

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Do species life history traits explain population responses to roads? A meta-analysis

Trina Rytwinski*, Lenore Fahrig

Geomatics and Landscape Ecology Laboratory (GLEL), Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6

ARTICLE INFO

Article history:

Received 13 September 2011
 Received in revised form 15 November 2011
 Accepted 25 November 2011
 Available online 24 January 2012

Keywords:

Landscape fragmentation
 Life history traits
 Population abundance
 Road mitigation
 Meta-analysis
 Road mortality

ABSTRACT

Efforts to mitigate road effects are now common in new highway construction projects. For effective mitigation of road effects it is important to identify the species whose populations are reduced by roads, so that mitigation efforts can be tailored to those species. We conducted a meta-analysis using data from 75 studies that quantified the relationship between roads and/or traffic and population abundance of at least one species to determine species life history characteristics and behavioral responses to roads and/or traffic that make species or species groups prone to negative road and/or traffic effects. We found that larger mammal species with lower reproductive rates, and greater mobilities, were more susceptible to negative road effects. In addition, more mobile birds were more susceptible to negative road and/or traffic effects than less mobile birds. Amphibians and reptiles were generally vulnerable to negative road effects, and anurans (frogs and toads) with lower reproductive rates, smaller body sizes, and younger ages at sexual maturity were more negatively affected by roads and/or traffic. Species that either do not avoid roads or are disturbed by traffic were more vulnerable to negative population-level effects of roads than species that avoid roads and are not disturbed by traffic. In general, our results imply that priority for mitigation should be directed towards wide-ranging large mammals with low reproductive rates, birds with larger territories, all amphibians and reptiles, and species that do not avoid roads or are disturbed by traffic.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Roads and traffic reduce populations of a wide variety of species (Fahrig and Rytwinski, 2009; Benítez-López et al., 2010), and efforts to mitigate road effects are now common in new highway construction projects (Beckmann and Hilty, 2010). To ensure effectiveness of such mitigation it is important to identify the species or species groups whose populations are most likely to be reduced by roads, so that mitigation efforts can be tailored to those species.

Several hypotheses have been suggested for the types of species whose populations should be most negatively affected by roads (summarized in Fig. 2 in Fahrig and Rytwinski, 2009). These hypotheses fall into two main sets: (i) hypotheses based on species life history traits and (ii) hypotheses based on species behavioral responses to roads and traffic. The first set of hypotheses argues that highly mobile species should be more negatively affected because they interact with roads more often than do less-mobile species (Carr and Fahrig, 2001; Gibbs and Shriver, 2002; Forman et al., 2003; Rytwinski and Fahrig, 2011). Similarly, species with larger territories or home ranges should be more susceptible to road effects than those with smaller territories or home ranges. Species with lower reproductive rates, later sexual maturity, and

longer generation times, should also be more susceptible to road effects because they will be less able to rebound quickly from population declines (Gibbs and Shriver, 2002; Rytwinski and Fahrig, 2011). Since species with large home ranges and low reproductive rates naturally occur at low densities, we also expect that species that naturally occur at low densities should be more susceptible to road effects than those that occur at high densities. Taken together, these hypotheses also suggest that, in general, larger species should be more negatively affected by roads than smaller species because larger species generally occur naturally at lower densities, have lower reproductive rates, longer generation times, and are more mobile than smaller species (Gibbs and Shriver, 2002; Forman et al., 2003). Interestingly, since larger species are often predators on smaller species, it is also possible that negative effects of roads on populations of large animals could lead to reduced predation on small animals in areas of high road density. This could indirectly reduce the impact of roads on animals. In fact, release from predation has been suggested as a possible cause for the frequently observed positive effects of roads on small mammal populations (Johnson and Collinge, 2004; Rytwinski and Fahrig, 2007; Bissonette and Rosa, 2009; Fahrig and Rytwinski, 2009).

The second set of hypotheses suggests that species behavioral responses to roads and traffic moderate the population-level effects of roads. Jaeger et al. (2005) discussed three avoidance responses to roads and traffic: (i) avoidance of the road surface,

* Corresponding author. Tel.: +1 613 425 0583; fax: +1 613 520 3539.
 E-mail address: trytwinski@hotmail.com (T. Rytwinski).

(ii) avoidance of traffic disturbance (noise, lights, chemical emissions), and (iii) vehicle avoidance (the ability to move out of the path of an oncoming vehicle). All of these avoidance behaviors should make species populations less susceptible to traffic mortality. However, on the negative side, road and traffic avoidance may cause populations to become fragmented into smaller, partially isolated local populations that are more vulnerable to extinction. This should be particularly the case for species that avoid the road surface itself because the road will remain a barrier to movement even when there is no traffic on it. Species that avoid roads at a distance due to traffic disturbance will suffer an additional loss of habitat (beyond the road itself) since the habitat near the road becomes unusable or of lower quality because of the traffic disturbance. On the other hand, species that are able to avoid oncoming vehicles should have low road mortality and should be able to cross the road when traffic volumes are not too high. Populations of these species should be less negatively affected by roads than populations of species in the other two avoidance categories. A fourth possible behavioral response to roads is road attraction. Some species for example, may be attracted to a road for a resource such as food (road-killed animals) (e.g. some birds: Haug, 1985; Watson, 1986; Knight and Kawashima, 1993; Meunier et al., 2000; Lambertucci et al., 2009), nesting sites (e.g. some turtles: Haxton, 2000; Aresco, 2005a; Steen et al., 2006) or to thermoregulate (e.g. some snakes: Sullivan, 1981; Rosen and Lowe, 1994). Species that are attracted to roads or that move onto roads irrespective of traffic should be strongly susceptible to road mortality (Forman et al., 2003) unless they are also able to avoid oncoming vehicles (vehicle avoidance).

The purpose of this study was to conduct a meta-analysis to test the following predictions arising from the hypotheses above: (1) the effects of roads and/or traffic on animal population abundance should be increasingly negative with (i) decreasing reproductive rate and/or age at sexual maturity, (ii) increasing mobility, and (iii) increasing body size; (2) species that are attracted to roads and have vehicle avoidance should be least negatively affected by roads, while the effect of roads should increase from (i) species with vehicle avoidance to (ii) species with road surface avoidance (suffering habitat fragmentation) to (iii) species with traffic disturbance avoidance (suffering habitat loss) to (iv) species with no road or traffic disturbance avoidance (suffering road mortality) to (v) species that are attracted to roads and have no vehicle avoidance (suffering high road mortality).

2. Materials and methods

2.1. Search and selection of studies for meta-analysis

We conducted a thorough literature search to find all relevant studies that quantify the relationship between roads and/or traffic and population abundance of at least one species. Here we use a broad definition of “population abundance” to include population size (or relative size), population density (or relative density), and species presence or absence (as an index of high vs. low abundance). Only studies based on quantitative data were included. We limited our analyses to include only animals that are terrestrial for at least part of their life cycle. Studies were excluded if they combined abundance or presence/absence data across species, such that values for individual species could not be extracted. To be included in the analysis, studies had to report (a) the test statistic for the effect of roads and/or traffic on animal abundance, and/or summary statistics (e.g. mean and variance) from which an effect size could be calculated and (b) the sample size (or the *P* value of the test if a test statistic was reported). In some cases where these values were not provided, we calculated them using raw data if

they were provided in the paper, could be extracted from graphs using GetData Graph Digitizer 2.24 (Fedorov, S. (2008), *unpublished internet freeware*), or were provided to us by authors. To reduce publication bias, we attempted a thorough search, including data available in theses.

2.2. Database and data extraction

We divided the studies into six categories, based on study design (see Appendix A). This was necessary in order to calculate comparable sample sizes across studies. “Landscape or region” studies documented animal abundance within landscapes or regions that varied in road density, traffic density, or length of roads. In these studies author(s) measured roads within buffers around focal species sampling areas, where the buffer size was usually selected based on the organism’s dispersal distance or average home range size. The results were usually reported as correlation coefficients or regression coefficients relating animal abundance to road density, traffic density, or length of roads. “Home range/territory area” studies compared the mean road density (or mean traffic density or mean length of roads) within individual animals territories to mean road density (or mean traffic density or mean length of roads) within randomly selected non-territory areas of equal size (to the territories), or within the entire study area (including areas both with and without territories). Results of such studies were usually reported as means and variances of road density within home range areas and random/study areas. Although the road density value for an entire study area is not a mean, for calculation of effect size, we treated this value as a mean with a standard deviation of zero. “Plot size” studies compared the mean road density (or mean traffic density or mean length of roads) within plots centered over species presence locations to the mean road density (or mean traffic density or mean length of roads) of random points or areas of equal size where the species was known to be absent. The results were usually in the form of means and variances of road density (or length of roads) within presence plots compared to within random or absence plots. “Distance from road: multiple distances” studies documented animal abundance at several distances from a road; the results of such studies were usually reported as correlation coefficients or regression coefficients of the relationship between animal abundance and distance from a road. “Distance from road: near vs. far” studies documented mean animal abundance at only two distances from a road: adjacent to the road vs. farther from the road (e.g. forest interior). The outcomes were usually in the form of means and variances in the two distance categories. “Road presence/absence” studies compared mean species abundance in areas where roads were present to mean species abundance in areas where roads were absent. The results of these studies were usually reported as means and variances of species abundance within road present areas and within road absent areas.

