

# Why are some animal populations unaffected or positively affected by roads?

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Received: 29 July 2012 / Accepted: 6 May 2013 / Published online: 29 May 2013  
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**Abstract** In reviews on effects of roads on animal population abundance we found that most effects are negative; however, there are also many neutral and positive responses [Fahrig and Rytwinski (Ecol Soc 14:21, 2009; Rytwinski and Fahrig (Biol Conserv 147:87–98, 2012)]. Here we use an individual-based simulation model to: (1) confirm predictions from the existing literature of the combinations of species traits and behavioural responses to roads that lead to negative effects of roads on animal population abundance, and (2) improve prediction of the combinations of species traits and behavioural responses to roads that lead to neutral and positive effects of roads on animal population abundance. Simulations represented a typical situation in which road mitigation is contemplated, i.e. rural landscapes containing a relatively low density (up to 1.86 km/km<sup>2</sup>) of high-traffic roads, with continuous habitat between the roads. In these landscapes, the simulations predict that populations of species with small territories and movement ranges, and high reproductive rates, i.e. many small mammals and birds, should not be reduced by roads. Contrary to previous suggestions, the results also predict that populations of species that obtain a resource from roads (e.g. vultures) do not increase with increasing road density. In addition, our simulations support the

predation release hypothesis for positive road effects on prey (both small- and large-bodied prey), whereby abundance of a prey species increased with increasing road density due to reduced predation by generalist road-affected predators. The simulations also predict an optimal road density for the large-bodied prey species if it avoids roads or traffic emissions. Overall, the simulation results suggest that in rural landscapes containing high-traffic roads, there are many species for which road mitigation may not be necessary; mitigation efforts should be tailored to the species that show negative population responses to roads.

**Keywords** Landscape connectivity · Landscape fragmentation · Landscape structure · Population density · Road mitigation

## Introduction

In a review of the empirical literature on effects of roads on animal population abundance and distribution, we found that most, about 59 %, of such effects are negative (Fahrig and Rytwinski 2009). The negative effects of roads on population abundance and distribution are thought to be mainly due to road mortality, population fragmentation, and traffic disturbance, and they are largely concentrated on amphibians and reptiles, large mammal species with low reproductive rates and large home ranges, and the more mobile birds (Rytwinski and Fahrig 2011, 2012). In addition, populations of species that avoid roads from a distance due to traffic disturbance (e.g. noise, lights) [e.g. elk (*Cervus elaphus*) and caribou (*Rangifer tarandus*)] and species that show no ability to avoid oncoming traffic on roads, therefore suffering high road mortality [e.g. northern leopard frog (*Rana pipiens*)], are more likely to be

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Communicated by Christopher Johnson.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-013-2684-x) contains supplementary material, which is available to authorized users.

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negatively affected by roads (Jaeger et al. 2005; Rytwinski and Fahrig 2012).

Although the majority of population-level responses to roads are negative, there are many species whose populations are apparently unaffected or even increase in response to roads. In our 2009 review we found that about 29 % of responses were neutral and about 12 % were positive. Following the addition of unpublished data from theses, and results of several recent studies, the estimated proportion of positive effects increased to about 24 % (Rytwinski and Fahrig 2012).

There are several possible explanations for neutral and positive effects of roads on wildlife populations. First, populations of species that avoid going onto roads but are not disturbed by road traffic, have small territory sizes, and have high reproductive rates should show weak or no effect of roads since traffic mortality should be low and viable populations should be able to exist within areas bounded by roads. This combination of conditions has been suggested as an explanation for observed lack of effect or weak effects on small mammals (Garland and Bradley 1984; McGregor et al. 2008). Second, as suggested by Jaeger et al. (2005), populations of some species may be unaffected by roads if they are able to avoid being killed by oncoming vehicles. Third, populations of animals that are attracted to roads for a resource (e.g. carrion-feeders such as ravens and some raptor species) and are able to avoid oncoming vehicles should show a net positive effect of roads (Knight and Kawashima 1993; Meunier et al. 2000). Finally, roads could indirectly produce a net increase in abundance of species whose predators show negative population-level responses to roads, through predation release. This has been suggested as a possible cause for the observed positive effects of roads on populations of several small mammal species (Johnson and Collinge 2004; Rytwinski and Fahrig 2007; Fahrig and Rytwinski 2009) and the white-tailed deer (*Odocoileus virginianus*) (Munro et al. 2012).

Several of the potential explanations for effects of roads on animal abundance (above) involve specific behavioural responses to roads or to individual vehicles. To date there are very few species for which there are quantitative data on such behavioural responses to roads [only 17 species globally (see Rytwinski and Fahrig 2012)], and consequently, hypotheses predicting species responses to roads based on behavioural responses are not empirically testable. In addition, the predation release hypothesis for positive road effects on prey has been proposed but not quantitatively evaluated. In this study we use an individual-based simulation model to study the circumstances—life history traits, behavioural responses to roads, and predation pressure—leading to negative, positive and neutral effects of roads on animal abundance. We first confirm that the model

is able to derive the known relationships between life history attributes and negative population level responses to roads. We then focus mainly on the conditions leading to neutral and positive effects of roads on animal population abundance. Our purpose is to derive a set of generalized predictions that could be tested in future empirical work.

## Materials and methods

### Overview

We developed a stochastic, individual-based, spatially explicit simulation model using the NetLogo modelling environment (Wilensky 1999). We used an individual-based approach because we wanted the effects of roads on population size to emerge as model output from the sum of individual behavioural responses to the roads (e.g. road avoidance by individuals). We felt this approach was preferable to a population modelling approach, which would have required us to make a priori assumptions about how behavioural responses to roads influence population parameters, potentially leading to self-evident model results.

The main goal of the simulations was to derive a set of generalized predictions of the circumstances leading to negative, positive and neutral effects of roads on animal abundance. We did not intend these predictions to be applicable to particular species, but rather our goal was to identify general species types, characterized by sets of traits (see below), that differ in the predicted effects of roads. The predictions are meant as working hypotheses on which future empirical work can be based. To do this, the model simulated the dynamics of a hypothetical animal population in hypothetical landscapes with different road densities. The simulation landscape was scaled to represent an area  $7.5 \times 7.5$  km, to allow realistic representation of species types with different territory sizes and movement ranges (below). A second version of the model represented the population dynamics of a prey species under predation by generalist predators. To determine whether behavioural responses to roads affected the abundance of the hypothetical animal populations, we conducted simulations in which each behavioural response to roads and traffic was set at one of two extremes, either 0 or 100 % (with the exception of traffic mortality, described below). There were two general species types characterized by a set of life history traits representing either a typical small-bodied species (small territory size, small movement range, and high reproductive rate) or a typical large-bodied species (large territory size, large movement range, and low reproductive rate). We combined each of these species types with each of six possible behavioural responses to roads, producing 12 general species categories. Each of

these was simulated across a range of eight different road densities to develop generalized predictions of the relative effects of roads on the abundances of the different species types and behavioural response categories. The behavioural responses to roads were: (1) road attraction + vehicle avoidance (e.g. vultures); (2) road attraction + no vehicle avoidance (e.g. turtles, snakes); (3) vehicle avoidance only (e.g. caribou); (4) traffic disturbance avoidance (e.g. grizzly bear, elk); (5) road surface avoidance (e.g. some small mammals); and (6) no avoidance (e.g. amphibians) (see Tables 1, 2 for model parameters; see EMS, Table S1 for definitions of behavioural responses to roads).

