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Ecological Modelling 185 (2005) 329–348
ECOLOGICAL MODELLING
www.elsevier.com/locate/ecolmodel

Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior

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Received 14 June 2004; received in revised form 14 December 2004; accepted 17 December 2004

Abstract

Roads and traffic affect animal populations detrimentally in four ways: they decrease habitat amount and quality, enhance mortality due to collisions with vehicles, prevent access to resources on the other side of the road, and subdivide animal populations into smaller and more vulnerable fractions. Roads will affect persistence of animal populations differently depending on (1) road avoidance behavior of the animals (i.e., noise avoidance, road surface avoidance, and car avoidance); (2) population sensitivity to the four road effects; (3) road size; and (4) traffic volume. We have created a model based on these population and road characteristics to study the questions: (1) what types of road avoidance behaviors make populations more vulnerable to roads?; (2) what types of roads have the greatest impact on population persistence?; and (3) how much does the impact of roads vary with the relative population sensitivity to the four road effects?

Our results suggest that, in general, the most vulnerable populations are those with high noise and high road surface avoidance, and secondly, those with high noise avoidance only. Conversely, the least vulnerable populations are those with high car avoidance only, and secondly, high road surface and high car avoidance. Populations with low overall road avoidance and those with high

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doi:10.1016/j.ecolmodel.2004.12.015

overall road avoidance tend to respond in opposite ways when the sensitivity to the four road effects is varied. The same is true of populations with high road surface avoidance when compared to those with high car and high noise avoidance. The model further predicted that traffic volume has a larger effect than road size on the impact of roads on population persistence. One potential application of our model (to run the model on the web or to download it go to www.glel.carleton.ca/ or www.nls.ethz.ch/roadmodel/index.htm or contact the first author) is to generate predictions for more structured field studies of road avoidance behavior and its influence on persistence of wildlife populations.

Keywords: Avoidance behavior; Barrier effect; Car avoidance; Habitat fragmentation; Habitat loss; Noise avoidance; Roads; Road avoidance; Road crossings; Road effects; Traffic; Traffic mortality

1. Introduction

Roads and other types of traffic lines are common occurrences everywhere humans have settled, and it is now becoming widely accepted that roads affect many aspects of ecosystems (Oxley et al., 1974; Institut für Naturschutz und Tierökologie, 1977; Ellenberg et al., 1981; Reck and Kaule, 1993; Glitzner et al., 1999; Trombulak and Frissell, 2000; Holzgang et al., 2000; Underhill and Angold, 2000; Carr et al., 2002; Spellerberg, 2002; Forman et al., 2003). For example, Forman (2000) estimates that the system of public roads affects ecologically about one-fifth of the United States land area. Based on results reported in the aforementioned literature, we infer that roads and their associated vehicular traffic affect persistence of wildlife populations in four main ways: (1) habitat loss; (2) traffic mortality; (3) resource inaccessibility; and (4) population subdivision (Fig. 1).

Habitat loss can be direct, where habitat is removed to build roads and their verges, or indirect, where habitat quality close to roads is reduced due to emissions from traffic (e.g., noise, light, pollutants). Reproduction is interrupted in areas of habitat destruction; furthermore, reproductive rates are likely reduced and mortality rates increased in lower quality habitat close to roads, leading to lowered chances of population persistence (Brody and Pelton, 1989; Reijnen and Foppen, 1994; Reijnen et al., 1995, 1996; Ortega and Capen, 1999; Forman et al., 2003, pp. 123–126).

Traffic mortality is due to collisions of individuals with vehicles on the road. If a significant proportion of a population is killed on roads, and this increased mortality is not compensated by higher birth rates, population persistence can be compromised (Fuller, 1989; Bangs et al., 1989; Andrews, 1990; Newton et al., 1991; van der Zee et al., 1992; Ferreras et al., 1992; Fahrig et al., 1995; Mumme et al., 2000; Hels and Buchwald, 2001; Gibbs and Shriver, 2002). In addition, traffic mortality contributes to population subdivision by reducing the flow of individuals between subpopulations separated by roads (Swihart and Slade, 1984; Reh and Seitz, 1990; Baker, 1998; Gerlach and Musolf, 2000; Keller and Largiadèr, 2003).

For some species, roads can act as barriers to movement and lead to resource inaccessibility. Individuals that do not cross roads cannot access resources such as food, mates, and breeding sites on the other side. Reduced access to such complementary or supplementary resources can lead to lower reproductive and survival rates, which in turn may reduce population persistence (Oxley et al., 1974; Mader, 1984; Mader et al., 1990; Dunning et al., 1992; Weidemann and Reich, 1995; Noss et al., 1996; Vos and Chardon, 1998; Clark et al., 2001). In addition, movement barriers contribute to population subdivision by reducing the flow of individuals between subpopulations separated by roads.

Population subdivision occurs when populations become separated into smaller, isolated subpopulations. As mentioned above, both traffic mortality and resource inaccessibility contribute to population subdivision. Populations living in habitat surrounded by roads are less likely to receive immigrants from other habitats, and thus may suffer from lack of genetic input and inbreeding. An increase in genetic defects may lower the probability of population persistence. Moreover, small populations are known to be particularly vulnerable to stochasticity: the smaller a population, the greater its chance of going extinct due to a random demographic, genetic, or environmental event (Wissel and Stöcker, 1991; Boyce, 1992; Remmert, 1994). Because chances of recolonization after extinction are reduced in isolated populations, extinct populations are unlikely to benefit from the rescue effect (Hanski, 1999).

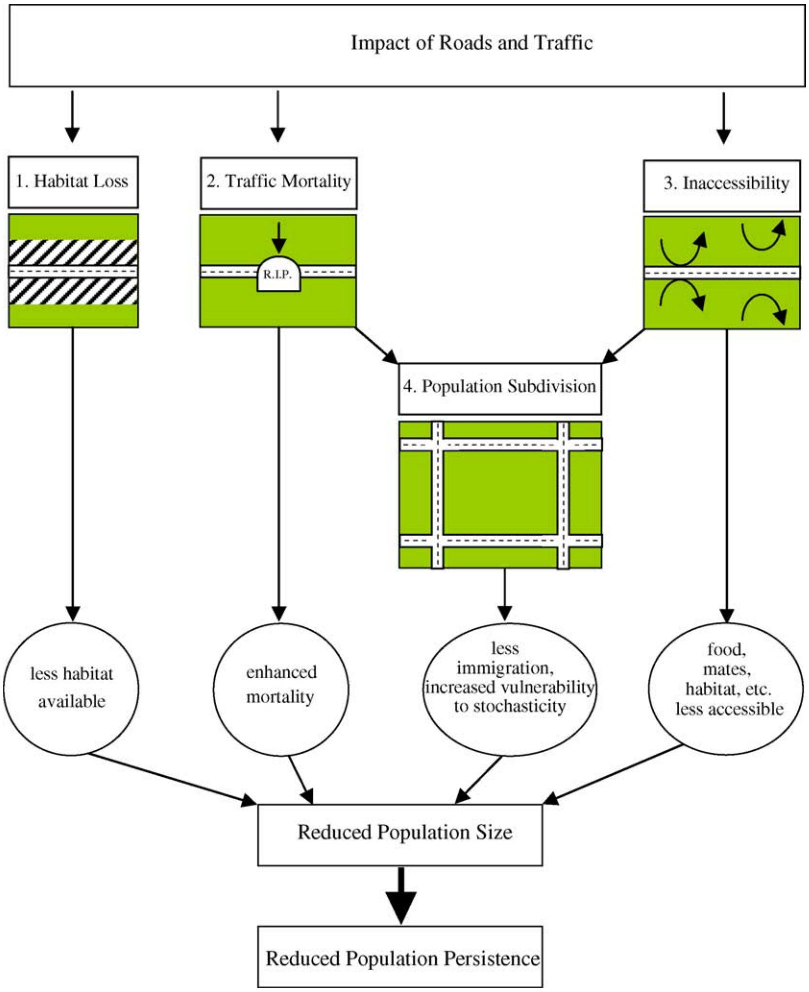

Fig. 1. Four ways roads and traffic are thought to impact persistence of wildlife populations. Both traffic mortality and inaccessibility contribute to population subdivision and isolation.