When a single study reported results for more than one species, we entered each species data as an independent estimate. When a single study presented data using the same study design in multiple years and/or in two or more habitat types, we averaged estimates across years and/or habitat types; however, if study design varied across years or habitats, we selected the results from the year or habitat with the largest sample size. When studies presented means or correlations of road effects calculated at multiple spatial scales, we selected the largest estimate, on the assumption that this scale was closest to the relevant scale for that species. Road type was included as a moderator variable in the meta-analysis (see below), and was categorized into four groups: category 1 = 4-lane divided highways; category 2 = 2-lane paved roads; category 3 = 1-lane paved or gravel/dirt roads; and category 4 = studies which combined multiple road types. In the latter case,

we included the estimates from each road type, unless one road type was a subset of another, in which case we selected the road category that included the most road types.

2.3. Effect size calculations

The first step in the meta-analysis was to convert the various estimates of the effects of roads and traffic on animal population abundance into a common measure, the Pearson correlation coefficient r . For studies reporting regressions, r was the square root of the regression R^2 with the sign of the slope added. Note we could not include studies reporting partial R^2 values (Hullett and Levine, 2003).

When the study reported means and variances of two groups (e.g. mean road density within animal home range areas vs. in randomly selected areas, or mean animal abundance near vs. far from roads), we first calculated the standardized mean difference;

$$ES_{sm} = \frac{\bar{X}_{G1} - \bar{X}_{G2}}{S_{pooled}} J \quad (1)$$

where \bar{X}_{G1} and \bar{X}_{G2} are the means of group 1 (G1) and group 2 (G2), S_{pooled} is the pooled standard deviation of the two groups,

$$S_{pooled} = \sqrt{\frac{(n_{G1} - 1)s_{G1}^2 + (n_{G2} - 1)s_{G2}^2}{(n_{G1} - 1) + (n_{G2} - 1)}} \quad (2)$$

where s = standard deviation and n = sample size of each group, and J is a correction term that removes small sample size bias (Gurevitch and Hedges, 1993),

$$J = \left[1 - \frac{3}{4N - 9} \right] \quad \text{where } N = \text{total sample size.} \quad (3)$$

We then transformed ES_{sm} into r (Lipsey and Wilson, 2001),

$$r = \frac{ES_{sm}}{\sqrt{(ES_{sm})^2 + \frac{1}{p(1-p)}}} \quad (4)$$

where p = proportion of the total sample in one of the two groups. As suggested by Hedges and Olkin (1985), we transformed correlation coefficients using Fisher's z -transform, $ES_{zr} = 0.5 \log_e \left[\frac{1+r}{1-r} \right]$.

2.4. Adjustments prior to analysis

After obtaining the z -transformed r value for each effect (ES_{zr}), the next step was to weight them. This is often done by taking the inverse variance ($w = n - 3$ for z -transformed r) (Lipsey and Wilson, 2001). However, this gives more weight to studies with larger sample sizes, which would overweight studies such as those based on individual Global Positioning System (GPS) co-ordinates compared to those based on number of individuals. For example, Palma et al. (1999) compared the mean road density within 25-km² grid cells centered over lynx (*Lynx pardinus*) presence records (size of grid cell based on known size of annual home ranges of male lynx) to the mean road density within an equal number of randomly selected cells of the same size, resulting in a total sample size of fifty 25-km² grid cells. In contrast, Mace et al. (1996) constructed a composite female grizzly bear (*Ursus arctos horribilis*) home range by overlaying the home ranges of 14 female grizzly bears and then obtained the mean road density of 4668 random 1-km² areas within the composite home range. They compared this to the mean road density from 2447 1-km² areas outside the composite home range, resulting in a total sample size of 7115 1-km² areas. While both studies provide relevant information on the relationship between animal density and road density, their different design and analysis approaches result in different apparent sample sizes. To adjust the sample sizes, we worked from the assumption that we should attribute one data point to each spatially-indepen-

dent sample in each data set. We assumed that an independent sample is equivalent to an independent individual in a spatially independent location. Where independent individuals were not known (e.g. where sampling was based on fecal pellets or footprint tracking stations), sample size was the likely number of individuals present, using information from the literature on territory sizes. For each of the six study categories, sample sizes were estimated as follows.

For landscape or region studies we used the number of landscapes or regions as the sample size, on the assumption that the authors selected independent landscapes or regions based on the biology of the organism. For home range area studies, the sample size was the number of home ranges, plus one, to account for the comparison with the non-home-range areas. For the plot size studies, the sample size was the number of individuals used in the study, when provided; otherwise it was the number of spatially independent "presence" plots +1, such that the distance between presence plots had to be greater than or equal to the linear home range area. For the distance from road: multiple distances studies, the sample size depended on the type of abundance measure: (1) species abundance or fecal density; (2) the number of territories or nest density; or (3) mean density of GPS locations or mean number of GPS locations per individual. For species abundance or fecal density with distance from the road along transects in rows parallel to the road, the sample size was the number of spatially independent rows (distance intervals) where spatial independence was determined using the species home range size, multiplied by the number of roads sampled in the study (or the number of spatially independent sampling locations if only one road was sampled). If the number of roads was not stated, we assumed there was one road when 'road' was used in the singular form and two roads when 'roads' was used. For studies that correlated the number of territories or nest density with distance from the road, the sample size was the number of rows multiplied by the number of roads (or the number of sampling locations if only one road sampled), in this case we did not assess spatial independence of rows because the abundance measure was already equivalent to the number of individuals. For studies that correlated mean number of GPS fixes per individual or mean density of GPS locations with distance from the road, the sample size was the number of collared individuals. For distance from road: near vs. far studies that compared mean species abundance or mean density at two distances from a road, the sample size was the number of spatially independent sites multiplied by 2 (for near vs. far), or by 1 if the distance between the near and far sampling locations was too close for spatial independence. For studies that compared abundance in the presence or absence of a road, the sample size was the number of locations sampled where a road was present plus one.

After determining the adjusted sample size of each study (n) we converted it to an inverse variance weight ($w = n - 3$) (Lipsey and Wilson, 2001). Studies with $w < 1$ were not included in the meta-analysis. Refer to Appendix B for study and species lists, effect sizes, adjusted sample sizes, and study design categories for each study.

2.5. Data analysis

Our main objective was to determine species characteristics and behavioral responses to roads and/or traffic that make species prone to negative road and/or traffic effects. We collected information on the following species characteristics from published papers, dissertations, and species guides/accounts: (1) body mass (average body mass of the two sexes in grams), (2) body length (average total body length of the two sexes in centimeters), (3) reproductive rate (mean number of offspring per litter or clutch multiplied by the maximum number of litters or clutches per year),

(4) age at sexual maturity (mean age at sexual maturity of the two sexes in months), (5) species mobility (see below) and (6) species behavioral response to roads and/or traffic (see below). Species mobility information for mammals was indexed as home range area (ha) (Bowman et al., 2002) and for birds as territory size (ha) (Bowman, 2003). For amphibians and reptiles, when home range information was not available we took the reported seasonal migration distance divided by two to obtain a radius which was then converted to a circular home range area (ha). Species mobility was averaged across the two sexes. Life history characteristics were taken from sources as close to the study region (for each study) as possible. Where studies reported ranges instead of individual values, we used the median of these ranges. Details on species values and information sources are in Appendix C.

Information on species behavioral responses to roads and/or traffic was collected from published papers and dissertations. To be included in the analysis, studies had to clearly quantitatively document a species behavioral response to roads and/or traffic. For example, studies showing distributions of animals with respect to roads cannot distinguish between mortality (suggesting low road avoidance) and avoidance of traffic disturbance since animal numbers may be low near roads either because mortality rate is high in these areas, which depresses the populations, or because animals avoid these locations because of traffic disturbance. To distinguish between these two cases, studies needed to either show higher mortality rates in roaded areas to support the former, or analyze movement paths showing deviations away from roads to support the latter (Fahrig and Rytwinski, 2009). Similarly, a common issue with past empirical studies of road avoidance is that studies were conducted across a range of road sizes, where larger roads were both wider and had higher traffic volumes (e.g. Oxley et al., 1974; Lovallo and Anderson, 1996; Rondinini and Doncaster, 2002). If animals are less likely to cross larger roads, it is not clear from these studies whether this is due to road avoidance or to avoidance of traffic disturbance. Where studies documented lower crossing frequencies by animals on roads with higher traffic volumes compared to roads with lower traffic volumes, unless there was quantitative documentation of vehicle avoidance, we assumed species were avoiding the road (i.e. the opening or clearing created by the road) (McGregor et al., 2008). Studies could document responses by either: (1) direct observations, (2) radio-telemetry or GPS telemetry, and/or (3) other study designs that allowed clear inference as to the mechanism.

All analyses were conducted in R 2.12.2 (R Development Core Team, 2011), using the 'metafor' package (version 1.5–0) (Viechtbauer, 2010). A random effects meta-analysis was conducted using the DerSimonian–Laird method to derive a pooled effect size. Despite our effort to reduce publication bias by including data available in theses, the results could still be flawed if there was a bias towards publishing only significant negative effects of roads/traffic on animal abundance. Therefore, we tested for publication bias using funnel plots of asymmetry (graphical detection of publication bias using a scatterplot of effect size vs. sample size). If no bias is present, the funnel plot should be shaped like an inverted cone, with a wider spread of effect sizes for studies with small sample sizes at the bottom (less precision) and decreasing spread as the sample size increases. In addition, the magnitude of the effect size should be independent of the sample size (i.e. points should be symmetrically distributed around the mean for all sample sizes). Homogeneity of effects sizes was tested based on the statistic Q to determine whether multiple effect sizes all estimate the same population mean i.e., the dispersion of the effect sizes around their mean is no greater than that expected from sampling error alone (Hedges and Olkin, 1985). A larger Q indicates greater heterogeneity in effects sizes (i.e., individual effect sizes do not estimate a common population mean), suggesting there are differ-

ences among effect sizes that have some cause other than sampling error. For both categorical and continuous data analysis, total heterogeneity, Q , can be partitioned into heterogeneity explained by the model, Q_M , and heterogeneity not explained by the model, Q_E (i.e., $Q = Q_M + Q_E$). The significance of Q is tested using a χ^2 distribution (Hedges and Olkin, 1985). To determine whether separate meta-analyses were needed for different taxonomic classes, we performed a mixed effects model including taxon (at the class level). Amphibians and reptiles were combined due to the small sample size for reptiles. We report the mean effect size (ES_r) of each class, and between groups heterogeneity (Q_M).

Since the effect of roads and traffic on animal abundance varied by taxonomic class, we conducted pairwise correlations to assess independence of the life history characteristics for each class separately. Since information on life history characteristics was not always available, and since we expected life history traits to be inter-correlated, we removed highly redundant traits, while maximizing the number of complete datasets (Table 1). For example, for mammals, reproductive rate and age to sexual maturity were highly correlated ($r = -0.812$, $p < 0.0001$), as expected. Since age at sexual maturity was more highly correlated to the other life history characteristics than reproductive rate, and there were fewer datasets containing information on age at sexual maturity than reproductive rate, we removed age at sexual maturity as an explanatory variable from analyses. We performed chi-squared tests to assess independence of study design and road category.

To test the importance of life history characteristics and/or study-level moderators in determining the sign and magnitude of the correlations between road and traffic effects and abundance, we ran univariate mixed-effects models using the *rma.uni* function in the metafor package with restricted maximum-likelihood estimation, for each taxonomic class separately. All continuous life history variables were log-transformed to meet test assumptions. To deal with non-independence of life history characteristics, we then proceeded in one of two ways. If differences among study designs or road categories did not explain variation in population-level responses to roads effects, we conducted an AIC-based model selection procedure using the life history characteristic(s) (if any) that were found to explain variation in the magnitude of population-level responses to roads and/or traffic. Alternatively, if a study-level moderator(s) were found to explain variation in population-level responses to roads and/or traffic for a particular class, we analyzed the effects of life history characteristics (using AICc) within the largest subgroup(s) of data (based on the study-level moderators) separately. In this case we used only the largest subgroup(s) since most remaining subgroups had sample sizes too small to allow for meaningful tests of the life history moderators.

We had initially hoped to include species-specific behavioral responses to roads and/or traffic as a moderator variable in the meta-analyses. However, there was too little information available for too few species to do this (see below). Instead, we tabulated the species in the six behavioral response categories, in order of increasing predicted negative effects of roads – (i) species that are attracted to roads and have vehicle avoidance, (ii) species with vehicle avoidance, (iii) species with road surface avoidance, (iv) species with traffic disturbance avoidance, (v) species with no road surface or traffic disturbance avoidance, (vi) species that are attracted to roads – and conducted a qualitative analysis of the tabulated results. For categories iii–vi, we assumed species had no vehicle avoidance unless there was quantitative evidence suggesting otherwise. It is also important to note that behavioral responses to roads and/or traffic are not necessarily mutually exclusive, in that a particular species could exhibit more than one response and that different combinations of responses can exist. In such cases, species were placed in more than one behavioral response category.

Table 1

Pearson correlations (above diagonals), their *p*-values (below diagonals) and sample sizes (on diagonals), between life history characteristics for: (a) mammals database, (b) birds database, (c) amphibians + reptiles database and, (d) anurans (frogs and toads) database. Life history characteristics in gray were removed from mixed-effects meta-analytical models to reduce highly redundant traits, while trying to maximize the number of complete datasets (i.e., information on certain life history characteristics was not always available).

	Reproductive rate	Mobility	Body mass	Body length	Age at sexual maturity
<i>(a)</i>					
Reproductive rate	120	–0.737	–0.763	–0.705	–0.812
Mobility	<0.0001	114	0.879	0.901	0.820
Body mass	<0.0001	<0.0001	126	0.956	0.834
Body length	<0.0001	<0.0001	<0.0001	120	0.782
Age at sexual maturity	<0.0001	<0.0001	<0.0001	<0.0001	114
<i>(b)</i>					
Reproductive rate	247	–0.286	–0.246	–0.393	–0.316
Mobility	<0.0001	171	0.549	0.587	0.506
Body mass	<0.0001	<0.0001	252	0.957	0.629
Body length	<0.0001	<0.0001	<0.0001	227	0.666
Age at sexual maturity	<0.0001	<0.0001	<0.0001	<0.0001	141
<i>(c)</i>					
Reproductive rate	55	0.133	–0.800	–0.625	–0.532
Mobility	<0.0001	53	0.424	0.354	0.190
Body mass	<0.0001	<0.0001	35	0.809	0.828
Body length	<0.0001	<0.0001	<0.0001	58	0.549
Age at sexual maturity	<0.0001	<0.0001	<0.0001	<0.0001	54
<i>(d)</i>					
Reproductive rate	22	0.155	0.689	0.617	0.617
Mobility	0.492	22	0.146	–0.297	–0.297
Body length	<0.0001	0.517	22	0.753	0.753
Age at sexual maturity	0.002	0.179	<0.0001	22	0.753

3. Results

3.1. Review statistics

We found 75 studies published during 1979–early 2011 that met the selection criteria. Studies were predominantly in either North America (49) or Europe (19), but there were also studies from Oceania (3), Africa (2), and Asia (2). Thirty-four studies from twelve countries included 84 mammal species, and 127 road and/or traffic effects on mammals were extracted for the meta-analysis. Sixteen studies from eight countries included 194 bird species, and 270 road and/or traffic effects on birds were extracted. For amphibians, 16 studies from six different countries included 23 species, resulting in 42 amphibian datasets. For reptiles, nine studies from three different countries included 11 species, resulting in 16 reptile datasets (Appendix B).

3.2. Global analysis and publication bias

The grand weighted-mean effect size derived from all effect size values in a random effects meta-analysis indicated that overall, roads and/or traffic have a weak, negative affect on animal population abundance and this mean was significantly different from zero, as indicated by their 95% confidence intervals ($ES_r = -0.077$ (95% CI: $-0.117, -0.036$)). The overall heterogeneity of effect sizes was large ($Q = 2541.88, p < 0.0001, n = 455$), indicating that the individual effect sizes in our data did not estimate a common population mean. Plotting effect sizes against sample sizes produced a typical funnel plot with greater scatter in studies based on smaller sample sizes and a lack of significant relationship between the magnitude of effect size and sample size ($r = -0.010, p = 0.837, n = 455$), patterns consistent with an absence of publication bias (Appendix D).

The effects of roads and/or traffic on animal abundance varied by taxonomic class (heterogeneity of the model $Q_M = 21.64,$

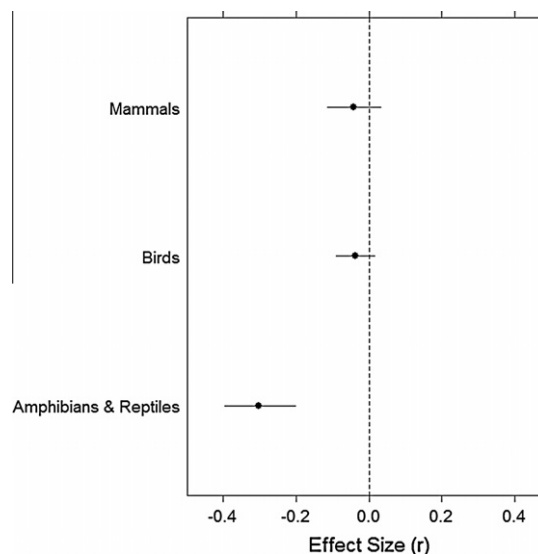


Fig. 1. Weighted-mean effect sizes (ES_r) for each animal class derived from a mixed effects meta-analytical model. Error bars indicate 95% confidence intervals.

$p < 0.0001, n = 455$ datasets). The weighted-mean effect sizes for mammals and birds were negative, but weak, and did not differ significantly from zero, as indicated by their 95% CI (Fig. 1). The weighted-mean effect size for amphibians + reptiles was negative and significantly different from zero, and the magnitude of population-level responses to roads and/or traffic was larger than that of either birds or mammals (Fig. 1). There was however large heterogeneity of effect sizes within each taxon separately (mammals: $Q = 1503.15, p < 0.0001, n = 127$; birds: $Q = 453.47, p < 0.0001, n = 270$; amphibians + reptiles: $Q = 481.87, p < 0.0001, n = 58$), suggesting other sources of variation maybe influencing the population-level response to road effects.

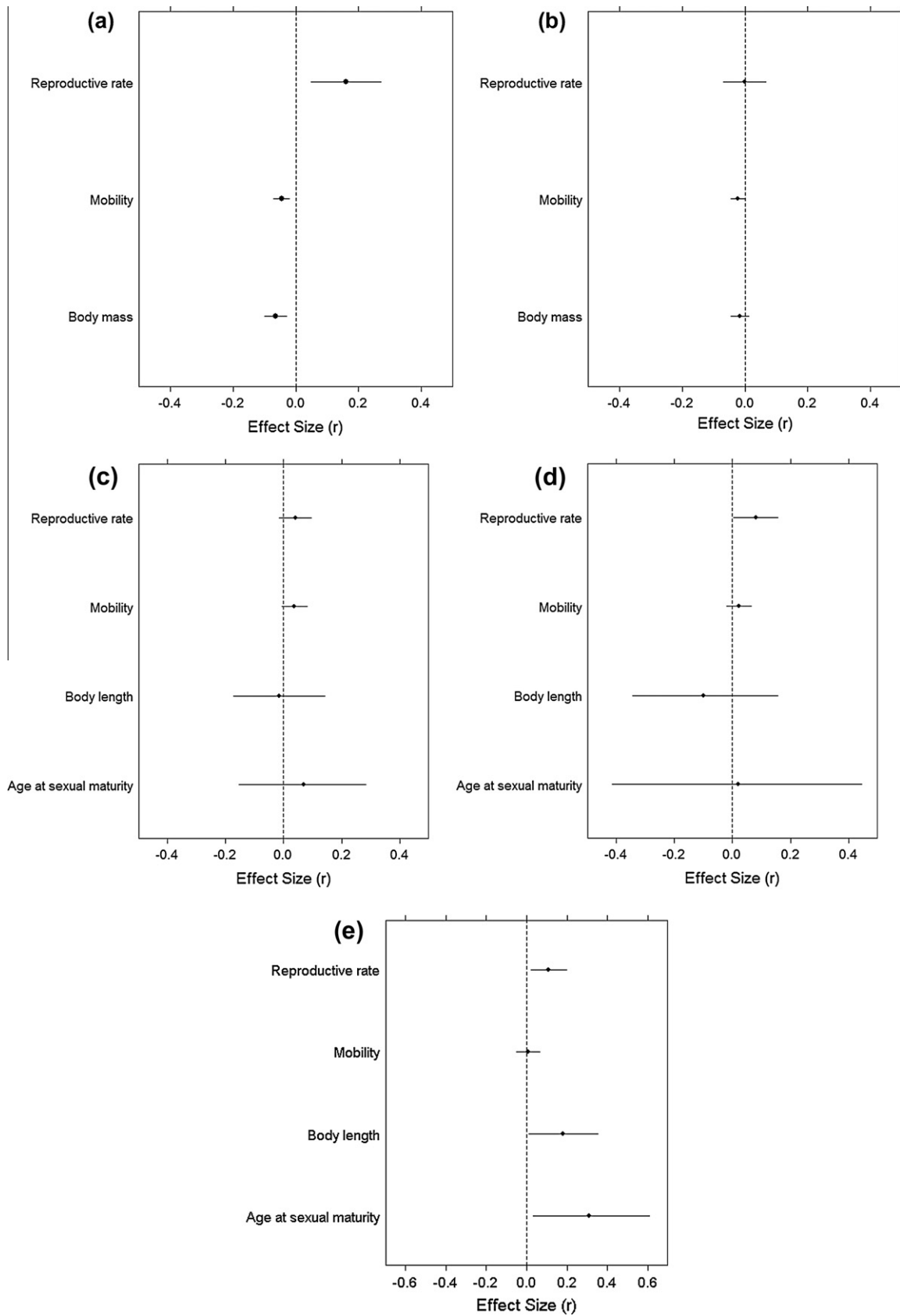


Fig. 2. Weighted-mean effect sizes (ES_i) from univariate meta-analytical regression models testing the effects of life history traits on species responses to roads and/or traffic at the population-level for (a) mammals, (b) birds, (c) amphibians + reptiles, (d) amphibians only, and (e) anurans only. Error bars indicate 95% confidence intervals.

3.3. Analysis of life history attributes

As expected there were high correlations among life history characteristics, with correlations higher ($r > 0.7$) for mammals than for birds and/or amphibians + reptiles (Table 1). After removing the redundant life history characteristics from each database (i.e., body mass for amphibians + reptiles, and body length and age at sexual maturity for birds, and mammals), the number of datasets within each database was reduced to 108 datasets for mammals, 170 for birds, and 50 for amphibians + reptiles.

3.3.1. Mammals

Reproductive rate, species mobility, and body mass were related to population-level effects of roads for mammals in univariate models (Fig. 2a; Appendix E Table E1; $Q_M = 7.90$, $p = 0.0049$; $Q_M = 10.12$, $p = 0.0015$; $Q_M = 11.16$, $p = 0.0008$, $n = 108$ respectively). As predicted, species with lower reproductive rates, higher mobility, and larger body sizes showed more negative responses to roads and/or traffic (Fig. 2a; Appendix E Table E1). Since the magnitude of population-level responses to roads effects was not significantly different among datasets using different study designs or road categories, we did not subgroup the data by these study-level moderators ($Q_M = 2.29$, $p = 0.6830$; $Q_M = 6.07$, $p = 0.1081$, $n = 108$ respectively; Appendix E Table E1). Based on the multiple meta-analytical model selection, the most parsimonious model was that containing only the explanatory variable body mass (AICc = 271.71 compared to 272.60 and 273.37 for reproductive rate and species mobility respectively; Appendix F Table F1a). However, all three models had substantial support, with $\Delta AICc$ less than 2 and models including combinations of two or more of these traits did not improve model fit (Appendix F Table F1a).

3.3.2. Birds

For birds, the magnitude of population-level responses to road effects varied according to species taxon as well as species mobility ($Q_M = 29.89$, $p = 0.0009$; $Q_M = 4.24$, $p = 0.0395$, $n = 169$ respectively; Appendix E Table E2). As predicted, more mobile birds (larger territory sizes) showed a more negative response to roads and/or traffic (Fig. 2b).

The magnitude of population-level effects of roads varied according to study design and road category for birds ($Q_M = 39.75$, $p < 0.0001$; $Q_M = 66.01$, $p < 0.0001$, $n = 169$ respectively; Appendix E Table E2). Therefore it was necessary to determine whether the effect of mobility remained significant after controlling for these study-level moderators. Study design and road category were not independent (Table 2a). We therefore subdivided the datasets by study design only, and to increase sample size, we grouped the data into two study design categories: (a) designs using area based measurements (i.e. home range and plot size study designs), and (b) designs using distance based measurements (i.e. distance from road (multiple distances) and distance from road (near vs. far)). The largest group was distance from road studies ($n = 106$ vs. $n = 62$). We then tested the effect of mobility within this group, after removing the single dataset from the order Charadriiformes to control for among-taxon heterogeneity (Appendix E Table E2). After controlling for study-level moderators, there was no longer a relationship between species mobility and the population-level effects of roads on birds ($Q_M = 1.12$, $p = 0.2900$, $n = 106$; Appendix G Table G1).

3.3.3. Amphibians and reptiles (combined)

For amphibians + reptiles, the magnitude of effect sizes did not vary among taxa ($Q_M = 4.69$, $p = 0.1956$, $n = 50$; Appendix E Table E3), and none of the life history characteristics were related to the population-level effects of roads (Fig. 2c; Appendix E Table E3; reproductive rate: $Q_M = 2.04$, $p = 0.1531$; mobility: $Q_M = 2.82$,

Table 2

Chi-squared contingency analysis for independence of study-level moderators (study design and road category) for: (a) bird database and (b) amphibians + reptiles database. Road categories: 1 = 4-lane divided highways, 2 = 2-lane paved roads, 3 = 1-lane paved or gravel/dirt roads, and 4 = all or multiple road types. Study designs (see Appendix A): 1 = landscape or region scale, 2 = home range area scale, 3 = plot size scale, 4 = distance from road (multiple distances), 5 = distance from road (near vs. far), and 6 = road presence/absence. Note that there were no landscape or region scale study designs for birds or distance from road (near vs. far) study designs for amphibians + reptiles.

	Road Category				Total
	1	2	3	4	
(a)					
Study design					
2	0	1	0	2	3
3	12	3	44	0	59
4	0	10	2	2	14
5	35	27	31	0	93
Total	47	41	77	4	169
Pearson chi-square	114.63				
Asymp. sig. (2-sided)	<0.0001				
(b)					
Study design					
1	0	0	0	13	13
2	1	2	1	5	9
3	0	3	1	14	18
4	1	4	1	1	7
6	0	0	3	0	3
Total	2	9	6	33	50
Pearson chi-square	42.49				
Asymp. sig. (2-sided)	<0.0001				

$p = 0.0929$; body length: $Q_M = 0.04$, $p = 0.8420$; age at sexual maturity: $Q_M = 0.37$, $p = 0.5453$, $n = 50$). However, the magnitude of population-level effects of roads varied according to study design and road category for amphibians + reptiles ($Q_M = 18.08$, $p = 0.0012$; $Q_M = 11.89$, $p = 0.0078$, $n = 50$ respectively; Appendix E Table E3) and these two moderators were not independent (Table 2b). Since the sample sizes in the road category levels were too small to allow meaningful tests of life history characteristics within sub-groups, and since study design and road category shared similar information, we removed road category from further analyses. For the study design moderator, we grouped the data into the same two categories as for the bird analysis (above). For amphibians + reptiles the largest subgroup was area-based studies ($n = 40$ vs. $n = 10$). After controlling for the effect of study design (i.e., using area based studies only), there were still no significant relationships between life history characteristics and population-level responses to roads and/or traffic for amphibians + reptiles (Appendix G Table G2).

3.3.4. Amphibians

In a separate analysis for amphibians only (sample size for reptiles was too small to allow a separate analysis), reproductive rate was related to the magnitude of the population-level effects of roads: amphibians with lower reproductive rates showed more negative responses to roads and/or traffic (Fig. 2d; Appendix E Table E4; $Q_M = 4.15$, $p = 0.0416$, $n = 35$). While both amphibian orders showed substantial negative responses to roads and/or traffic, the population-level response to roads was larger for the order Caudata compared to anurans ($ES_r = -0.441$ (95% CI: -0.609 , -0.235) and $ES_r = -0.193$ (95% CI: -0.336 , -0.041) respectively; Appendix E Table E4). Differences in study design or road category did not explain variation in the magnitude of population-level effects of roads for amphibians ($Q_M = 6.28$, $p = 0.1791$; $Q_M = 3.90$, $p = 0.2723$, $n = 35$ respectively; Appendix E Table E4). For anurans only (anurans was the larger subgroup), reproductive rate, body length, and age at sexual maturity all explained variation in the

Table 3
Species for which quantitative information exists on both (i) population-level responses to roads and/or traffic and (ii) behavioural responses to roads and/or traffic. Possible responses to roads are listed in order of increasing predicted negative effect of roads and/or traffic at the population level, i.e., increasing predicted effect sizes. References for documented behavioural responses are given. Note that one species may have more than one behavioural response and therefore may appear more than once in the table. Effect sizes in bold are weighted average effect sizes for each response category (or the actual effect size if only one species in a category). Effect sizes for species within categories (regular font) are weighted average effect sizes for a species (or the actual effect size if only one dataset for a species). Asterisks identify species that have been documented not to avoid areas adjacent to roads.

Behavioural response	References	Effect size (r)
i. Attracted to roads and vehicle avoidance		
no data		n/a
ii. Vehicle avoidance		
<i>Rangifer tarandus</i> (woodland caribou)	Curatolo and Murphy (1986)	-0.293 -0.293
iii. Road surface avoidance		
* <i>Peromyscus leucopus</i> (white-footed mouse)	McGregor et al. (2008)	0.145 0.145
* <i>Tamias striatus</i> (eastern chipmunk)	Ford and Fahrig (2008), McGregor et al. (2008)	-0.005 -0.005
<i>Erinaceus europaeus</i> (hedgehog)	Rondinini and Doncaster (2002)	-0.167
<i>Lynx rufus</i> (bobcat)	Lovallo and Anderson (1996), Riley et al. (2006)	-0.016
* <i>Canis lupus</i> (Gray wolf)	Whittington et al. (2004)	0.022
* <i>Puma concolor</i> (cougar)	Dickson et al. (2005)	-0.066
* <i>Ursus americanus</i> (black bear)	Brody and Pelton (1989), Beringer et al. (1990), Brandenburg (1996), McCoy (2005)	-0.207
<i>Crotalus horridus</i> (timber rattlesnake)	Andrews and Gibbons (2005)	-0.225
<i>Heterodon platirhinos</i> (eastern hog-nosed snake)	Andrews and Gibbons (2005)	-0.032
<i>Sistrurus catenatus</i> (eastern massasauga rattlesnake)	Andrews and Gibbons (2005)	-0.076
iv. Traffic disturbance avoidance		
<i>Rangifer tarandus</i> (woodland caribou)	James and Stuart-Smith (2000), Dyer et al. (2001), Schindler et al. (2006)	-0.293 -0.293
<i>Cervus elaphus</i> (elk)	Rowland et al. (2000), Gagnon et al. (2007), Dodd et al. (2007), Stewart et al. (2010)	-0.568
<i>Alces alces</i> (moose)	Laurian et al. (2008)	0.247
<i>Ursus arctos</i> (grizzly bear)	McLellan and Shackleton (1988), Mace et al. (1996), Gibeau (2000), Chruszcz et al. (2003), Waller and Servheen (2005)	-0.230
v. No road/traffic avoidance		
<i>Rana pipiens</i> (northern leopard frog)	Bouchard et al. (2009)	-0.189 -0.189
vi. Attracted to roads		
<i>Corvus corax</i> (common raven)	Knight and Kawashima (1993)	-0.042 -0.042
<i>Milvus migrans</i> (black kite)	Meunier et al. (2000)	0.073

magnitude of population-level effects of roads in univariate models (Fig. 2e; Appendix E Table E5; $Q_M = 5.71$, $p = 0.0169$; $Q_M = 4.34$, $p = 0.0371$; $Q_M = 4.72$, $p = 0.0297$, $n = 22$ respectively;). Anuran species with lower reproductive rates, smaller body sizes, and younger ages at sexual maturity were more negatively affected by roads and/or traffic than species with higher reproductive rates, larger body size, and older ages at sexual maturity (Fig. 2e; Appendix E Table E5). Since the magnitude of the population-level response to roads effects did not vary with study design or road category for anurans, we did not subgroup the data by these study level moderators ($Q_M = 1.40$, $p = 0.7062$; $Q_M = 0.15$, $p = 0.6977$, $n = 22$ respectively; Appendix E Table E5). Based on multiple meta-analytical regression models, the most parsimonious model was that containing only the explanatory variable age at sexual maturity, with earlier-maturing species showing more negative effects of roads and/or traffic (AICc = -0.60 compared to 1.72 and 1.80 for body length and reproductive rate respectively) (Appendix F Table F1b). Models including combinations of 2 or more traits did not improve model fit (Appendix F Table F1b; see Table 1d for correlations between anuran traits).

3.4. Analysis of behavioral responses to roads

We found 17 species for which data on both population-level responses to roads and/or traffic and behavioral responses to roads existed (11 mammals, 2 birds, 3 reptiles, and 1 amphibian) (Table 3). Qualitatively, results did not follow our predictions that the negative effects of roads on animal abundance will increase with increasing order of behavioral response categories (i → vi). Species that exhibit road surface avoidance and species that are attracted

to roads (with no evidence of vehicle avoidance) showed overall weak population-level responses to roads/traffic, whereas species that avoid roads from a distance due to traffic disturbance or have no road and/or traffic avoidance, showed the most negative population-level responses to roads/traffic (Table 3). While the vehicle avoidance response category showed the strongest negative effect of roads/traffic on animal abundance, there was only one species, woodland caribou (*Rangifer tarandus*) which was reported to show this behavior, and this same species was also documented to avoid roads from a distance due to traffic disturbance.

4. Discussion

4.1. Mammals and life history attributes

Our results support the prediction that mammal species with lower reproductive rates, greater mobilities, and larger body sizes, are most negatively affected by roads and/or traffic. Of these three traits, body mass was the main explanatory variable for population-level responses to road effects, but all three models were essentially indistinguishable in terms of model support, due to the high correlations among the life history variables (Table 1a; Appendix F Table F1a).

While previous studies, both theoretical and empirical, have found effects of reproductive rate and species mobility on species responses to habitat loss for various taxa (With and King, 1999; Fahrig, 2001; Vance et al., 2003; Holland et al., 2005; Gibbs, 1998; Casagrandi and Gatto, 1999; Flather and Bevers, 2002; León-Cortés et al., 2003; Van Houtan et al., 2007), only one previous study investigated the effects of species traits on mammal

responses to roads and/or traffic at the population level. In an empirical study of 13 mammal species we (Rytwinski and Fahrig, 2011) found that reproductive rate, and body size explained 77% of the variation in the slope of the relationship between road density and mammal abundance, with the effect of reproductive rate clearly the stronger. Our ability to isolate the effect of reproductive rate in our previous study was due to the relatively low correlation between reproductive rate and body size ($r = -0.521$) in that study. In contrast, the correlations among life history traits were much higher in the current study ($r > 7$; Table 1a). Note that the results for mammals in this meta-analysis do not depend on the inclusion of the empirical results from our previous study. The number of effect sizes extracted from that paper only represented 16% of the total number of effect sizes here, and excluding these effects from the current analysis does not qualitatively change the conclusions (Appendix G Table G3). Overall, this meta-analysis provides further support that mammals with lower reproductive rates, greater mobilities, and larger body sizes are most vulnerable to the negative effects of roads and/or traffic.

4.2. Birds and life history attributes

For birds, species mobility was the only life history trait that explained variability in the magnitude of population-level responses to roads (Fig. 2b; Appendix E Table E2), indicating that more mobile bird species are more susceptible than less mobile species to negative road effects. However this result is somewhat equivocal because the effect of mobility disappeared after we controlled for differences in study design (Appendix G Table G1). Although this is the first test of this hypothesis for road effects on birds, there are analogous results in the habitat loss literature. Van Houtan et al. (2007) suggest that species with high dispersal rates and long dispersal distances are more susceptible than less mobile species to habitat loss due to the higher risk of mortality in the matrix sustained by more mobile species. In the context of this meta-analysis, increased risk results from increased road mortality rather than decreased habitat amount. This result also provides indirect support for the hypothesis that road effects on birds are often due to mortality rather than noise disturbance as is commonly assumed (Summers et al., 2011).

The lack of support for predictions on the effect of reproductive rate and body size, and the weak support for an effect of species mobility on birds, maybe partly explained by the fact that the majority of population-level bird studies (87%) have been conducted on passerines. A lack of variation in species life history traits across passerines could explain this lack of effect (see Appendix H). On the other hand, there was large heterogeneity in effect sizes within passerines, suggesting that some other (untested) species trait(s) may explain variation among road/traffic effects in birds.

4.3. Amphibian and reptiles (combined) and life history attributes

Of the taxonomic classes in this meta-analysis, amphibians and reptiles (classes combined) were the most negatively affected by roads and/or traffic (Fig. 1), which is consistent with previous studies (e.g. Gibbons et al., 2000; Cushman, 2006; Eigenbrod et al., 2008; Fahrig and Rytwinski, 2009; Patrick and Gibbs, 2010). Despite having the highest threat status of all terrestrial vertebrates, with significantly more species at risk than either mammals or birds (IUCN, 2010), amphibians and reptiles are among the least studied taxa (Cushman, 2006; Taylor and Goldingay, 2010; Vetter et al., 2011). This was also true in our meta-analysis; amphibians and reptiles were the least represented classes, with a combined species total of 34 compared to 84 and 194 species for mammals and birds respectively. All four orders represented in the amphibian + reptile database showed negative mean effect sizes, but sala-

manders (Caudata) and snakes (Squamata) showed the strongest negative effects (Appendix E Table E3). In general our results confirm the notion that amphibians and reptiles are particularly vulnerable to road effects.

4.4. Reptiles and life history attributes

Due to the small number of studies on the effects of roads on reptile populations, we could not investigate the effects of life history traits on reptile responses to roads separately. Many turtles and squamate reptiles are long-lived, have high adult survival, low levels of recruitment and delayed sexual maturity (Brooks et al., 1991; Congdon et al., 1993, 1994). Furthermore, many turtle species make annual movements overland, moving between aquatic and terrestrial habitats (Gibbons, 1986) and many snakes have high movements rates associated with foraging and mate searching (King and Duvall, 1990). The above characteristics coupled with their typically slow movements across roads likely make reptile populations particularly vulnerable to the effects of road mortality. Moreover, studies have found a higher proportion of male turtles in populations near roads (Marchand and Litvaitis, 2004; Aresco, 2005a; Gibbs and Steen, 2005; Patrick and Gibbs, 2010), likely due to higher road mortality in females, which make frequent movements associated with nesting activity and often select highway shoulders and gravel roads for nest sites (Aresco, 2005b; Steen et al., 2006; pers. obs.). It has been suggested that even small increases in annual mortality rates of adult females can cause long-term population declines (Brooks et al., 1991; Congdon et al., 1993; Congdon et al., 1994). While we were not able to test the effects of life history traits on reptile responses to roads this meta-analysis and the literature to date suggest that reptiles in general should be a high priority for mitigation of road effects.

4.5. Amphibians and life history attributes

We did have enough datasets to test the life history predictions for amphibians separately. Reproductive rate was found to be related to the magnitude of population-level effects of roads, providing support for the prediction that species with lower reproductive rates show more negative responses to roads and/or traffic (Fig. d; Appendix E Table E4). While both amphibian orders showed substantial negative responses to roads and/or traffic, caudates showed a stronger and more negative response to roads and/or traffic than did anurans (Appendix E Table E4). This may be partly explained by the fact that caudates had lower reproductive rates (caudates: mean reproductive rate = 178.9 (range = 9–421, $n = 13$ datasets of eight species), anurans: mean reproductive rate = 2923.3 (range = 650–8000, $n = 22$ datasets of nine species)). We did not have enough datasets to test whether reproductive rate explained variation in effect sizes within the order Caudata. For anurans, species with lower reproductive rates, smaller body sizes, and shorter ages at sexual maturity were more negatively affected by roads and/or traffic (Fig. 2e; Appendix E Table E5). Of the three species traits, age at sexual maturity showed the strongest model fit (Appendix F Table F1b) although the traits were strongly inter-correlated (Table 1d). We suggest that for anurans, the effect of age at sexual maturity on the negative effect of roads functions through its correlation with reproductive rate. Species-specific estimates of reproductive rate and body size in amphibians are highly variable because growth is indeterminate and reproductive rate generally increases with body size (e.g. Wilbur, 1977; Kaplan and Saithe, 1979; Gibbons and McCarthy, 1986; Berven, 1988; Pupin et al., 2010) and therefore with age (Berven, 2009). Age at first reproduction is perhaps the best indicator of overall reproductive rate: species that mature earlier tend to be smaller and have

lower reproductive rates (Tinkle et al., 1970; Schwarzkopf, 1994). Therefore, our results support the prediction that the negative effects of roads on frog population abundance should be stronger on smaller bodied frogs because they will be less likely to rebound quickly from population declines due to traffic mortality.

Indeterminate growth in amphibians and reptiles likely contributes to their susceptibility as a group to road effects. Increased mortality due to road kill results in a shift in age distribution towards younger individuals. For amphibians and reptiles, this means a reduction in mean body size, with an associated reduction in reproductive rate (Hoskin and Goosem, 2010; Karraker and Gibbs, 2011). Therefore, road mortality on amphibians and reptiles reduces population abundance not only directly but also indirectly through reduced mean reproductive rate.

4.6. Behavioral responses to roads

Some of the variation in population-level responses to roads not explained by life history variables is likely explained by differences among species in their behavioral responses to roads and traffic (Jaeger et al., 2005; Fahrig and Rytwinski, 2009). Qualitatively, our results suggest that species that exhibit traffic disturbance avoidance (habitat loss) or no road and/or traffic avoidance (road mortality) are more vulnerable to negative population-level responses to roads compared to other behavioral responses to roads. The two species for which the population-level responses to roads were most negative were elk (*Cervus elaphus*) and caribou (*Rangifer tarandus*) which have been reported to avoid roads from long distances away, even when these roads are small, lightly used logging roads (James and Stuart-Smith, 2000; Rowland et al., 2000; Dyer et al., 2001; Gagnon et al., 2007; Schindler et al., 2006; Stewart et al., 2010). While these ungulates may still suffer from road mortality, since been reported to cross roads, the functional habitat loss or degradation as a result of avoiding roads from a distance likely causes their stronger negative responses to roads compared to other species that avoid crossing roads but do not avoid using the habitat adjacent to roads (e.g. eastern chipmunk (*Tamias striatus*), gray wolves (*Canis lupus*), cougars (*Puma concolor*), black bears (*Ursus americanus*)) (Table 3). We found that the vehicle avoidance response showed the strongest negative population-level response to roads out of all behavioral responses which intuitively does not seem logical. However, because the only species in this category was the woodland caribou, which as mentioned above, has also been reported to avoid roads from a distance due to traffic disturbance, the observed negative population-level response for caribou is likely a result of habitat loss associated with avoiding roads from a distance.

We predicted that species that are attracted to roads but are unable to avoid oncoming vehicles (i.e. slow moving) will be most vulnerable to population-level responses to roads, but overall weak population-level effects of roads were found for this behavioral response category. We assumed that the common raven (*Corvus corax*) and the black kite (*Milvus migrans*), are unable to avoid oncoming vehicles since there are no quantitative studies documenting vehicle avoidance behavior in these species. However, if they do show some vehicle avoidance and if they benefit from the food on roads in the form of road-kill carcasses, roads could have positive effects on reproduction which could balance or even outweigh negative effects of road mortality, resulting in overall weak road effects.

Overall, it is not yet possible to evaluate the effects of behavioral responses on the population-level effects of roads. To do so would require more studies of the behavioral responses to roads for more of the species in Appendix C. Such behavioral studies are particularly needed for: (1) any species that shows strong negative responses to roads and/or traffic, (2) mammal species that

show strong negative responses to roads and/or traffic and have higher reproductive rates than species of similar body size (e.g. *Meles meles* (European badger), *Vulpes vulpes* (red fox), *Lepus europaeus* (European hare), *Sus scrofa* (wild boar)), (3) bird species that show strong negative responses to roads and/or traffic and have lower mobility (e.g. water birds (e.g. *Vanellus vanellus* (northern lapwing)), *Parus major* (great tit), *Turdus merula* (common black-bird)), and (4) most amphibian and reptiles species with particular attention to squamates (i.e., snakes) and caudate species (i.e., salamanders and newts).

5. Conclusions

Our results support the prediction that mammal species with lower reproductive rates, greater mobilities, and larger body sizes are more susceptible to negative road and/or traffic effects at the population level. We also found weak support for the hypothesis that more mobile birds are more susceptible to negative road and/or traffic effects than less mobile bird species. Our results highlight the vulnerability of amphibians and reptile populations to negative road and/or traffic effects, and suggest that anuran species with lower reproductive rates, smaller body sizes, and younger ages at sexual maturity are more negatively affected by roads and/or traffic. Also, our results suggest that species that either do not avoid roads or are disturbed by traffic are more vulnerable to negative population-level effects of roads than species that avoid roads and are not disturbed by traffic. In general, our results imply that priority for mitigation should be directed towards wide-ranging large mammals with low reproductive rates, birds with larger territories, all amphibians and reptiles, and species that do not avoid roads or are disturbed by traffic. For species that are mainly affected by roads through road mortality, such as amphibians (Fahrig et al., 1995; Bouchard et al., 2009), reptiles (Boarman and Sazaki, 2006; Tanner and Perry, 2007), some birds (Summers et al., 2011), and some larger mammals (Fuller, 1989; Ferreras et al., 1992), mitigation should be mainly directed towards preventing animals from moving onto roads. For amphibians and reptiles this can be done by installing fencing with very small mesh (e.g., Aresco, 2005b) and/or reconstructing the road bed with the addition of “barrier walls” that have a lip to keep animals from climbing onto the road (e.g., Barachivich and Dodd, 2002). In locations where amphibians need to cross the road (e.g., to access breeding sites), wildlife crossing structures (ecopassages) can be used to allow safe passage under the road (Clevenger et al., 2001; Huijser and McGowen, 2010). These are best placed wherever streams intersect with roads: culverts should be replaced by “extended stream crossings” that allow the natural stream, with wide banks on either side, to flow under the road (Ruediger, 2001), thus allowing free movement of amphibians and reptiles. Such underpasses, if large enough, would also allow movement of larger mammals, but additional, substantial fencing is required to keep large mammals such as cougars off roads (e.g., Smith, 2004). For birds, avoiding 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 fencing in combination with wildlife crossing structures in key movement areas would also be beneficial.

Acknowledgements

We thank all the authors that responded to our enquiries. 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. Rytwinski and NSERC and Canada Foundation for Innovation grants to L. Fahrig.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.11.023.

References

- Andrews, K.M., Gibbons, J.W., 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia*, 772–782.
- Aresco, M.J., 2005a. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation* 123, 37–44.
- Aresco, M.J., 2005b. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. *Journal of Wildlife Management* 69, 549–560.
- Barachivich, W.J., Dodd, C.K., 2002. The Effectiveness of Wildlife Barriers and Underpasses on US Highway 41 across Paynes Prairie State Preserve, Alachua County, Florida. Phase II Post-Construction Final Report. Florida Department of Transportation.
- Beckmann, J.P., Hilty, J.A., 2010. Connecting wildlife populations in fractured landscapes. In: Beckman, J.P., Clevenger, A.P., Huijser, M.P., Hilty, J.A. (Eds.), *Safe Passages: Highways, Wildlife, and Habitat Connectivity*. Island Press, Washington, DC, USA, pp. 3–16.
- Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biological Conservation* 143, 1307–1316.
- Beringer, J.J., Seibert, S.G., Pelton, M.R., 1990. Incidence of road crossing by black bears on Pisgah National Forest, North Carolina. *International Conference of Bear Research and Management* 8, 85–92.
- Berven, K.A., 1988. Factors affecting variation in reproductive traits within a population of wood frogs (*Rana sylvatica*). *Copeia*, 605–615.
- Berven, K.A., 2009. Density dependence in the terrestrial stage of wood frogs: evidence from a 21-year population study. *Copeia*, 328–338.
- Bissonette, J., Rosa, S., 2009. Road zone effects in small-mammal communities. *Ecology and Society* 14, 27, <http://www.ecologyandsociety.org/vol14/iss1/art27/>.
- Boarman, W.I., Sazaki, M., 2006. A highway's road-effect zone for desert tortoises (*Gopherus agassizii*). *Journal of Arid Environments* 65, 94–101.
- Bouchard, J., Ford, A.T., Eigenbrod, F.E., Fahrig, L., 2009. Behavioral responses of northern leopard frogs (*Rana pipiens*) to roads and traffic: implications for population persistence. *Ecology and Society* 14, 23, <http://www.ecologyandsociety.org/vol14/iss2/art23/>.
- Bowman, J.C., 2003. Is dispersal distance of birds proportional to territory size? *Canadian Journal of Zoology* 81, 195–202.
- Bowman, J.C., Jaeger, J.A.G., Fahrig, L., 2002. Dispersal distance of mammals is proportional to home range size. *Ecology* 83, 2049–2055.
- Brandenburg, D.M., 1996. Effects of Roads on Behavior and Survival of Black Bears in Coastal North Carolina. Dissertation, University of Tennessee, Knoxville, Tennessee, USA.
- Brody, A.J., Pelton, M.R., 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* 17, 5–10.
- Brooks, R.J., Brown, G.P., Galbraith, D.A., 1991. Effects of a sudden increase in the natural mortality of adults in a population of the common snapping turtle (*Chelydra serpentina*). *Canadian Journal of Zoology* 69, 1314–1320.
- Carr, L.W., Fahrig, L., 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15, 1071–1078.
- Casagrandi, R., Gatto, M., 1999. A mesoscale approach to extinction risk in fragmented habitats. *Nature* 400, 560–562.
- Chruszcz, B., Clevenger, A.P., Gunson, K.E., Gibeau, M.L., 2003. Relationship among gizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81, 1378–1391.
- Clevenger, A.P., McIvor, M., McIvor, D., Chruszcz, B., Gunson, K., 2001. Tiger salamander (*Ambystoma tigrinum*) movements and mortality on the Trans-Canada Highway in southwestern Alberta. *Canadian Field Naturalist* 115, 199–204.
- Congdon, J.D., Dunham, A.E., van Loben Sels, R.C., 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7, 826–833.
- Congdon, J.D., Dunham, A.E., van Loben Sels, R.C., 1994. Demographics of common snapping turtles: implications for conservation and management of long-lived organisms. *American Zoologist* 34, 397–408.
- Curatolo, J.A., Murphy, S.M., 1986. The effects of pipelines, roads, and traffic on the movements of caribou, *Rangifer tarandus*. *The Canadian Field-Naturalist* 100, 218–224.
- Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128, 231–240.
- Dickson, B.G., Jenness, J.S., Beier, P., 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management* 69, 264–276.
- Dodd, N.L., Gagnon, J.W., Boe, S., Schweinsburg, R.E., 2007. Assessment of elk highway permeability by using global positioning system telemetry. *Journal of Wildlife Management* 71, 1107–1117.
- Dyer, S.J., O'Neill, J.P.S., Wasel, M., Boutin, S., 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* 65, 531–542.
- Eigenbrod, F., Hecnar, S.J., Fahrig, L., 2008. The relative effects of road traffic and forest cover on anuran populations. *Biological Conservation* 141, 35–46.
- Fahrig, L., 2001. How much habitat is enough? *Biological Conservation* 100, 65–74.
- Fahrig, L., Rytwinski, T., 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14, 21, <http://www.ecologyandsociety.org/vol14/iss1/art21/>.
- Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D., Wegner, J.F., 1995. Effect of road traffic on amphibian density. *Biological Conservation* 73, 177–182.
- Ferreras, P., Aldama, J.J., Beltran, J.F., Delibes, M., 1992. Rates and causes of mortality in a fragmented population of *Iberian lynx Felis pardini* (Temminck, 1824). *Biological Conservation* 61, 197–202.
- Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *The American Naturalist* 159, 40–56.
- Ford, A.T., Fahrig, L., 2008. Movement patterns of eastern chipmunks (*Tamias striatus*) near roads. *Journal of Mammalogy* 89, 895–903.
- Forman, R.T.T. et al., 2003. *Road Ecology: Science and Solutions*. Island Press, Washington, DC, USA.
- Fuller, T., 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105, 1–41.
- Gagnon, J.W., Theimer, T.C., Dodd, N.L., Boe, S., Schweinsburg, R.E., 2007. Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management* 71, 2318–2323.
- Gibbons, J.W., 1986. Movement patterns among turtle populations: applicability to management of the desert tortoise. *Herpetologica* 42, 104–113.
- Gibbons, M.M., McCarthy, T.K., 1986. The reproductive output of frogs *Rana temporaria* (L) with particular reference to body size and age. *Journal of Zoology* 209, 579–593.
- Gibbons, J.W. et al., 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50, 653–666.
- Gibbs, J.P., 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13, 263–268.
- Gibbs, J.P., Shriver, G., 2002. Estimating the effects of road mortality on turtle populations. *Conservation Biology* 16, 1647–1652.
- Gibbs, J.P., Steen, D.A., 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. *Conservation Biology* 19, 552–556.
- Gibeau, M.L., 2000. A Conservation Biology Approach to Management of Grizzly Bears in Banff National Park, Alberta. Dissertation, University of Calgary, Calgary Alberta, Canada.
- Gurevitch, J., Hedges, L., 1993. Meta-analysis: combining the results of independent experiments. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments*. Chapman and Hall, New York, NY, USA, pp. 378–425.
- Haug, E., 1985. Merlin feeding on road kills. *Journal of Raptor Research* 19, 103.
- Haxton, T., 2000. Road mortality of snapping turtles, *Chelydra serpentina*, in central Ontario during their nesting period. *Canadian Field Naturalist* 114, 106–110.
- Hedges, L.V., Olkin, I., 1985. *Statistical Methods for Meta-analysis*. Academic Press, Orlando, Florida.
- Holland, J.D., Fahrig, L., Cappuccino, N., 2005. Fecundity determines the extinction threshold in a Canadian assemblage of longhorned beetles (Coleoptera: Cerambycidae). *Journal of Insect Conservation* 9, 109–119.
- Hoskin, C.J., Goosem, M.W., 2010. Road impacts on abundance, call traits, and body size of rainforest frogs in Northeast Australia. *Ecology and Society* 14, 15, <http://www.ecologyandsociety.org/vol15/iss3/art15/>.
- Huijser, M.P., McGowen, P.T., 2010. Reducing wildlife-vehicle collisions. In: Beckman, J.P., Clevenger, A.P., Huijser, M.P., Hilty, J.A. (Eds.), *Safe Passages: Highways, Wildlife, and Habitat Connectivity*. Island Press, Washington, DC, USA, pp. 51–74.
- Hullett, C.R., Levine, T.R., 2003. The overestimation of effect sizes from *F* values in meta-analysis: the cause of a solution. *Communication Monographs* 70, 52–67.
- IUCN, 2010. IUCN Red list of Threatened Species 2010. International Union for the Conservation of Nature (IUCN), Gland, Switzerland. <<http://www.iucn.org>>.
- Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., Tluk von Toschanowitz, K., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* 185, 329–348.
- James, A.R.C., Stuart-Smith, K., 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64, 154–159.
- Johnson, W.C., Collinge, S.K., 2004. Landscape effects on black-tailed prairie dog colonies. *Biological Conservation* 115, 487–497.
- Kaplan, R.H., Salthe, S.N., 1979. The allometry of reproduction: an empirical view in salamanders. *The American Naturalist* 113, 671–689.

- Karraker, N.E., Gibbs, J.P., 2011. Contrasting road effect signals in reproduction of long- versus short-lived amphibians. *Hydrobiologia* 66, 213–218.
- King, M.B., Duval, D., 1990. Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging and sex differences. *Animal Behaviour* 39, 924–935.
- Knight, R.L., Kawashima, J.Y., 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management* 57, 266–271.
- Lambertucci, S.A., Speziale, K.L., Rogers, T.E., Morales, J.M., 2009. How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodiversity and Conservation* 18, 2063–2074.
- Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M., Breton, L., 2008. Behavior of moose relative to a road network. *Journal of Wildlife Management* 72, 1550–1557.
- León-Cortés, J.L., Lennon, J.J., Thomas, C.D., 2003. Ecological dynamics of extinct species in empty habitat networks. 1. The role of habitat pattern and quantity, stochasticity and dispersal. *Oikos* 102, 449–464.
- Lipsey, M.W., Wilson, D.B., 2001. *Practical Meta-analysis*. SAGE Publications, Thousand Oaks, California, USA.
- Lovall, M.J., Anderson, E.M., 1996. Bobcat movements and home ranges relative to roads in Wisconsin. *Wildlife Society Bulletin* 24, 71–76.
- Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., Zurring, H., 1996. Relationships among grizzly bears, roads, and habitat in the Swan Mountains, Montana. *The Journal of Applied Ecology* 33, 1395–1404.
- Marchand, M.N., Litvaitis, J.A., 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conservation Biology* 18, 758–767.
- McCoy, K., 2005. Effects of Transportation and Development on Black Bear Movement, Mortality, and Use of the Highway 93 Corridor in NW Montana. Dissertation, University of Montana, Missoula, MT, USA.
- McGregor, R.L., Bender, D.J., Fahrig, L., 2008. Do small mammals avoid roads because of the traffic? *Journal of Applied Ecology* 45, 117–123.
- McLellan, B.N., Shackleton, D.M., 1988. Grizzly bears and resource-extraction industries: effects of roads on behavior, habitat use and demography. *Journal of Applied Ecology* 25, 451–460.
- Meunier, F.P., Verheyden, C., Jouvantin, P., 2000. Use of road-sides by diurnal raptors in agricultural landscapes. *Biological Conservation* 92, 291–298.
- Oxley, D.J., Fenton, M.B., Carmody, G.R., 1974. The effect of roads on populations of small mammals. *Journal of Applied Ecology* 11, 51–59.
- Palma, L., Beja, P., Rodrigues, M., 1999. The use of sighting data to analyse *Iberian lynx* habitat and distribution. *Journal of Applied Ecology* 36, 812–824.
- Patrick, D.A., Gibbs, J.P., 2010. