) and genetic differentiation (F_{st}) between roadsides. Regressions were repeated across five levels of road-kill risk (RK). Model weights (i.e., probability a model is the "true" model) are 1.0 for the full model (*Pass* + *Fenc*) in all cases.

Resp.	Model	RK = 0.1		RK = 0.3		RK = 0.5		RK = 0.7		RK = 0.9	
		ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2
	Pass	37	0.01	1013	0.02	2337	0.02	3326	0.02	4187	0.02
N	*Fenc*	10	0.02	62	0.33	143	0.59	152	0.72	215	0.80
	Pass + *Fenc*	0	0.02	0	0.35	0	0.62	0	0.74	0	0.82
	Pass	2651	0.09	1551	0.16	639	0.19	1245	0.16	1831	0.12
F_{st}	*Fenc*	635	0.60	742	0.39	660	0.18	688	0.34	823	0.47
	Pass + *Fenc*	0	0.69	0	0.55	0	0.38	0	0.51	0	0.65

increasing the proportion of road fenced always led to higher N when compared to increasing the number of passages, in any level of comparison (Fig. 4 and Table 3). This was particularly visible at higher road-kill levels. For example, for RK = 0.7 the expected population size was 133 individuals when no road mitigation was in place. Installing between six and 24 passages on average added 10 (7.3%) to 42 (31.6%) individuals to the population. Fencing 25–100% of the road on average added between 68 (51.3%) and 261(195.4%) individuals (Table 3).

Interestingly, *Fenc* also explained the majority of the non-random variation in F_{st} (*Fenc*: R^2 = 0.18–0.60; *Pass*: R^2 = 0.09–0.19). Only in the case of intermediate road mortality risk (RK = 0.5) did fencing and passages explain similar amounts of variation in F_{st} (Table 2). Fencing generally leads to either neutral or negative effects on F_{st}. At low road kill levels (RK ≤ 0.3) fencing up to 75% of the road length could be achieved without increasing genetic differentiation above fenceless levels (Table 3). At higher road-kill levels (RK ≥ 0.5), increased fencing did lead to reduced F_{st}, although this effect generally leveled off or was reversed at 100% fencing (Fig. 4). Furthermore, the slope of this relationship increased as the probability of road mortality increased (Fig. 4 and Table 3).

As expected, installing passages generally decreased F_{st}, although this reduction was only evident for higher road-kill risk scenarios or when complete fencing was applied (Fig. 4). That is, the slope of this relationship increased as the probability of road mortality increased, as found for *Fenc*, but at a lower rate (Fig. 4 and Table 3). For example, for RK = 0.7, the expected F_{st} was 0.085 under zero mitigation, and adding between six and 24 passages on average reduced F_{st} by between −0.012 and −0.032, respectively. Applying fencing to between 25 and 75% of the road on average reduced F_{st} by −0.018 and −0.044 (Table 3). This difference was even more pronounced for the higher road-kill level, where complete fencing actually lead to lower F_{st} values than installing 24 passages (Fig. 4 and Table 3).

Models including both fences and passages always led to higher population size and lower F_{st} (Table 2). However, when one mitigation option must be selected over the other, building fences is always equally good or better at increasing abundance and decreasing genetic differentiation than building an equivalent number of passages (Fig. 4 and Table 3).

4. Discussion

Roads represent an important source of mortality for many species which can severely reduce the abundance and connectivity of natural populations. In this study we developed a stochastic, spatially explicit, individual-based model for stone martens in order to evaluate the relative performance of two approaches commonly adopted to mitigate the negative impacts of roads.

When any form of mitigation was absent, the population size (N) decreased with increasing road-kill risk. Road-kills are known to be a major contributor to population declines (Ramp and Ben-Ami, 2006; Row et al., 2007; Chambers and Bencini, 2011), and our model shows that once the probability of road mortality is 30% or higher, populations are no longer able to compensate increased road mortality with decreased competition for resources. Also as expected, the genetic differentiation between roadsides (F_{st}) increased with increasing road-kill risk, due to the combined effects of mortality and barrier effects, since potential crossers are killed during dispersal. This effect of mortality on genetic structure has been demonstrated previously (Riley et al., 2006; Jackson and Fahrig, 2011), and is well supported by population genetic expectations.

Table 3
Coefficient values for the number of passages (*Pass*) and proportion of fenced road (*Fenc*) for full models regarding each mortality risk level (RK).

Resp.	Coefficients	RK = 0.1	RK = 0.3	RK = 0.5	RK = 0.7	RK = 0.9
	Intercept	407	334	218	133	78
	Pass: 6	3	3	9	10	4
	Pass: 12	3	8	13	13	16
	Pass: 18	3	12	25	28	29
N	*Pass*: 24	4	17	38	42	48
	Fenc: 25%	2	28	61	68	55
	Fenc: 50%	4	51	118	152	150
	Fenc: 75%	6	66	161	225	257
	Fenc: 100%	4	71	179	261	318
	Intercept	0.011	0.020	0.045	0.085	0.128
	Pass: 6	−0.005	−0.006	−0.008	−0.012	−0.015
	Pass: 12	−0.008	−0.009	−0.012	−0.018	−0.025
	Pass: 18	−0.009	−0.011	−0.017	−0.026	−0.034
F_{st}	*Pass*: 24	−0.010	−0.012	−0.019	−0.032	−0.044
	Fenc: 25%	0.000	−0.003	−0.009	−0.018	−0.022
	Fenc: 50%	0.001	−0.003	−0.016	−0.035	−0.047
	Fenc: 75%	0.004	−0.002	−0.019	−0.044	−0.068
	Fenc: 100%	0.023	0.015	−0.007	−0.040	−0.077

Our results suggest that fences are much more effective at mitigating the effects of roads than are passages for our model species. As expected, fencing is an effective way to mitigate reduced abundance due to road mortality (e.g. Clevenger et al., 2001). Even incomplete fencing (75%) can effectively return population size to near that expected under roadless conditions when road mortality is extremely high. The mitigating capacity of passages is very weak by comparison. Implementing the highest number of passages in our model (24) is not as effective at mitigating abundance as is implementing the lowest proportion of fencing (25%; Table 3).

More surprising is how effectively fencing can also reduce genetic differentiation, a relationship opposite to that often assumed (Hepenstrick et al., 2012). When mortality risk is low to medium and the entire road is fenced, fencing does increase differentiation over the course of 30 years. However, when fencing is done partially, or when mortality risk is high, the more fencing implemented, the slower that differentiation will develop. Thus, fencing often appears to effectively promote rather than impede connectivity. This relationship makes sense in light of population genetic expectations: by promoting larger population sizes, fencing also promotes higher genetic diversity, thus diminishing the rate at which genetic drift differentiates populations. Conversely, many more passages would need to be constructed than we have simulated to equal the ability of fences at reducing genetic differentiation. Passage building is more effective at slowing differentiation than fence building only when mortality risk is low or when fencing is 100%.

Assessing the relative effect of fences and passages at mitigating road mortality effects requires the study of different populations inhabiting areas near roads with different levels of fencing and road passages. To our knowledge such a study has yet to be conducted and would be difficult to achieve in an empirical framework. Simulations are thus an ideal way to investigate the relative effectiveness of these two common mitigation techniques and our study is the first to quantitatively investigate this question while independently varying levels of fencing, passage construction, and road mortality. Our results suggest that fencing is much better at recouping lost abundance and genetic diversity (and under most conditions, reducing genetic differentiation) than passage building.

A second clear outcome from our simulations was that populations are predicted to be resilient to WVC events when risk of mortality is low ($\leq$10%). This resilience effect likely resulted from reduced competition for resources in response to increased road mortality, an effect facilitated by density dependent growth. This suggests that mitigation efforts may be wasteful and even harmful when road mortality is expected to be low. This point was previously made by Jaeger and Fahrig (2004), who predicted that fences could reduce population persistence when organisms are able to effectively avoid roads or traffic. Although we predict that populations may be robust to small levels of road mortality, extreme caution should be taken because WVC may have a cumulative effect with other sources of mortality, and may thus inflict a larger negative effect than expected (Forman, 2000).

Taken as a whole, our results demonstrate that for roads with medium to high WVC risk, both mitigation approaches can improve abundance and connectivity, but that fences are more effective in most cases. We suggest that partial fencing (particularly at ~75%) is a promising and underappreciated management option for mitigating negative road effects. Fencing 75% of the road achieved nearly all the improvements in abundance obtained by fencing 100% of the road, yet fencing at 75% also appears to have allowed for enough gene flow across the road to generally prevent the increased differentiation that can develop when dispersal is completely severed by 100% fencing. Surprisingly, the potential improvement in N or reduction in F_{st} by adding passages on top of partial fencing is apparently very small, which challenges previous claims (Jaeger and Fahrig, 2004). To our knowledge, the merits of partial fencing have not before been tested and our results highlight this as a good management option.

Our model may underestimate the pervasiveness of mortality risk from roads on populations. For example, in our model road mortality only affects dispersing sub-adults and male adults searching for females. Mortality effects are likely higher in nature where settled adults may also be vulnerable to roads that bisect their territories. In fact, recent studies have shown that large sections of highway often bisect marten home ranges (Grilo et al., 2012). In addition, our model assumed that martens cross roads over a minimum time period. However, there is evidence that some carnivores often hunt in highway verges where prey is abundant (Barrientos and Bolonio, 2009), and thus may linger near roads for long periods. This behavior would likely heighten the mortality risk for carnivores beyond that seen in our model under a given level of simulated risk.

The NetLogo code for REPoP is freely available at https://sites.google.com/site/roadmitigation/) and can be easily adapted to other species or management scenarios. Thus, the REPoP model can be a valuable tool when planning road mitigation actions, not only for martens and other small sized carnivores, but also for a variety of species. We stress that our model described here was based on martens and our results are most applicable to martens and other medium-sized carnivores. Extrapolation to other species with different behaviors—such as road avoidance (McGregor et al., 2008), high sensitivity to road passage characteristics (Clevenger et al., 2001), or seasonal migrations, which may require massive numbers of individuals (e.g., ungulates or amphibians) to cross roads over short periods—should be carefully pondered.

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