In the predation-effect version of the model, generalist predators (individual predators from an unspecified number of species) were assumed in all simulations to be large-bodied species types (large territory size, large movement range, and low reproductive rate) that were negatively affected by roads. There were two prey species types (in separate simulations), a small-bodied prey species (small territory size, small movement range, and high reproductive rate) and a large-bodied prey species (large territory size, large movement range, and low reproductive rate). The same six behavioural responses to roads as outlined for the single-species version were run for each prey species type (small and large) at the eight different road densities (Table 2).

### Model description

The simulated landscape comprised a two-dimensional uniform-grid landscape of  $751 \times 751$  square cells, each

**Table 1** Parameter values held constant among simulation runs

Parameters	Values
Landscape size	$751 \times 751$ Cells ( $\sim 56 \text{ km}^2$ )
Time steps in simulation	100 or until stable or extinct
Maximum cell occupancy	One individual per cell
Road attraction zone <sup>a</sup>	Within four cells of a road
Attracted-benefit <sup>b</sup> ( <i>B</i> ; proportion of reproductive output)	1
Traffic density (vehicles/10-m cell)	3 (High traffic)
Traffic disturbance zone (no. of cells)	
If movement distance = 1.5	Avoid road from 1 cell away
If movement distance = 500	Avoid road from 45 cells away

<sup>a</sup> Distance from which a road-attracted individual was attracted to a road, i.e. if a road-attracted individual is within a road attraction zone, it is moved to the centre of the nearest road cell

<sup>b</sup> Applied to those individuals that are attracted to a road, and that are reproducers in the current time step, and avoid oncoming vehicles. These individuals receive a benefit from the road in the form of extra offspring; the number of extra offspring is a proportion (*B*) of its nominal reproductive output

representing a  $10\text{-m} \times 10\text{-m}$  area. This landscape size ( $\sim 56 \text{ km}^2$ ) was large enough to allow for a population of up to 37 individuals of the large-bodied animal, with territory size  $1.5 \text{ km}^2$  and movement distance 5 km, but small enough to keep the maximum abundance of the small-bodied animal with small territory size computationally manageable ( $\leq 282,000$  individuals).

The simulation landscape represented a typical landscape situation where road mitigation measures are often considered, i.e. rural landscapes of mainly natural areas crossed by a few high-traffic roads. The simulation grid contained two kinds of cells, habitat and roads; roads were one cell (10 m) wide. We increased the number of roads from 0 to 14 in increments of 2, which corresponds to typical road densities in rural landscapes ( $0\text{--}1.86 \text{ km/km}^2$ ; Table 2), and covers the range of road densities where negative effects of roads on wildlife populations have been observed (e.g. van Dyke et al. 1986; Mech et al. 1988; Mladenoff et al. 1995; Rytwinski and Fahrig 2011). At the maximum road density of 14 roads, the resulting loss of habitat was less than 2 %, allowing us to be confident that effects of road density on the populations would not be a result of direct habitat loss. All non-road cells were assumed to be equal-quality habitat. The model proceeded in time steps equivalent to years (or generations). Each run continued until the population reached a steady state (i.e. it varied by less than 5 % from year to year for at least 10 years), the population went extinct, or 100 years, whichever came first.

### Submodels

The model includes three submodels—reproduction, movement, and density limit—applied in this order to each individual in each time step (Fig. 1). Each submodel is completed for all individuals before the next submodel begins.

### Setup

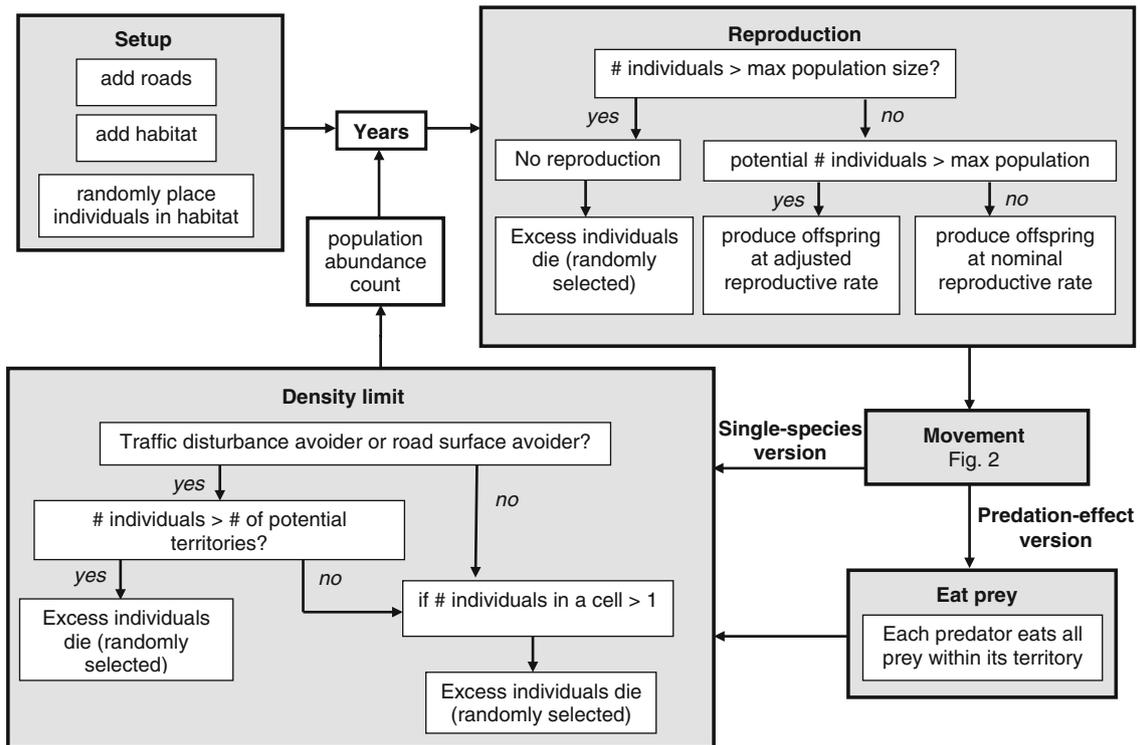
An individual simulation run begins by placing the roads in the landscape (if roads are present), followed by assigning the remaining grid cells to habitat. The spatial pattern of the landscape is constant throughout the simulation run. Roads were straight and formed a grid pattern, with an equal number of horizontal and vertical roads extending the entire width of the landscape. Parallel roads were equidistant from one another. Once the landscape was generated, in the single-species model version 1,000 individuals were distributed randomly across habitat i.e. individuals did not start the simulation on a road. In the predation-effect simulations, 1,000 prey and 50 generalist predators were distributed randomly across habitat.

**Table 2** Parameters that varied among the simulations

Simulations	Species type	Life history trait			Avoidance behaviour				
		Reproductive rate	Movement distance	Territory size	$T(k)$	$C(k)$	$M(d)$	$A$	$R$
1. Road attraction + vehicle avoidance	Small	32 (55)	1.5	2	0	200	2.5	1	0
	Large	1 (35)	500	15,000	0	200	2.5	1	0
2. Road attraction + no vehicle avoidance	Small	32 (55)	1.5	2	0	0	2.5	1	0
	Large	1 (35)	500	15,000	0	0	2.5	1	0
3. Vehicle avoidance	Small	32 (55)	1.5	2	0	200	2.5	0	0
	Large	1 (35)	500	15000	0	200	2.5	0	0
4. Traffic disturbance avoidance	Small	32 (55)	1.5	2	200	0	2.5	0	0
	Large	1 (35)	500	15,000	200	0	2.5	0	0
5. Road surface avoidance	Small	32 (55)	1.5	2	0	0	2.5	0	1
	Large	1 (35)	500	15,000	0	0	2.5	0	1
6. No avoidance	Small	32 (55)	1.5	2	0	0	2.5	0	0
	Large	1 (35)	500	15,000	0	0	2.5	0	0

The same simulations with the same parameter values were run for the single-species and predation-effect simulations, with the exception that the nominal reproductive rates differed (predation-effect rates are *in parentheses*); this was necessary to allow population persistence in the predation-effect model (see text). Note for the predation-effect version, the generalist predators were large-bodied species (reproductive rate = 35 offspring, movement distance = 500 cells, territory size = 15,000 cells) showing no road-avoidance behaviours and high traffic mortality in all simulations

$T$  Probability of an animal avoiding the road from a distance due to traffic disturbance, determined by the avoidance parameter  $k$ ;  $C$  probability that an animal on a road can avoid oncoming vehicles, determined by the avoidance parameter  $k$ ;  $M$  probability of an animal being killed on the road given it attempted to cross, determined by the mortality parameter  $d$  (0, 88, and 100 % probabilities, respectively);  $A$  probability of an animal being attracted to a road from a given distance;  $R$  probability of an animal avoiding moving onto or across roads, in the event that its randomly selected movement trajectory would have taken it onto or across a road (0 or 1 corresponded to 0 and 100 % probabilities, respectively)



**Fig. 1** Model flow chart

## Reproduction

At the beginning of each time step, each individual produces a number of offspring determined by the nominal reproductive rate, a constant value applied to all individuals in all time steps for a model run. Nominal reproductive rate was assumed to be the net of reproduction and natural mortality (with the exception of predation in the predation-effect version of the model). In the current runs, nominal reproductive rate was either high (32 offspring per year) or low (one offspring per year), representing small-bodied and large-bodied (respectively) generic species (Table 2). We chose the maximum value (32) in preliminary experiments: at a reproductive rate of 32, all six behaviour categories showed population persistence at the lowest road density (two roads), thus allowing us to observe the relative effects of increasing road density across the six behaviour categories. While an annual reproductive rate of 32 offspring may seem high, this is realistic for some species of birds and mammals that have high brood/litter sizes and multiple broods/litters per year [e.g. *Ochrotomys nuttalli* (golden mouse) (Linzey and Packard 1977)]. In the predation-effect version, the reproductive rate of the predators was held constant at 35 for all predators and runs. This is higher than the rate for the large-bodied animal in the single-species simulations (Table 2). This was necessary to ensure some predators survived at higher road densities, since the purpose was to evaluate the interacting effects of predation and road density on the prey species categories. The nominal reproductive rate for the large prey species was also 35 and for the small prey species was higher at 55 (Table 2).

The total number of individuals in the landscape is not allowed to exceed the maximum capacity of the landscape as determined from the territory size (natural density) (Fig. 1). This is determined by dividing the number of habitat cells in the landscape by the territory size (number of cells per individual). In the current runs, territory size was either small [two cells per individual or 200 m<sup>2</sup> (maximum population size = 282,000 individuals)] or large [15,000 cells per individual or 1.5 km<sup>2</sup> (maximum population size = 37 individuals)], representing small-bodied and large-bodied (respectively) generic species (Table 2). While a territory size of 200 m<sup>2</sup> may seem small, this is realistic for some species of birds and mammals [e.g. *Microtus californicus* (California vole) (Cudworth and Koprowski 2010)]. If the potential number of individuals prior to reproduction, based on the nominal reproductive rate (i.e. potential number of individuals = current number of individuals × nominal reproductive rate), was greater than the maximum population size, the reproductive rate was adjusted [actual reproductive rate = (potential number of individuals – maximum population size)/current number of individuals]. All individuals can potentially reproduce.

For behaviour category (road attraction + vehicle avoidance) the number of individuals can potentially exceed the maximum capacity of the landscape prior to reproduction because individuals receive a benefit from the road in the form of extra offspring at the end of the previous generation (year) (see the movement submodel below). To ensure that the total population does not exceed the maximum prior to movement in the current generation, excess individuals are killed off randomly if the number of individuals in the landscape exceeds the maximum population size (Fig. 1).

## Movement

Net movement per individual per time step is modeled one individual at a time (Fig. 2). A random movement angle is selected between 0° and 360°. Nominal movement distance is a constant applied to all individuals in all time steps. In the current runs, nominal movement distance was either small (1.5 cells = 15 m) or large (500 cells = 5 km), representing the small and large (respectively) generic species (Table 2). When a moving individual encounters the border of the landscape, it re-enters the landscape on the opposite side and continues moving in the same direction (wrapped grid). Actual movement distance is determined by the combination of nominal movement distance and the species behavioural response to roads and traffic.

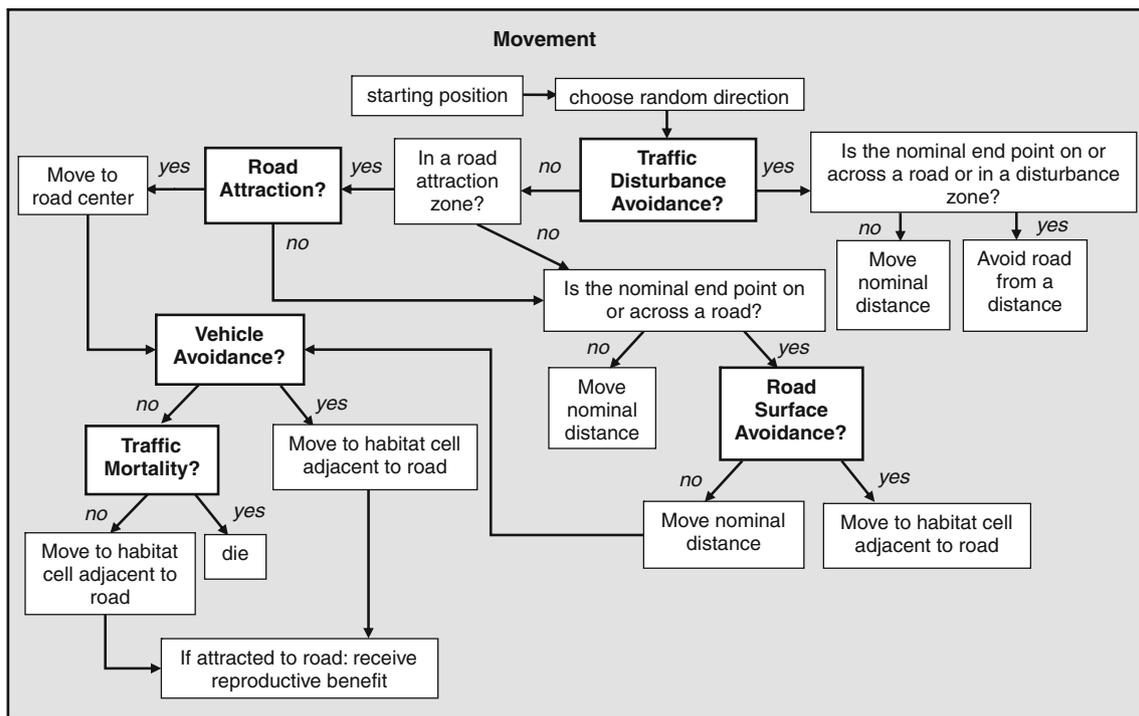
The following parameters determine behavioural responses to roads and traffic, and traffic mortality (Fig. 2; EMS, Fig. S1):

### 1. Traffic disturbance avoidance

The probability of an animal avoiding the road from a distance ( $T$ ) is a function of traffic density and is estimated using the following equation:

$$T = \frac{kV}{1 + kV}$$

where  $k$  is the avoidance parameter, and  $V$  is the traffic density (vehicles per road cell).  $k$  determines the probability of an animal avoiding the road from a distance (below) at a given traffic density (EMS, Fig. S2a). In the current simulations we held traffic density constant at three vehicles per cell for all model runs, and  $k$  was either 0 or 200, corresponding to 0 and 100 % probabilities (respectively) of avoiding the road (Tables 1, 2; EMS, Fig. S2a). Note that we modelled traffic only indirectly, by incorporating it into the above probability of road avoidance from a distance (as well as vehicle avoidance and traffic mortality; see below). The traffic density experienced by an individual animal encountering a road cell is high; three vehicles in a 10 m-long two-lane road cell might represent



**Fig. 2** Flow chart of the movement submodel

two vehicles in one lane and one vehicle in the opposing lane. We intentionally modelled high-traffic roads since our goal was to model the type of roads for which mitigation is usually contemplated. Note, however, that we cannot translate this traffic density into an hourly or daily traffic volume since the traffic volume experienced by the animal is instantaneous, and the animal might have (notionally) encountered the road any time during the 1-year model time step.

The avoidance distance is a function of the animal's nominal movement distance so that larger-bodied road-avoiding animals avoid the road from farther away than do smaller-bodied road-avoiding animals (EMS, Fig. S3). Given the dimensions of the landscape and the road densities we investigated, the maximum avoidance distance possible in the current runs was 450 m, which is consistent with road effect zones reported for large species such as woodland caribou [250 m (Dyer et al. 2001)], grizzly bears [500 m (Waller and Servheen 2005)]; and moose [ $\geq 500$  m (Laurian et al. 2008)]. If at the beginning of a simulation an individual is closer to a road than its avoidance distance, it is moved to the nearest cell out of the disturbance zone before the simulation begins. If an individual's nominal movement end point would place it on or across a road, or inside a disturbance zone, the individual avoiding the road due to traffic disturbance moves in its current direction until it reaches the disturbance zone.

## 2. Road attraction

The probability of an animal being attracted to a road (A) [e.g. for food i.e. road-kill animals (some birds), a nesting site (some turtles), a mate (all animals), or thermoregulation (some snakes)] was set at either 0 (no road attraction) or 1 (100 % road attraction) (Table 2). Here again we set the behavioural response to roads i.e. road attraction, to the extremes to determine whether this response to roads could have a large effect on the abundance of the hypothetical animal populations. The road attraction zone for those attracted was set at four cells (Table 1). We made this simplifying assumption because road attraction zones are generally unknown. It is known that perceptual ranges in animals are highly variable depending on both the species (Zollner 2000; Mech and Zollner 2002; Forero-Medina and Vieira 2009) and the particular context (Yeomans 1995; Zollner and Lima 1999; Schooley and Wiens 2003; Olden et al. 2004; Flaherty et al. 2008; Forero-Medina and Vieira 2009; Prevedello et al. 2011). If a road-attracted individual is within a road attraction zone, it is moved to the centre of the nearest road cell and the vehicle avoidance submodel (below) is then applied.

Individuals that are attracted to a road, and that are reproducers in the current time step (from the reproduction submodel), and avoid oncoming vehicles (below), receive a benefit from the road in the form of extra offspring. The

number of extra offspring is a proportion,  $B$ , of its “normal” reproductive output. In the current runs  $B$  was set at 1 for all model runs, so reproductive output was doubled for animals receiving the benefit.

### 3. Road surface avoidance

The probability of an animal avoiding moving onto a road, in the event that its randomly selected movement trajectory would have taken it onto the road ( $R$ ). Road surface avoidance occurs in species, such as some small mammals (Ford and Fahrig 2008; McGregor et al. 2008), that are unlikely to move onto exposed surfaces such as roads (probably to avoid predation), but are not repulsed by traffic disturbance itself. In the current runs, the probability of avoiding the road surface was either 0 (no surface avoidance) or 1 (100 % surface avoidance) (Table 2). If an individual avoids the road surface, it is moved back to the habitat cell adjacent to the road on the side from which it came (Fig. 2).

### 4. Vehicle avoidance

The probability that an animal on a road avoids oncoming vehicles ( $C$ ), is a function of traffic density and is estimated using the same equation as for traffic disturbance avoidance (above), replacing  $T$  with  $C$ .  $k$  is the avoidance parameter and  $V$  is the traffic density.  $k$  is the probability of an animal avoiding vehicles(s) at a given traffic density (EMS, Fig. S2a). In the current runs we held traffic density constant at three vehicles per road cell, and  $k$  was either 0 or 200, corresponding to 0 and 100 % probabilities, respectively, of avoiding oncoming vehicles (Tables 1, 2). If an individual on a road shows vehicle avoidance, 70 % of the time, it is returned to the habitat cell adjacent to the road on the side of the road it came from; otherwise it moves to the habitat cell adjacent to the road on the opposite side of the road (i.e. it crosses the road). We made the arbitrary assumption of a 70 % return probability, based on the idea that animals frightened by vehicles are more likely to return to a familiar location than move to an unfamiliar one, unless they are close to the unfamiliar side.

### 5. Road (traffic) mortality

The probability of an animal being killed on the road given it attempted to cross ( $M$ ), is a function of traffic density and is estimated using the same equation as for traffic disturbance avoidance (above), replacing  $T$  with  $M$ .  $d$  is the mortality parameter and  $V$  is the traffic density.  $d$  is the probability of an animal being killed at a given traffic density (EMS, Fig. S2b). In the current runs traffic density was held constant at three vehicles per road cell and  $d$  was either 0 or 2.5, corresponding to probabilities of road mortality of 0 and 88 %, respectively (Tables 1, 2). We used an upper limit of 88 % to ensure that in all parameter combinations at least a few individuals would survive.

### Density limit

In addition to the maximum population size for the whole landscape, as determined from the territory size (see reproduction submodel above), the density of species that avoid roads is not allowed to exceed a maximum in each habitat block (habitat area bounded by roads), given the number of territories available in the block. For individuals that avoid roads from a distance (traffic disturbance avoidance; above), the effective block area is reduced to exclude the parts of the block within the traffic avoidance zone. For both of the density limitation steps i.e. the maximum number of individuals for the landscape and the maximum number for a habitat block, if the number of individuals exceeds the maximum, individuals die at random until the maximum density is reached. Therefore, in this model individual territories overlap, although at any given time the position of each individual is assigned to a unique cell (Table 1; Fig. 1).

### Predation effect

The predation release hypothesis (above) does not invoke a paired predator–prey dynamic. Rather, it hypothesizes that release from predation pressure in landscapes with high road density may compensate or even over-compensate for road mortality on a prey species. Therefore, we did not model a paired predator–prey dynamic; rather, we modelled generalist predators (from an unspecified number of species). The population of predators is not dependent on the prey population abundance.

The predation-effect version of the model contains individual generalist predators and a prey species (Table 2). In the current runs the predators were modelled as large-bodied species (large territory sizes, large movement ranges, and low reproductive rates) that should be negatively affected by road mortality i.e. showing no road avoidance behaviour. These characteristics were held constant for all predators in all simulations. The reproductive rate of the predators was 35. This is higher than the rate for the large animal in the single-species simulations (Table 2), which was necessary to ensure that some predator individuals survived at higher road densities. Two prey species types were modeled in separate runs, a large prey species (e.g. deer, moose) and a small prey species (e.g. small mammal, bird) (Table 2). Reproductive rate for the small prey species was 55 and for the large prey species was 35 (Table 2). After the movement submodel is applied to both predators and prey, individual predators create circular territories (15,000 cells in the current runs), within which all prey are eaten (Fig. 1). Note that trial runs in which we reduced predation efficiency to 50 % did not qualitatively affect the results.

## Number of simulation runs

The total number of runs possible was limited because of the large spatial extent represented by the model, resulting in very large population sizes for many of the runs for the small-bodied species types. Some runs took longer than 3 months to run on high-performance computers [(1) Dell Precision T7500–2 × Intel (R) Xeon (R) 2.67 GHz, total RAM 48 GB, and (2) Beowulf Cluster–64 nodes 4 × 2.2 GHz Opteron Cores w/8 GB RAM per node–three nodes with 12 × 2.53 GHz Intel Xeron E5649 w/24 GB RAM per node], thus restricting us to one replicate per parameter combination (above). We checked the impact of this by running up to 100 replicates for selected parameter combinations that ran more quickly, and found that model results did not qualitatively vary, with the exception of the large-bodied prey species runs. Thus for the large-bodied prey species runs, we ran 50 replicates per parameter combination. The limitation on the number of runs possible is also the reason that we only simulated the two extreme values of each of the life history and road response parameters (Table 2). In all, 192 simulations were run. The outcome of each run was recorded as the mean abundance over the last ten generations (zero if the population went extinct).

## Results

### Small species types

There was no behaviour category predicted to result in a negative effect of increasing road density on the abundance of a small species type in either the single-species or

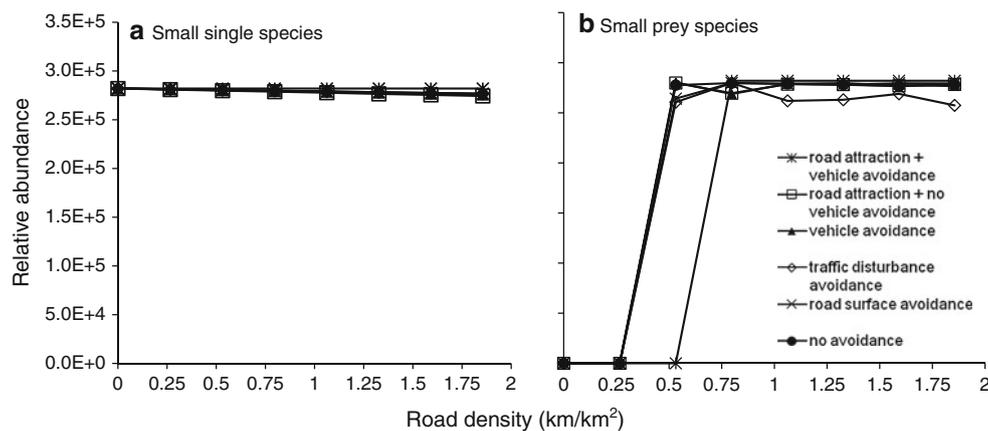
predation-effect runs (Fig. 3). In single-species runs the abundance of the small-bodied species type was predicted to be unaffected by increasing road density for all behaviour categories (Fig. 3a). In the presence of generalist predators that were negatively affected by increasing road density, the small-bodied prey species type was positively affected by increasing road density for all behaviour categories (Fig. 3b).

### Large species types

Neutral effects of roads on the large-bodied species occurred in single-species runs when the species was able to avoid oncoming vehicles and either (1) showed no road or traffic disturbance avoidance, or (2) was attracted to the road for a resource (Fig. 4a). In predation-effect scenarios, these behaviour categories led to positive effects of roads on the abundance of the large-bodied prey species (Fig. 4b). In addition, the abundance of large-bodied prey species that either (1) avoided roads from a distance due to traffic, or (2) avoided the road surface, increased with increasing road density until an optimum, above which it decreased (Fig. 4d). For all other behaviour categories the large-bodied species type was predicted to decrease in abundance with increasing road density (Fig. 4c, e and f).

## Discussion

The results support several previously suggested hypotheses to explain neutral or positive effects of roads on animal abundance. First, small-bodied species that avoid going onto roads but are not disturbed by road traffic are predicted to be unaffected by increasing road density



**Fig. 3** Simulated predictions of the relative abundance [mean abundance over the last ten generations (zero if the population went extinct)] of the small-bodied species types as a function of increasing road density, for different assumed behavioural responses to roads. Small-bodied species types had small territory sizes/high natural

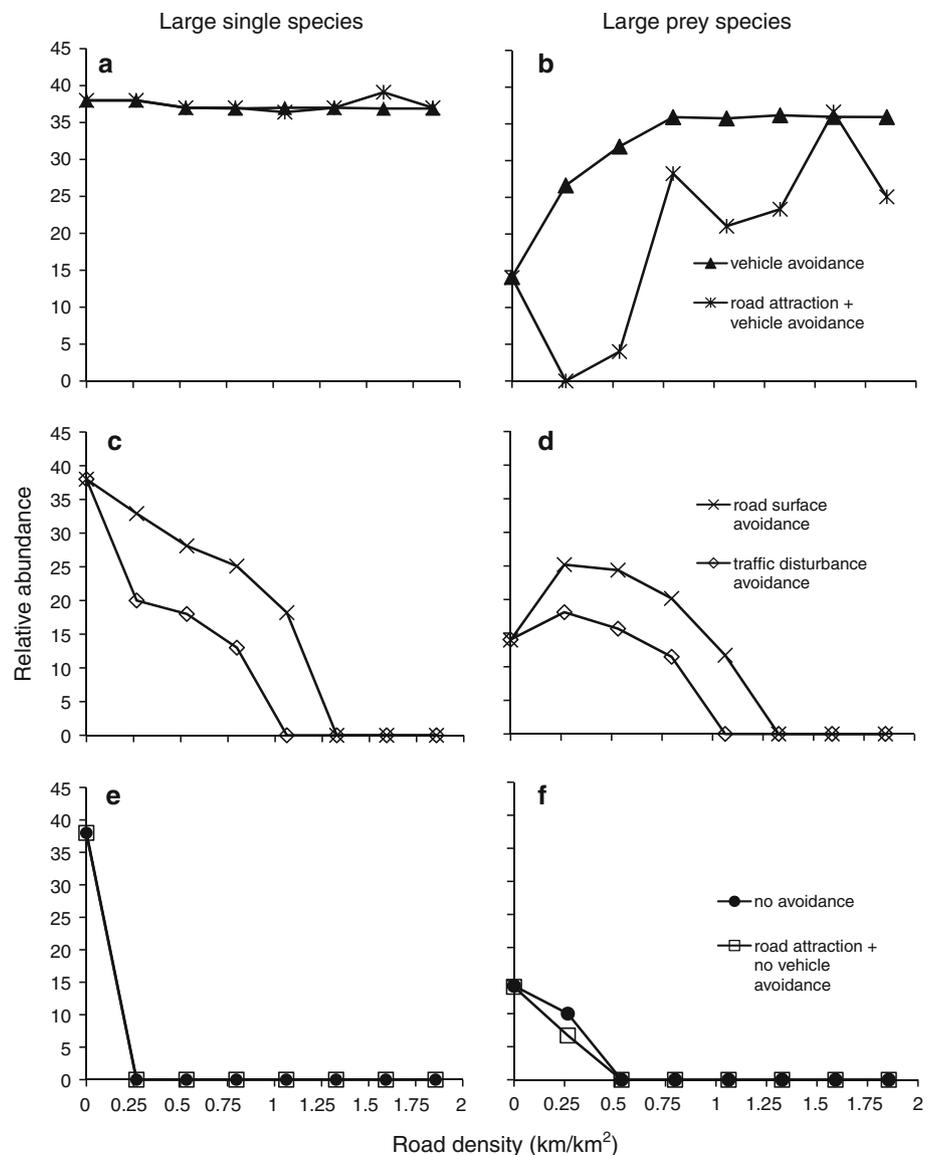
densities, small movement ranges, and high reproductive rates. **a** Single-species version with no predators in the model, **b** predation-effect version, where the small-bodied species was prey for road mortality-affected large generalist predators

(Fig. 3a). These conditions likely explain the observed lack of effect or weak effects for many small mammals and small birds. We note, however, that this result would likely not hold in urban situations where road density, along with associated habitat loss and road mortality, may be high enough to cause negative road effects even on such small-bodied animals. Second, the abundance of both a large-bodied and small-bodied species is predicted to be unaffected by roads if the species can avoid oncoming vehicles (Figs. 3a, 4a). These conditions might explain the lack of effect or weak effects of roads on some large-bodied and small-bodied mammal populations; however, despite many anecdotal observations, to our knowledge there are no studies that quantify vehicle avoidance behaviour in animals. Third, increasing road density is predicted to produce a net increase in abundance of small-bodied prey species

whose generalist predators are negatively affected by road mortality (Fig. 3b), supporting the predation release hypothesis for observed positive effects of roads on populations of several small mammal species (Johnson and Collinge 2004; Rytwinski and Fahrig 2007; Fahrig and Rytwinski 2009). Interestingly, our model also predicts a positive effect of roads on a large-bodied prey species in the presence of road mortality-affected predators, when the large prey species is able to avoid oncoming vehicles (Fig. 4b), which may explain an observed positive effect of road density on abundance of white-tailed deer (Munro et al. 2012).

Based on our simulation results we propose several new hypotheses to explain neutral or positive effects of roads on animal abundance. The single-species simulations predict that species with small territories and movement ranges

**Fig. 4** Simulated predictions of the relative abundance [mean abundance over the last ten generations (zero if the population went extinct)] of large-bodied species types as a function of increasing road density, for different assumed behavioural responses to roads. Large-bodied species types had large territory sizes/low natural densities, large movement ranges, and low reproductive rates. Predictions are separated into columns for results from the single-species runs with no predation in the model (large single species) (a, c, and e), and the predation-effect runs (large prey species)



and high reproductive rates are generally unaffected by roads, with all behavioural scenarios predicting neutral effects (Fig. 3a). Furthermore, in our simulated landscapes there were no circumstances predicted to lead to negative effects of roads on this species type. These results suggest that the combination of high reproductive output, low mobility, and small territory sizes (high density) render populations resilient to effects of traffic mortality, resource inaccessibility and population subdivision as road density increases in a landscape containing habitat blocks surrounded by roads. Such small animals can maintain viable populations within these blocks. Again note that this result applies to the landscape scenario we simulated i.e. high-traffic roads within a mainly natural area. Negative effects of roads on small-bodied species would be observed if the number of roads were greatly increased, say to the density of an urban landscape. In the extreme, no habitat would be remaining. Even if there is habitat remaining, small-bodied species that show no avoidance behaviour towards roads or traffic would suffer from high road mortality, and species that avoid traffic disturbance from a distance would suffer from effective habitat loss and resource inaccessibility. As Forman et al. (2003) noted, road networks can vary greatly in density, with urban centres typically having a road density of about 40 km/km<sup>2</sup>, suburban areas about 10 km/km<sup>2</sup>, and rural agricultural landscapes having a road density of about 2 km/km<sup>2</sup>. We designed our simulated landscapes to reflect landscapes containing mainly natural cover, crossed by high-traffic roads at rural road densities, and therefore this is the scenario to which the results apply.

We simulated this relatively low road density, using narrow roads (10 m), not only to represent situations where road mitigation is commonly considered (high-traffic roads through mainly natural areas), but also because our aim was to determine the situations in which roads affects populations beyond their direct effect on habitat loss. In our simulations the maximum road density of 1.86 km/km<sup>2</sup> represented less than 2 % habitat loss, allowing us to be confident that effects of road density we observed were not mainly a result of direct habitat loss. Habitat loss due to roads can be mitigated only by removing (or deciding not to build or not to widen) roads, whereas the mortality, movement barrier, or disturbance impacts of roads can be mitigated by measures such as wildlife fencing, ecopassages, and noise barriers. Therefore, it is important to understand the effects of roads other than their direct effects on habitat loss (Eigenbrod et al. 2008).

All non-road cells in our simulated landscapes were the same type of habitat. This is certainly atypical of many rural landscapes, which are usually composed of multiple cover types (e.g. forest, agriculture, aquatic etc.) that vary in both amount and quality. The modelled landscape more closely represents a rural landscape containing mainly

natural and semi-natural habitats, e.g. a predominantly forested landscape. We did not include spatial variation in habitat quality because our goal was to develop generalized predictions. Including information on the pattern of habitat quality would require specific information about the habitat associations of a particular species of interest, identifying the cover types where it finds food, mates, nests, etc. and the cover types through which it is most likely to move. This level of detail could be included in model runs representing a particular species in a particular landscape, but would be impractical for the kinds of generalized predictions that were our aim. Similarly, we simulated only grid road patterns with evenly spaced roads. The actual road configuration of a real landscape could be modelled in simulations tailored to a specific real situation.

Since there are many documented negative effects of roads on abundance of amphibians and reptiles (reviewed in Rytwinski and Fahrig 2012), the “small-bodied animal type” in our simulations clearly does not represent these species well. The model must be missing important elements of these species life histories that would make them susceptible to roads. For amphibians we hypothesize that a missing element is their need to knit together different habitat types—aquatic breeding habitats, upland feeding habitats, and specialized overwintering habitats—to complete a life cycle (Wilbur 1980; Hecnar and M'Closkey 1996). This places a high premium on “landscape complementation” (Dunning et al. 1992), or the easy access of multiple required resources in the landscape. When the required resources are not in close proximity, amphibians must move large distances to find them (Laan and Verboom 1990; Reh and Seitz 1990). As road density increases, the likelihood of all required resources occurring within a single road-delineated area becomes unlikely. In some cases, all animals in the population must cross roads to obtain required resources, which can impose exceptionally high mortality rates on these populations, producing negative road effects (Fahrig et al. 1995; Carr and Fahrig 2001; Eigenbrod et al. 2008). In addition, both reptiles and amphibians display indeterminate growth, in which reproductive rate increases with body size and thus with age (e.g. Wilbur 1977; Kaplan and Salthe 1979; Gibbons and McCarthy 1986; Berven 1988; Berven 2009; Pupin 2010). For such species the impact of road mortality may be much higher than the impact on the small-bodied species type we modelled here. Increased mortality results in a shift in age distribution towards younger individuals, which would reduce the population reproductive rate of species with indeterminate growth (Hoskin and Goosem 2010; Karraker and Gibbs 2011), thus increasing the negative impact of road mortality on these populations. Therefore, while our model predictions for the small-bodied species types likely apply to many small mammals and

small birds, amphibians and reptiles have attributes not captured by the model that augment the negative impacts of road mortality on their populations.

Our simulations predict that roads generally negatively affect populations of the large-bodied species types (Fig. 4c, e, f), as expected a priori (e.g. Mladenoff et al. 1995; Mech et al. 1988; Mace et al. 1996; Newmark et al. 1996; Reijnen et al. 1996; Dyer et al. 2001; Roedenbeck and Köhler 2006). However, there are situations in which there is either a positive predicted effect (see above), no effect, or a hump-shaped predicted effect of roads on large-bodied species. Populations of species that do not avoid roads or traffic emissions (e.g. noise) and are able to avoid oncoming vehicles when attempting to cross roads are predicted to be unaffected by roads (Fig. 4a), as suggested by Jaeger et al. (2005). One could interpret this as indicating an imperative for studies quantifying vehicle-avoidance behaviour in animals, so that road mitigation projects can be directed to species that are unable to avoid oncoming vehicles. However, we suggest that such studies may be unnecessary, since the presence of road-killed animals indirectly indicates an inability (or at least a lack of perfect ability) to avoid oncoming vehicles. This tends to support the current intuitive practice of planning mitigation for large species that are found killed on roads [e.g. Florida Panther (*Puma concolor coryi*), black bear (*Ursus americanus*), Key deer (*Odocoileus virginianus clavium*) (Florida), grizzly bear (*Ursus arctos horribilis*), wolf (*Canis lupus*), wolverine (*Gulo gulo*) (Banff National Park Canada), large ungulates (British Columbia) (Evink 1996; Leeson 1996; Sielecki 2007)], particularly when there is sufficient information on population size to estimate the per capita road mortality rate [e.g. Florida Panther (Maehr et al. 1991); Key deer (Calvo and Silvy 1996)].

The simulations do not support the idea that a species, either large or small, that is attracted to the road for a resource and able to avoid oncoming vehicles should show a positive population-level response to roads; rather, the simulations predict a neutral effect in these cases (Figs. 3a, 4a). In our model, it seems that the territory size of the species limits the extent to which the added resources near roads can increase the population, as the populations of both the large-bodied and small-bodied species types were predicted to remain close to the maximum capacity for the landscape even as road density increased. If true, this suggests that the apparent positive effects of road attraction on animal abundance [e.g. vultures and raptors (Knight and Kawashima 1993; Meunier et al. 2000; Benítez-López et al. 2010)] may be illusory in some cases; they may actually represent increased time spent within the portion of habitat near to roads, and a benefit at the individual level i.e. extra offspring to individuals near roads, rather than a positive effect of roads on the overall population, which

would require an increase in the number of territories. On the other hand, food availability has been identified as the most important determinant of home-range size and shape in birds (Roland 2002), with home ranges often being smaller when resource density is higher (Zabel et al. 1995). Therefore, it may be possible that landscape containing higher road densities can support a larger number of smaller territories of some species that obtain resources from roads. To our knowledge, however, to date there are no studies showing smaller territory sizes near roads for animals such as birds of prey which are attracted to roads.

Interestingly, the simulations predict an optimal road density for the large-bodied prey species type that avoids the road or traffic emissions (Fig. 4d). For these species road mortality is low due to their road/traffic avoidance. As road density increases, the benefit of reduced predation can out-weigh the habitat loss/resource inaccessibility associated with roads and traffic avoidance. However, above an intermediate road density these negative road effects prevail. This indicates that, unlike the effects of road mortality, the effects of habitat loss and subdivision due to roads are only evident at high road densities. This is supported by previous simulations where traffic mortality had a much stronger effect on animal population persistence than did road avoidance alone (Jaeger and Fahrig 2004). In addition, Jaeger and Fahrig (2004) found that road mortality decreased persistence time, whereas road avoidance led to longer persistence times in most simulated cases. This result is also supported by some empirical studies of large species showing differences in road density thresholds. For example, numerous studies have found that wolves are absent from areas with road densities exceeding 0.6 km/km<sup>2</sup> (more than four roads in our model) (Thiel 1985; Mech et al. 1988; Mladenoff et al. 1995), most likely due to road mortality (Fuller 1989). For species such as elk (*Cervus elaphus*), which avoid roads from a distance (Rowland et al. 2000; Gagnon 2007; Dodd et al. 2007; Stewart et al. 2010), and are therefore affected by habitat loss and resource inaccessibility rather than mortality, much higher road density thresholds have been reported e.g. 3.2 km/km<sup>2</sup> for a 25 % decline in usable elk habitat (Lyon 1983).

A common challenge in modelling is the trade-off between realism and generality. As researchers, we want to provide information that is useful and accurate, yet applicable across multiple locations and species. Various tools have been used to study the effects of roads and/or traffic on the viability of animals; however, the majority of these models are species-specific, requiring detailed field research to validate the parameters used (van der Grift et al. 2004). Obtaining species demographic information is both expensive and time consuming, with some species attributes nearly impossible to accurately determine (e.g.

dispersal distance). This is further complicated by the fact that roads simultaneously impact multiple interacting species. The general goal of our simulations was to identify the general situations where road impacts are almost certain to be strong from those where they are likely weak or even non-existent. To obtain such general results, we made the model both as general and as realistic as possible. For example, our simulated landscape had a realistically large spatial extent that allowed for representation of different species with different territory sizes and movement ranges. In addition, we modelled life history traits that have been shown to affect species responses to roads in previous studies i.e. territory size, mobility, and reproductive rate (see Rytwinski and Fahrig 2012). The trade-off between generality and realism entailed some compromises. First, due to the realistic spatial extent of the model, computing demands were heavy, and so we were not logistically able to simulate full gradients of the parameters. We chose instead to model extreme contrasts in life history and behavioural responses to roads. Many real combinations are therefore missing from our runs. For example, the short-tailed weasel (*Mustela erminea*) has a relatively large home range (13 ha) for its small body size (75 g) [Ontario, Canada (Simms 1979; Eder 2002)] compared to the similar sized eastern chipmunk (*Tamias striatus*) with a home range size of 0.1 ha (Yerger 1953); thus the weasel is neither a typical small-bodied species nor a typical large-bodied species type. Second, we limited characterization of the small- and large-bodied species types to the three life history traits mentioned above. It is possible that other demographic and movement attributes may also affect species responses to roads (e.g. age at sexual maturity, age or sex differences in movement, density-dependent dispersal). However, even with the set of parameter combinations that we evaluated, several new working hypotheses emerged (above), representing generalized conditions of the circumstances which lead to neutral and positive road effects. As mentioned above, the model could be tailored in future to develop predictions for particular species population-level responses to road density.

This study represents the first to develop general hypotheses and predictions specifically of the circumstances leading to neutral and positive effects of roads on population abundance. Our results suggest that there are many situations where road mitigation may not be necessary (18 of 24 scenarios predicted neutral or positive effects of roads). Specifically, in landscapes containing high-traffic roads at relatively low densities, with habitat between the roads, priority for mitigating road effects should be directed towards the predators of small mammals and birds, rather than the small mammals and birds themselves. Although the small-bodied species were predicted to benefit from reduced predation, they were also

predicted to be largely unaffected by roads even in the absence of predation, suggesting again that mitigation for them is unnecessary. In contrast, for large-bodied prey species, if mitigation is directed towards their predators, increased predation may result in negative road effects on the large-bodied prey; therefore road mitigation should be directed towards all large species types. For large-bodied species that are mainly affected by roads through road mortality, mitigation should be mainly directed towards preventing animals from moving onto roads through complete fencing of the road and wildlife crossing structures in key movement areas. For birds, mitigating for road mortality would require installation of tall structures along roads that encourage or force birds to fly above the height of traffic. For the larger mammals that are disturbed by traffic, road effects can be mitigated by measures aimed at reducing road and traffic density in the landscape. In addition, engineering solutions to reducing traffic noise, e.g. changes to pavement or tires, could partially mitigate the disturbance effects. However, since many of the species that have been reported to avoid roads from a distance, have been reported to nevertheless cross roads in certain locations and thus potentially suffer from road mortality, providing complete fencing in combination with wildlife crossing structures in key movement areas would also be beneficial.

In conclusion, our results provide working hypotheses for future empirical work and road mitigation design, for the type of landscape we modelled i.e. continuous habitat crossed by high-traffic roads at densities equivalent to rural North American landscapes. Our simulations suggest that species with small territories and movement ranges and high reproductive rates are not negatively affected by roads in such landscapes. The results also suggest, contrary to previous suggestions, that populations of species that obtain resources from a road are not positively affected by increasing road density. In addition, our results support the predation release hypothesis for positive road effects on populations of both small-bodied and large-bodied prey species. Interestingly, the simulations predict an optimal road density for large-bodied prey species that avoid roads or traffic emissions and have predators that are negatively affected by roads. Therefore, unlike the effects of road mortality, the effects of habitat loss and subdivision due to roads are only evident at high road densities. Overall, the simulation results suggest that there are many species in many landscapes for which road mitigation may not be necessary; mitigation efforts should be tailored to the species, such as large predators, that show negative population-level responses to roads.

**Acknowledgments** We are grateful to L. Tischendorf for modelling assistance. We also thank the reviewers for their constructive

comments. This study was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) scholarship to T. R. and NSERC and Canada Foundation for Innovation grants to L. F.

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