Roads will affect persistence of animal populations differently depending on (1) road avoidance behavior; (2) population sensitivity to the four aforementioned road effects; (3) size of the road; and (4) traffic volume. We have created a model to predict the impact of roads on population persistence based on these population and road characteristics (to run the model on the web or to download it go to www.glel.carleton.ca/ or www.nls.ethz.ch/roadmodel/index.htm or contact the first author). In this study, we use the model to address the following questions: (1) what types of road avoidance behaviors make populations more (or less) vulnerable to roads?; (2) for given types of roads and of road avoidance behavior, does the impact of roads vary with the relative population sensitivity to the four road effects?; (3) what types of roads have the greatest (or the least) impact on population persistence?

2. Methods

Very few quantitative data are available on the impact of roads on population persistence. Therefore, our approach in creating this model was to develop relative rankings that could be used to compare the impact of

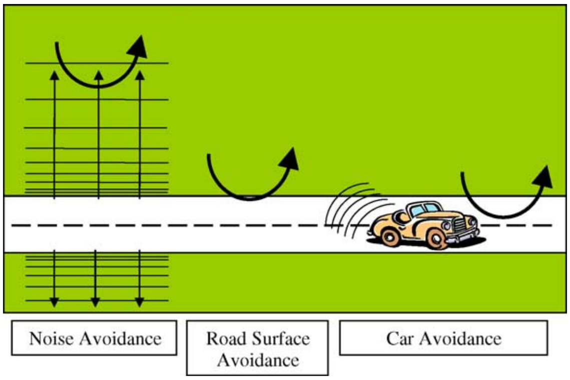

Fig. 2. Three components of road avoidance behavior. "*Noise avoidance*" is avoidance of the road from a long distance according to traffic emissions such as noise, light, or smell. "*Road surface avoidance*" is a short distance avoidance due to lack of cover and to the character of embankment and pavement which is different from natural habitat. "*Car avoidance*" includes perceiving single cars that are approaching the location where the animal wants to cross the road.

roads in various combinations of population and road characteristics.

2.1. Road avoidance behavior

The model considers three components of road avoidance behavior: (1) noise avoidance; (2) road surface avoidance; and (3) car avoidance (Fig. 2). Each component can be either low or high.

For our purposes, noise avoidance behavior is assumed to include avoidance of any long-ranging traffic emissions such as noise, light and pollutants. This component of road avoidance depends on traffic volume, but not on the size of the road. Animals with high noise avoidance will avoid crossing and will stay away from noisy roads, resulting in resource inaccessibility and habitat loss wherever noise from the road is audible. High noise avoidance spatially extends the road effect zone (Forman, 2000). For example, many bird species in The Netherlands exhibit noise avoidance behavior (Reijnen et al., 1995, 1996, 1997).

Road surface avoidance (abbreviated as "surface avoidance") is a short-range phenomenon because it occurs only at the physical border of the road, or on the road itself. It is a tendency to avoid going onto the road because of inhospitable conditions, e.g., lack of shelter, pavement, different microclimate conditions, changes in vegetation at the edge, etc. This component of road avoidance behavior depends on the size of the road, but not on traffic volume. Animals with high surface avoidance may approach the road, but will be hesitant to venture onto the road surface, contributing to resource inaccessibility and habitat loss in the area of the road itself. Examples of species that avoid the road surface are small mammals (Merriam et al., 1989; McGregor, 2004) and hedgehogs (*Erinaceus europaeus*; Reeve, 1994; Mulder, 1999).

Car avoidance is also a short-range phenomenon. This component of road avoidance behavior depends on traffic volume, but not on the size of the road. Animals with high car avoidance will avoid approaching or crossing roads when vehicles are passing by, decreasing traffic mortality, but increasing resource inaccessibility. This obviously corresponds to the way that humans behave when they want to cross a road. Wildlife biologists have reported that black bears (*Ursus americanus*) are able to learn how to successfully cross roads and avoid cars (R. Serrouya, personal communication). This behavior seems to be very similar to the behavior of humans but so far no systematic studies are available.

2.2. Sensitivity to the four road effects

Persistence of different populations will be affected differently by habitat loss, traffic mortality, resource inaccessibility and population subdivision. For example, populations that can compensate increasing mortality with increasing reproduction will be relatively insensitive to traffic mortality (e.g., roe deer [*Capreolus capreolus*], Pielowski and Bresinski, 1982; white-tailed deer [*Odocoileus virginianus*], Cheatum and Severinghaus, 1950). Populations that require different habitat types to complete their life history will be sensitive to resource inaccessibility (e.g., northern leopard frogs [*Rana pipiens*], Pope et al., 2000). Populations that naturally occur at low densities will be sensitive to population subdivision (e.g., Eurasian lynx [*Lynx lynx*], Kramer-Schadt et al., 2004; Florida panther [*Puma concolor coryi*], Meegan and Maehr, 2002). (For more details on which characteristics make a species or population vulnerable to specific road effects, see Table 5.3 in Forman et al. (2003), p. 121.) This variable sensitivity of populations is included in the model by applying weights to each road effect, where the sum of all weights is 100%. For example, to simulate a population of a species sensitive to all four road effects equally, a weight of 25% would be assigned to each effect. In the case of a species that is very sensitive to habitat loss, but only slightly affected by the other three effects, habitat loss could receive a weight of 85%, and traffic mortality, resource inaccessibility, and population subdivision could each receive a weight of 5%.

2.3. Size of the road

In our model, roads can either be small or large. A small road has one lane in each direction, whereas a large road has two or more lanes in each direction. We assume all roads are paved.

2.4. Traffic volume

Traffic volume can either be low or high. The model considers traffic volume independently of the size of the road, even though in reality large roads are more likely to have high traffic, and vice versa. However, large roads with low traffic and small roads with high traffic do exist, and therefore our model includes these possibilities. We assume that high traffic on a small road represents the same amount of traffic as high traffic on a large road.

2.5. Creating relative ranks

Our goal when creating the model was to compare the impact of roads on population persistence when the various species and road characteristics were varied. To build the model, we began by considering habitat loss, traffic mortality and resource inaccessibility separately (population subdivision will be discussed shortly). For each of these three road effects, we listed the 32 possible combinations of road avoidance behavior and road type. We then assigned points to each combination according to the magnitude of the expected road effect under this set of conditions (Tables 1–3). A high number of points represented a large negative impact of the road effect on population persistence. For example, the combination low noise avoidance, low surface avoidance, low car avoidance, small road, low traffic received one point for habitat loss, while the combination high noise avoidance, low surface avoidance, low car avoidance, large road, high traffic received five points (Table 1). The second set of conditions would result in higher habitat loss. The specific rules used for assigning points are described in Appendix A.

As discussed earlier, population subdivision is a result of both traffic mortality and barriers to movement. Therefore, points for this road effect (Table 4) were calculated from the points assigned to traffic mortality (Table 2) and resource inaccessibility (Table 3). See Appendix A for details.

The model calculates the impact of the road as a relative rank value. A high rank represents a large negative impact of the road on population persistence. The relative rank for a specific set of road avoidance and road type conditions is calculated by first multiplying the points for each road effect by the weight of that effect, and then adding up the weighted points of the four effects together. As the range of ranks in the tables differs for the different effects, the points for each road effect were rescaled (before multiplying them with the effect weights) to correct for the differences in range.

Table 1
Predicted relative effect (in ranks of increasing effect from 1 to 5) of reduced habitat amount caused by habitat loss on population persistence

	Low noise avoidance				High noise avoidance			
	Low road surface avoidance		High road surface avoidance		Low road surface avoidance		High road surface avoidance	
	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance
Small road/low traffic	1	1	1	1	3	3	3	3
Small road/high traffic	2	2	2	2	4	4	4	4
Large road/low traffic	2	2	2	2	4	4	4	4
Large road/high traffic	3	3	3	3	5	5	5	5

Table 2
Predicted relative effect (in ranks of increasing effect from 1 to 12) of enhanced mortality caused by collisions with traffic on population persistence

	Low noise avoidance				High noise avoidance			
	Low road surface avoidance		High road surface avoidance		Low road surface avoidance		High road surface avoidance	
	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance
Small road/low traffic	9	6	7	4	7	4	5	2
Small road/high traffic	12	9	10	7	10	7	8	5
Large road/low traffic	8	5	6	3	6	3	4	1
Large road/high traffic	11	8	9	6	9	6	7	4

Table 3
Predicted relative effect (in ranks of increasing effect from 1 to 10) of resource inaccessibility on population persistence

	Low noise avoidance				High noise avoidance			
	Low road surface avoidance		High road surface avoidance		Low road surface avoidance		High road surface avoidance	
	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance
Small road/low traffic	1	2	3	4	3	4	5	6
Small road/high traffic	4	5	6	7	6	7	8	9
Large road/low traffic	2	3	4	5	4	5	6	7
Large road/high traffic	5	6	7	8	7	8	9	10

The resulting sum of points was then converted into a rank between 1 and 10 in such a way that the smallest sums correspond with rank 1 and the largest sums with rank 10 (the intervals of points corresponding to each rank are of similar size). A rank system of 1–10 was chosen because a finer resolution (i.e., higher number of ranks) would not be reliable given that the input variables can assume only two values (low or high), and a lower number of ranks would not reveal some of the influences of input variables on population persistence.

2.6. Using the model

To answer our research questions, we ran the model 480 times and recorded the impact of the road (relative rank) for each iteration. Each run had different input parameters. We varied the road avoidance

Table 4
Predicted relative effect (in ranks of increasing effect from 1 to 12) on population persistence of higher demographic and environmental stochasticity and lack of immigrants caused by population subdivision

	Low noise avoidance				High noise avoidance			
	Low road surface avoidance		High road surface avoidance		Low road surface avoidance		High road surface avoidance	
	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance
Small road/low traffic	4	1	5	2	5	2	6	3
Small road/high traffic	10	7	11	8	11	8	12	9
Large road/low traffic	4	1	5	2	5	2	6	3
Large road/high traffic	10	7	11	8	11	8	12	9

behavior among the eight possible combinations, and the road characteristics among the four possible combinations. We varied the population sensitivity to the four road effects using 15 different combinations. In the first combination, all road effects had equal importance (25% each). In the next four combinations, three effects had weights of 31.67% and the remaining effect had a weight of 5%. In six combinations, two effects had weights of 45% and two had weights of 5%. In the last four combinations, one effect had a weight of 85% and the remaining three effects had weights of 5%.

For each road type separately, we calculated the median rank obtained for each type of road avoidance behavior across the range of population sensitivities to the four road effects. We also calculated the associated quartile deviation as a measure of rank dispersion about the median (Zar, 1999).

3. Results

Results of all 480 iterations are shown graphically in Appendix B, and a summary of the median rank values for each type of road avoidance behavior is presented in Table 5.

Our first objective was to identify behaviors that make populations more or less vulnerable to roads. Our model predicted that, in general, the most vulnerable populations are those with high noise and high surface avoidance, and secondly, those with high noise avoidance only (Fig. 3). Populations with these two behaviors consistently had the highest and second highest median ranks across all road types (Table 5). Conversely, the least vulnerable populations are those with high car avoidance, and secondly, high road surface and high car avoidance (Fig. 3). Populations with these two behavior types consistently had the lowest and second lowest median ranks across all road types (Table 5).

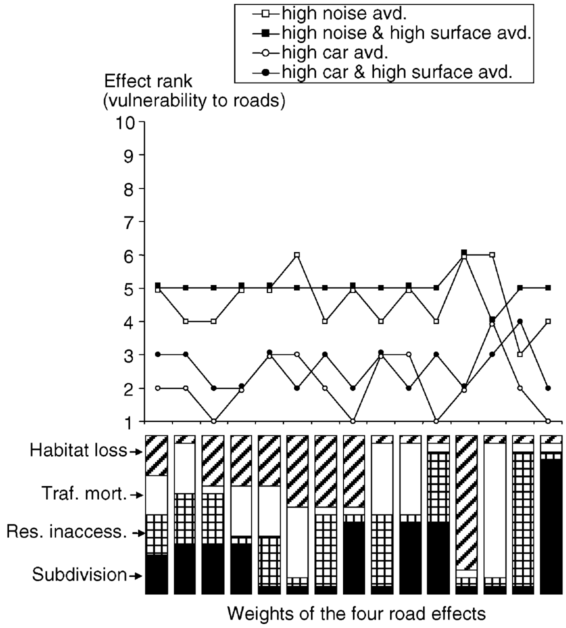

Fig. 3. Avoidance behaviors consistently resulting in more, or less, vulnerable populations: Two types of road avoidance behavior: (1) high noise avoidance only and (2) high noise and high surface avoidance, consistently result in populations more vulnerable to roads (higher relative effect ranks). Conversely, two types of road avoidance behaviors: (1) high car avoidance and (2) high car and high surface avoidance, consistently result in populations less vulnerable to roads (lower relative effect ranks). This graph shows a small road with low traffic as an example; the same pattern holds across all road types (see Appendix B). 1 is the lowest, 10 is the highest impact on populations.

Table 5
Median ranks produced by different avoidance behaviors across 15 combinations of the weights for the four main road effects (same as in Figs. 3–5)

	Low noise avoidance				High noise avoidance			
	Low road surface avoidance		High road surface avoidance		Low road surface avoidance		High road surface avoidance	
	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance
Small road/low traffic	3 (1)	2 (0.75)	3 (0.5)	3 (0.5)	5 (0.5)	4 (0.5)	5 (0)	4 (0.75)
Small road/high traffic	7 (0.75)	6 (0.5)	7 (1)	6 (0.5)	8 (0.5)	7 (0)	8 (0.5)	7 (0.5)
Large road/low traffic	4 (0.5)	3 (0.5)	4 (0)	3 (0.5)	5 (0.5)	4 (1)	6 (0.5)	4 (0.75)
Large road/high traffic	7 (0.5)	6 (0)	8 (0.5)	7 (0.5)	9 (0.5)	8 (0.5)	9 (0.75)	8 (1)

The quartile deviations (i.e., semi-interquartile range (Q3–Q1)/2) describe the dispersion of the ranks around the median rank.

Table 6
Examples of road avoidance behavior leading to high, medium, or low vulnerability to roads

Vulnerability to roads	Type of road avoidance behavior (specific conditions, if any)
High	High noise avoidance and high surface avoidance
	High noise avoidance
	High noise avoidance and high car avoidance (when high sensitivity to habitat loss)
	Low overall avoidance (when high sensitivity to traffic mortality)
	High overall avoidance (when high sensitivity to habitat loss and resource inaccessibility)
	High overall avoidance (when high sensitivity to resource inaccessibility)
Medium	High noise avoidance and high car avoidance (when sensitivity to all four road effects is equal)
	High road surface avoidance (when high sensitivity to habitat loss and population subdivision)
	High road surface avoidance (when low sensitivity to traffic mortality)
Low	High car avoidance
	High surface avoidance and high car avoidance
	High road surface avoidance (when high sensitivity to habitat loss)
	Low overall avoidance (when high sensitivity to resource inaccessibility)
	Low overall avoidance (when high sensitivity to habitat loss)
	Low overall avoidance (when high sensitivity to habitat loss and resource inaccessibility)
	High overall avoidance (when high sensitivity to traffic mortality)

When sensitivity to road effects is specified, the vulnerability rating is valid only under these conditions. The patterns are consistent across road types.

Fig. 3 shows this distinction between behaviors resulting in high and low vulnerability to roads. However, as will be discussed below, classification of road avoidance behavior types as “most vulnerable” or “least vulnerable” can depend on the sensitivity of the population to the four road effects. Table 6 lists examples of road avoidance behaviors resulting in high, medium and low vulnerability to roads. These patterns were consistent across road types.

Our second objective was to determine whether the impact of roads varied with population sensitivity to the four road effects, given a certain road type and avoidance behavior. The quartile deviations in Table 5 indicate how much the rank values varied as we varied the degree of sensitivity of the population to the four road effects. The quartile deviations vary with road type and avoidance behavior. For example, on a small road with low traffic, populations with high overall avoidance (i.e., of noise, surface, and cars) showed high variability in their responses to roads (quartile deviation = 0.75, Table 5). On the same type of road, populations with high noise and high surface avoidance showed very little variation in their responses to roads (quartile deviation = 0, Table 5). We detected no pattern in variability across road types, with the exception that populations with low overall avoidance (low noise avoidance + low surface avoidance + low car avoidance) or high overall avoidance generally show highly variable responses to roads as sensitivity values are changed. Therefore, it is very difficult to predict the impact of a road on such populations if their sensitivities to the four road effects are not known. Responses to roads for populations with low and high overall avoidance tended to show opposite trends as sensitivity values were varied (Fig. 4a). Similarly, populations with high surface avoidance tended to show opposite trends to species with high noise and high car avoidance (Fig. 4b). Finally, the variability in response to roads tended to increase as population sensitivity values were increasingly dominated by one road effect (Fig. 4a and b).

Our third objective was to identify road characteristics that make populations more or less vulnerable to roads. The model suggested that traffic volume has the greatest effect on the magnitude of the road impact. A small or large road with high traffic nearly always resulted in higher relative ranks than a small or large road with low traffic, across all behaviors and population sensitivity values. The size of the road also influences the response to the road; large roads nearly always resulted in higher relative ranks than small roads. However, the magnitude of this effect was much smaller than that of traffic volume (Fig. 5).

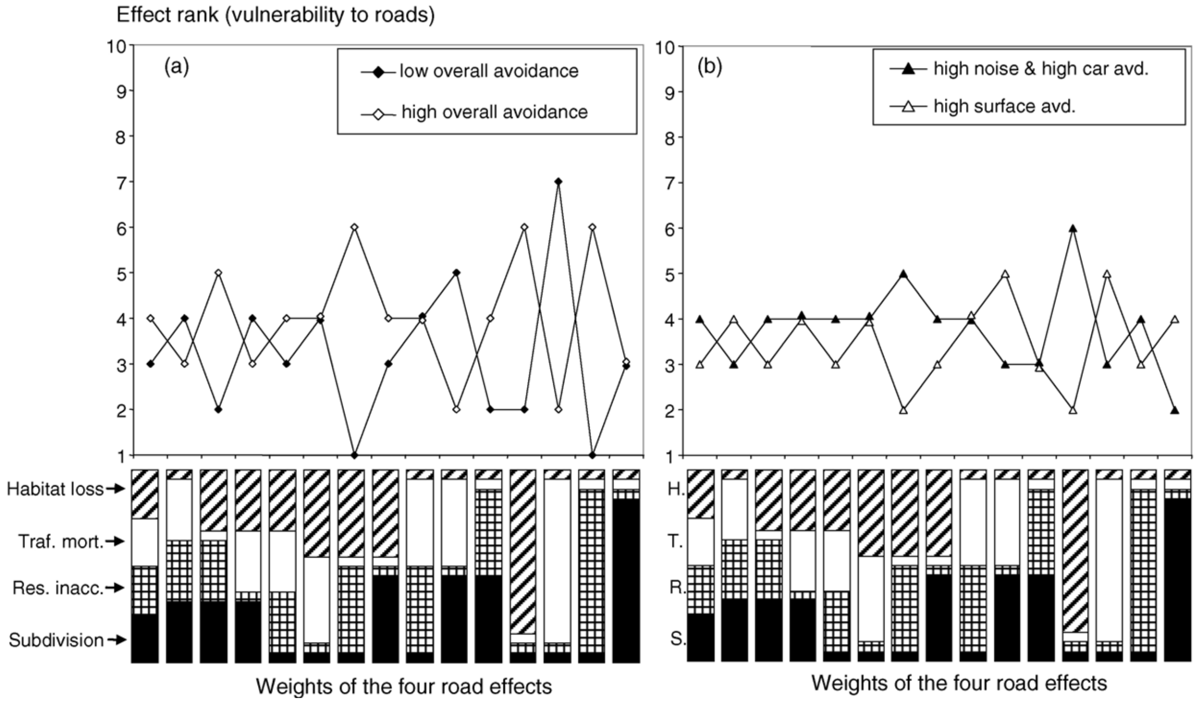

Fig. 4. Avoidance behaviors resulting in opposing trends of vulnerability: Two pairs of road avoidance behaviors: (a) low overall avoidance and high overall avoidance and (b) high surface avoidance and high noise and high car avoidance, show opposing trends as sensitivities of the four road effects are varied. Also notice the increasing variability of relative ranks when species become more and more sensitive to a single road effect. These graphs show a small road with low traffic as an example; the same patterns hold across all road types (see Appendix B). 1 is the lowest, 10 is the highest impact on populations.

4. Discussion

Our results suggest that populations with high noise and high surface avoidance, and populations with high noise avoidance only are most vulnerable to roads. We also predict that populations with high car avoidance, and populations with high surface and high car avoidance are least vulnerable to roads. These patterns are consistent across road types and most combinations of population sensitivity to the four road effects (Fig. 3). Therefore, our model suggests that it is possible to predict the impact of roads on these populations, even when information about the road characteristics or the sensitivity to the four road effects is not available. However, for populations exhibiting other types of avoidance behaviors, road avoidance behavior alone is not sufficient to predict the road impact; information about the sensitivities to the four road effects must be obtained. The model results also suggest that variability in response to roads tends to increase as populations become increasingly sensitive to a single road effect (Fig. 4a and b). For such populations, good information about avoidance behavior and the road characteristics are needed to predict the impact of roads.

Populations with low overall avoidance and those with high overall avoidance tend to respond in opposite ways when the importance of the four road effects is varied (Fig. 4a). The same is true of populations with high surface avoidance when compared to those with high car and high noise avoidance (Fig. 4b). This is because of the trade-off between avoiding a road and therefore limiting the problem of traffic mortality, and crossing the road and therefore limiting the problems of resource inaccessibility and population subdivision. For populations that are sensitive to traffic mortality, high overall avoidance or high noise and high car avoidance increase persistence by reducing traffic mortality. In contrast, for populations that are sensitive to

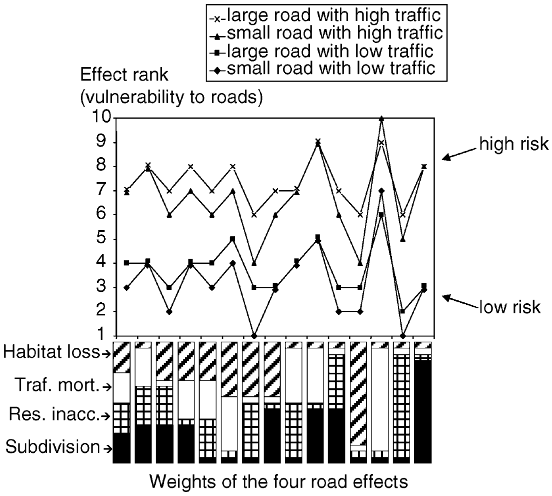

Fig. 5. Relative effect of road characteristics: roads with high traffic (small or large) have a greater impact on population persistence (higher relative ranks) than roads with low traffic. The relative ranks presented here are for low overall avoidance; the pattern is consistent across all types of road avoidance behavior. 1 is the lowest, 10 is the highest impact on populations.

resource inaccessibility and habitat subdivision, high overall avoidance or high noise and high car avoidance reduce persistence by exacerbating habitat inaccessibility and population subdivision.

The model predicts that traffic volume has a larger effect than road size on the impact of the road on population persistence (Fig. 5). This is mainly because road size alone (with no associated increase in traffic) does not affect traffic mortality. In addition, road size only affects resource inaccessibility and population subdivision for populations that avoid the road surface itself.

Various classifications have been proposed in the literature to distinguish different types of models (e.g., Verboom et al., 1993; Jørgensen and Bendoricchio, 2001; McIntosh, 2003; Seppelt, 2003). According to the terminology used by Jørgensen and Bendoricchio (2001), our model can be characterized as being deterministic (i.e., the response of the model is completely determined by a knowledge of the inputs), static (not dependent on time), causal, or mechanistic (i.e., the inputs, the states and the outputs are interrelated by using causal relationships) and fuzzy (i.e., observations are indicated as ranges or classes, e.g., high, medium and low). Our model can also be called a conceptual model (Jørgensen and Bendoricchio, 2001, p. 211ff; Wissel, 1989) in the sense that it focuses on the most important components and connections that are relevant for a certain research question but does not consider species-specific or site-specific details that would be included in a more complex simulation model. A conceptual model may serve as a first stage in developing more detailed models if more details are required to be included depending on the purposes of the models. May (1973) called this type of conceptual model 'strategic' in the sense of being general, simple and parameter sparse and leading to general insight, as opposed to 'tactical' models which are specific, complex, detailed and have many parameters (Verboom et al., 1993).

The situation that expert knowledge is characterised as being incomplete, sparse and non-formalised is rather common in ecology. Qualitative reasoning leading to qualitative (not quantitative), or fuzzy, models is applied in data-poor situations to capture such knowledge provided by experts (McIntosh, 2003; Salles et al., 2003; Adriaenssens et al., 2004). In this sense, our model can be regarded as being a rule-based expert system (Puppe, 1993; Metternicht, 2001). The input to the model is based mainly on "expert opinion" which is different from an empirically-based model. To a certain degree our model is similar, for example, to the expert system TESTEX which helps choose statistical tests (White, 1995). The main part of this system is a test selection procedure, which operates by asking the user questions about the data and the experimental design and builds up a picture of the problem until it is able to advise the use of a particular statistical procedure. The system was intended for use by medical and dental postgraduates and academic staff who could be assumed to have some knowledge of the application of statistics within their medical discipline without being very sure about exactly how to go about selecting the appropriate tests. However, our model differs from White's model in that it does not include a decision tree but combines the four impacts of roads according to a set of causal rules to predict the risk that roads pose to animal populations (a second difference is that White's model was not developed under the condition of incomplete knowledge). With respect to this logical structure, our model is a new model. We used *Science Direct* and *ISI Web of Science* to search for similar models but did not find any structurally similar model.

The most important feature of our model is the use of rules that represent the causal relationships between the various road avoidance behaviors and road effects. The purpose of our modelling exercise was to create a series of hypotheses. The hypotheses we have proposed based on the model results still need to be tested. We suggest that models similar to ours are very useful to capture and handle expert knowledge in order to develop hypotheses in data-poor situations and for qualitative impact assessments (Verboom et al., 1993; Metternicht, 2001; Adriaenssens et al., 2004). We see a huge potential for this type of model to be applied more often in ecology and environmental science.

5. Conclusion and speculation

Studies on road avoidance behavior are scarce. Some studies document a reduction in density of species in habitat near roads (Thiel, 1985; Mech et al., 1988; McLellan and Shackleton, 1988; Belden and Hagedorn, 1993; Mace et al., 1996; Mladenoff et al., 1999; Robitaille and Aubry, 2000; Nellemann et al., 2003). Such information is ambiguous because the reduced density can either be a result of avoidance behavior or a reduction in population size due to traffic mortality (Fahrig et al., 1995). Many bird species of The Netherlands show evidence of noise avoidance (Reijnen et al., 1995, 1996, 1997). Caribou in northern Alberta (*Rangifer tarandus*) have been shown to avoid habitat up to 250 m on either side of roads (Dyer et al., 2001). In contrast, caribou in Alaska do not seem to reduce their use of habitat in proximity to roads (Cronin et al., 1998; Yost and Wright, 2001), probably due to lower traffic volume. Therefore, the avoidance observed in northern Alberta is likely related to traffic noise, not road surface avoidance. According to a study by Whittington et al. (2004), wolves crossed all roads, trails, and a railway line about 10% less often than expected, but avoided crossing high-use roads more than low-use trails. Wolf path tortuosity increased near high-use trails and within areas of high-trail and road density. The results suggest that although roads and trails in this study were not absolute barriers to wolf movement, they altered wolf movements across their territories. However, wolves equally avoided trails and roads even though roads received well over 100 times the daily traffic of trails and presented wolves with a risk of mortality. Wolves, therefore, appeared to either not recognize, or have difficulty learning about, the danger posed by vehicles. In a similar study, Papouchis et al. (2001) found that bighorn sheep in Utah fled at least three times more often from hikers than from vehicles. Whittington et al. (2004) concluded that wildlife disproportionately avoid humans for three reasons. First, hikers are less predictable than vehicles and often directly approach animals. Second, vehicles appear relatively static compared to the body motions associated with animal and human movement. Consequently, it may be difficult for animals to gauge the speed of vehicles. Third, vehicles do not have organic scent and may, therefore, not deter animals as strongly as people. Merriam et al. (1989) found that the white-footed mouse (*Peromyscus leucopus*) avoids crossing roads, independently of traffic volume, indicating that they avoid the surface of the road itself. Flying squirrels (*Glaucomys volans*) also show evidence of road avoidance behavior that is related to road size; they do not cross very wide roads, probably because they cannot glide far enough to reach the other side (Bednarczuk et al., submitted for publication). Hedgehogs (*Erinaceus europaeus*) have been shown to avoid crossing roads, with avoidance increasing in proportion to road width (Rondinini and Doncaster, 2002). Results by Reeve (1994) and Mulder (1999) suggest that reluctance of hedgehogs to cross roads may reflect an aversion to the synthetic surface of the road, i.e., road surface avoidance. Falk et al. (1978) argue that mortality of white-tailed deer (*Odocoileus virginianus*) was high when highways were first opened to public use but later, when traffic volume increased drastically, deer “no longer presented a significant hazard”, because “traffic itself, when continuously heavy, prevented deer from venturing onto highways”. This tentative observation could be explained by either noise avoidance or car avoidance if deer, even though they may not be very successful in avoiding single cars, avoid continuous flows of vehicles.

The model does not include the effect of increased human access to a species’ habitat due to roads because these effects do not depend on the road avoidance behavior of the animals and the road characteristics. Examples of species in North America that are affected by increased road access, leading to overharvest are elk (*Cervus elaphus*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*); to overtrapping are wolverine (*Gulo gulo*), lynx (*Felis lynx*), fisher (*Martes pennanti*), and marten (*Martes americana*); to poaching are grizzly bear (*Ursus arctos*), wolf (*Canis lupus*), woodland caribou (*Rangifer tarandus caribou*); and to increased collection for pet merchants include most reptile species (Bailey et al., 1986; Knight et al., 1988; Horejsi, 1989; Leptich and Zager, 1991; Unsworth et al., 1993; Hodgman et al., 1994; Hayes et al., 2002). For these species, this effect could be accounted for in using the model by giving traffic mortality a higher relative weight, i.e., high sensitivity of the species to additional mortality due to collisions with traffic. This effect can be reduced only when humans refrain from hunting these species.

In addition to direct habitat loss and habitat loss due to traffic emissions, habitat loss may also be caused by the road allowing establishment of invasive plants, distributing livestock that may cause habitat loss from overgrazing, and increasing frequency of man-made fires (Lonsdale and Lane, 1994; Milberg and Lamont, 1995; Angold, 1997; Gelbard and Belnap, 2003; Gelbard and Harrison, 2003). These effects could be accounted for in using the model by giving habitat loss a higher relative weight, i.e., high sensitivity of the species to additional habitat loss.

The spatial extent of model application needs to be matched well with the spatial extent of the species' population. Application of the model over millions of hectares may dilute local effects of roads on small species with restricted movements. By contrast, application of the model over only a few hectares would be misleading for wide-ranging species whose persistence depends on cumulative management of road effects over expansive areas. Therefore, wider-ranging animals require analysis over larger areas, whereas species with more limited movement ranges require modeling applications over smaller spatial extents.

One potential application of our model is to generate predictions for more structured field studies of road avoidance behavior and its influence on persistence of wildlife populations. For example, Table 7 shows types of avoidance behaviors predicted to result in high or low vulnerability to roads for species very sensitive to only one road effect. The following predictions can be made:

1. A population very sensitive to habitat loss will be most vulnerable to roads if the individuals tend to avoid noise.
2. A population very sensitive to traffic mortality (or any form of additional mortality) will be most vulnerable to roads if individuals do not avoid crossing roads.
3. A population very sensitive to resource inaccessibility will be most vulnerable to roads if both noise and surface avoidance are high.
4. A population very sensitive to population subdivision will be most vulnerable to roads if car avoidance is low and either noise or surface avoidance are high.

These predictions can be tested in the field. For instance, one could compare two populations known to be very sensitive to habitat loss, using one population that shows noise avoidance and another that does not. Our model predicts that the noise avoiders should see their persistence reduced by roads (prediction 1 above).

Table 7
Types of avoidance behaviors predicted to result in high or low vulnerability to roads for species very sensitive to only one road effect (listed in the very left column)

	Low noise avoidance				High noise avoidance			
	Low road surface avoidance		High road surface avoidance		Low road surface avoidance		High road surface avoidance	
	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance	Low car avoidance	High car avoidance
Habitat loss	○	○	○	○	●	●	●	●
Traffic mortality	●			○		○		○
Resource inaccessibility	○	○					●	●
Population subdivision		○	●		●		●	

High vulnerability (●); low vulnerability (○).

This model could also be used to formulate other types of predictions to be tested in the field, or to predict the impact of roads under a particular set of conditions, e.g., managers of wildlife populations can download the model and put their own susceptibility values in (Appendix C; to run the model on the web or to download it go to www.glel.carleton.ca/ or www.nls.ethz.ch/roadmodel/index.htm or contact the first author).

Our model results indicate that the type of road avoidance behavior may be of major importance for understanding the effects of roads on animal populations and for identifying groups of species that are particularly vulnerable to roads. Therefore, we want to stimulate empirical studies on the road avoidance behavior of species and to encourage the use of the model to create more systematic hypotheses.

Acknowledgments

We thank Jason Nicolaides and Sarah Brown for assistance with preparing the model and the members of the Geomatics and Landscape Ecology Laboratory (GLEL) at Carleton University, Ottawa, for stimulating discussions about road effects. This work was supported through a postdoctoral scholarship from the German Academy of Natural Scientists Leopoldina to J.A.G.J. (grant number BMBF-LPD 9901/8-27) and through a Natural Sciences and Engineering Research Council of Canada grant to L.F.

Appendix A. Rules for assigning points to get relative ranks and for combining the four tables

For each of the four road effects, we listed the 32 possible combinations of road avoidance behavior and road type. A high number of points represent a large negative impact of the road on population persistence. The rules for assigning points for the three effects habitat loss, traffic mortality, and resource inaccessibility are created separately (Tables 1–3), and the points for population subdivision (Table 4) were calculated from the points assigned to traffic mortality (Table 2) and resource inaccessibility (Table 3) as population subdivision is a result of both traffic mortality and resource inaccessibility.

A.1. Habitat loss

We start with the situation where the road has the lowest impact (rank 1) and add points to get the rankings. We assume the effects of the various factors are additive.

A.1.1. Road size

Building large roads removes more habitat than building small roads due to wider embankments, broader trenches, and larger radii of the curves (large road: +1 over small roads). This is valid for both low and high noise avoidance as noise avoidance leads to a reduction of the density of the individuals whereas building a road removes the habitat entirely (see below).

A.1.2. Traffic amount

Habitat loss depends on traffic amount only via the behavior of the animals (see below) but not on traffic volume per se (+0).

A.1.3. Road surface avoidance

Road surface avoidance does not change the amount of habitat lost (+0).

A.1.4. Car avoidance

The avoidance of cars does not reduce or enhance habitat loss (+0).

A.1.5. Noise avoidance

Noise avoidance results in an additional loss of habitat because the animals have reduced densities in the road noise zone. Therefore, noise avoidance adds a band of less hospitable area on either side of the road. The effect of noise avoidance strongly depends on the amount of traffic but not on the size of the road. High noise avoidance (at low traffic) has a bigger effect than high traffic (at low noise avoidance) when the animal chooses its habitat: We assume that a species avoiding noise would not live in a place with even a little traffic whereas of a species that only slightly avoids noise a higher proportion of the animals would breed at a similar distance from the road (low noise avoidance: +1 for high traffic over low traffic; high noise avoidance: +2 over low noise avoidance in case of low traffic and +3 in case of high traffic).

We start with the situation that has the lowest level of habitat loss giving it a rank of 1. This is the situation of a small road with low traffic and low noise avoidance (car avoidance and road surface avoidance do not have an influence here).

A.2. Traffic mortality

Here, we start with the situation of highest impact state (because it is easier to identify than the situation with the least impact) and subtract points to get the rankings. As before, we assume the effects of the various factors are additive. In addition, we assume that the effect of any of the three avoidance behaviors has the same strength on the reduction of road mortality. Therefore, we keep the average and the range of the points the same for each avoidance behavior.

The highest impact is for a small road with high traffic at low avoidance (low noise avoidance, low road surface avoidance, low car avoidance). It is lower for a large road because for a large road as opposed to a small road, the low road surface avoidance already leads to a reduction of traffic mortality (see below).

A.2.1. Road size

If traffic amount is the same then the probability of a collision is assumed to be the same for small and large roads. Mortality depends on road size only via the behavior of the animals (see below) but not on road size per se (+0).

A.2.2. Traffic amount

The probability of a collision with a vehicle is significantly lower on a road with low traffic than on a road with high traffic, i.e., the animal will be able to successfully cross the road more often (low traffic: −4).

A.2.3. Road surface avoidance

Low road surface avoidance means that the animal undertakes fewer attempts to cross the road, compared to no road surface avoidance. This will slightly reduce traffic collisions. This effect is stronger for large roads. High road surface avoidance means even fewer attempts to cross the road. At some point there would be no crossings any more and, therefore, no collisions. We assume that road surface avoidance is stronger for large roads because they represent a greater expanse of inhospitable cover type (low road surface avoidance: −1 for large roads over small roads; high road surface avoidance: −2 over low road surface avoidance in case of a small road and −3 in case of a large road).

A.2.4. Car avoidance

Low car avoidance leads to fewer attempts to cross the road and reduces traffic collisions. It does not significantly depend on traffic amount as the animal avoids cars in both situations (‘low traffic’ and ‘high traffic’) in a similar manner (+0). High car avoidance leads to even fewer attempts to cross the road. If there is very dense traffic the animal will not try to cross the road at all. This results in no road mortality. So, the reduction in potential mortality is great in both cases, on high traffic roads because there are no crossing attempts at all and on low traffic roads because the animals will always find a sufficiently large break in the traffic to cross the road safely (high car avoidance: −3 over low car avoidance for low traffic as well as for high traffic).

A.2.5. Noise avoidance

The effect of noise avoidance depends on traffic volume, i.e., noise avoidance leads to a higher reduction of mortality on roads with high traffic. The effect of noise avoidance is independent of road size. The proportion of animals that do not try to cross the road is assumed to be higher for high noise avoidance at low traffic (because these animals stay farther away) than it is for low noise avoidance at high traffic (low noise avoidance: +1 for low traffic as opposed to high traffic; high noise avoidance: −2 over low noise avoidance in case of high traffic and −1 in case of low traffic).

The rank of the highest impact situation is set to 12 for a small road with high traffic, indicating a high probability of road mortality. The number of 12 was chosen because it results in a value of 1 for the conditions under which road mortality is expected to be lowest.

A.3. Resource inaccessibility

The lowest effect of resource inaccessibility is expected for a small road with low traffic when all three types of avoidance behavior are low. There we start with a rank of 1 and add points to get the rankings.

A.3.1. Size of the road and traffic amount

The effect of resource inaccessibility depends on road size and traffic amount only via the behavior of the animals (see below) but not on road size and traffic amount per se. Without avoidance behavior the animals would always try to cross the road (+0).

A.3.2. Road surface avoidance

Large roads will be avoided more than small roads. Therefore, the fence effect is higher for large roads. High road surface avoidance at small roads has a bigger fence effect than low road surface avoidance at large roads. The difference between high and low road surface avoidance is bigger than the difference between a small and a large road (low road surface avoidance: +1 for large road over small road; high road surface avoidance: +3 over low road surface avoidance in case of a large road and +2 in case of a small road).

A.3.3. Car avoidance

If the individuals do not try to cross the road when there are vehicles on the road they will not be killed but they cannot contribute to the exchange of individuals, either. This effect does not depend on the size of the road but it strongly depends on the amount of traffic. High car avoidance at low traffic leads to a similar degree of retaining from crossing as low car avoidance in a high traffic situation. At low traffic the individual can cross, at high traffic it will not be able to cross, i.e., the effect is bigger for high traffic at low car avoidance than for low traffic at high car avoidance (low car avoidance: +2 for high traffic over low traffic; high car avoidance: +3 over low car avoidance in case of high traffic and +1 in case of low traffic).

A.3.4. Noise avoidance

The animals do not go close to the road which reduces the number of crossing attempts. This effect does not depend on the degree of road surface avoidance. As in Table 3 (for road mortality), we assume that the proportion of animals that do not try to cross the road is higher for high noise avoidance at low traffic than it is for low noise avoidance at high traffic (low noise avoidance: +1 for high traffic over low traffic; high noise avoidance: +3 over low noise avoidance in case of high traffic and +2 in case of low traffic).

Note that we again have used the same averages and ranges of the points for all three avoidance behaviors which implies that all three can have the same strength of effect.

A.4. Population subdivision

The reduction of the number of successful crossings is a consequence of reducing both the number of animals killed by collisions with traffic and the number of animals that do not venture onto the road (Fig. 1). Therefore, points for this road effect (Table 4) were calculated from the points assigned to traffic mortality (Table 2) and resource inaccessibility (Table 3).

Before the tables can be added they have to have equal weights. Therefore, the two tables are rewritten in ranks from 1 to 60 because 60 is the smallest common multiple of 12 (Table 2) and 10 (Table 3). Therefore, the points in Table 2 are multiplied by 5 and the points in Table 3 by 6. Then the points of the two tables were added and then rearranged into ranks by combining short series of points that were close together to be in the same rank and by giving those points that were separated by gaps different ranks. This procedure resulted in ranks between 1 and 12 (Table 4).

A.5. Combining the four tables

The relative rank for a specific set of road avoidance and road type conditions is calculated by first multiplying the points for each road effect by the weight of that effect, and then adding up the weighted points of the four effects together. As the range of ranks in the tables differs for the different effects, the points for each road effect were rescaled to correct for the difference in range before they were multiplied by the weights. The ranks for habitat loss were rescaled from a range of 1 to 5 into a range of 2 to 12, and for resource inaccessibility from a range of 1 to 10 to a range of 1 to 12. The resulting sum of points was converted into a rank between 1 and 10 by multiplying by 0.9 and rounding to integer numbers. The smallest sums then correspond with rank 1 and the largest sums with rank 10 while the intervals of points corresponding to each rank are of similar size. Therefore, using the model while assigning a weight of 100% to one road effect and 0% to the other three will result in the ranks between 1 and 10 based on the values given in Tables 1–4, but rescaled, multiplied by 0.9 and rounded. For example, when habitat loss has a weight of 100%, the result for low noise avoidance, low sur-

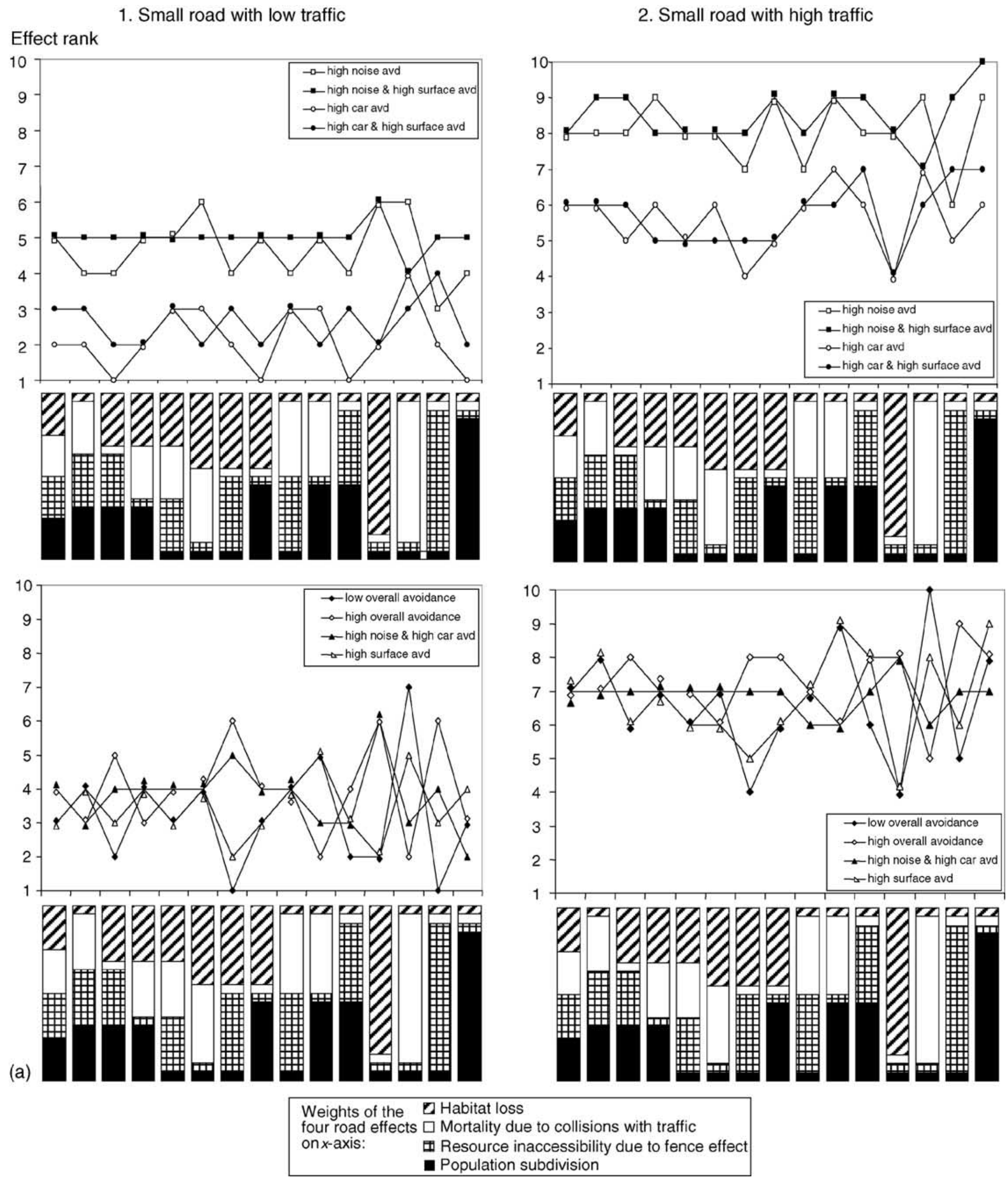

Fig. 6. (a) Full results for small road: predicted overall effect severity (effect ranks) for the eight types of avoidance behaviors of the animals for low and high traffic on a small road. The weights of the four road effects are varied from 25% each to 5% for one effect and equal weights for the other three, to 5% for two effects and 45% for each of the other two, and to 85% for one effect and 5% for each of the other three. 1 is the lowest, 10 is the highest impact on populations (to Appendix B). (b) Full results for large road: predicted overall effect severity (effect ranks) for the eight types of avoidance behaviors of the animals for low and high traffic on a large road. The weights of the four road effects are varied from 25% each to 5% for one effect and equal weights for the other three, to 5% for two effects and 45% for each of the other two, and to 85% for one effect and 5% for each of the other three. 1 is the lowest, 10 is the highest impact on populations (to Appendix B).

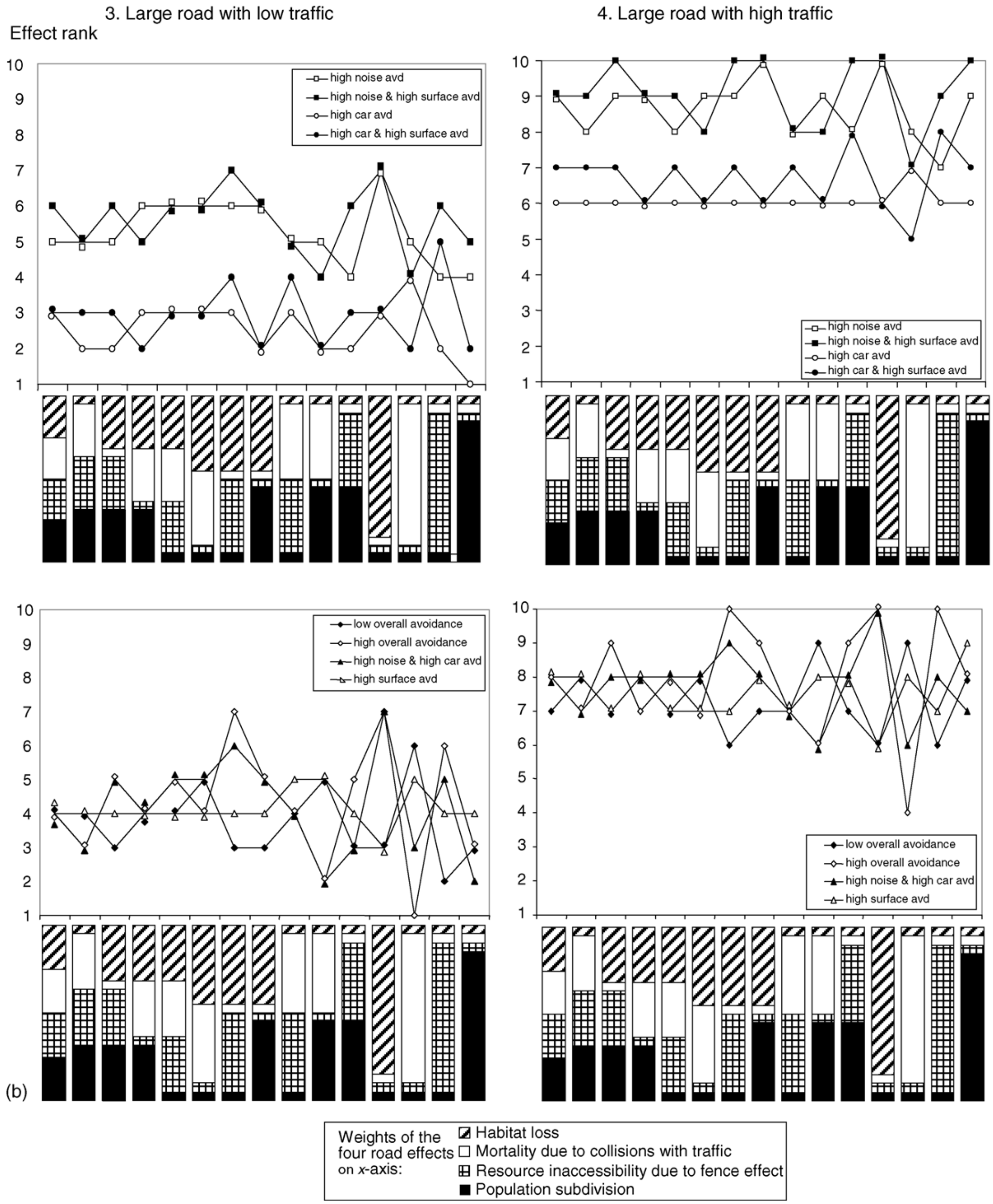

Fig. 6. (*Continued*).

face avoidance, and low car avoidance at a small road with low traffic volume is an effect rank of 1; while it is 10 for high noise avoidance, high surface avoidance, and high car avoidance at a large road with high traffic volume.

Appendix B. Full results

Fig. 6 shows the effect ranks for all combinations of road type and animal behavior using 15 different combinations for the weights of the four road effects. Selections of these are shown in Figs. 3–5 in the main body of the paper. For all types of roads, two types of road avoidance behavior: (1) high noise avoidance only and (2) high noise and high surface avoidance, consistently result in populations more vulnerable to roads (higher relative ranks), and two types of road avoidance behavior: (1) high car avoidance and (2) high car and high surface avoidance, consistently result in populations less vulnerable to roads (lower relative ranks; upper row of diagrams). In addition, two pairs of road avoidance behaviors: (1) low overall avoidance and high overall avoidance and (2) high surface avoidance and high noise and high car avoidance, consistently show opposing trends as sensitivities of the four road effects are varied (lower row of diagrams). Also notice the increasing variability of relative ranks when species become more and more sensitive to a single road effect. Roads with high traffic (small or large; second and fourth column of diagrams) have a greater impact on population persistence (higher relative ranks) than roads with low traffic (first and third column of diagrams).

Appendix C. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2004.12.015.

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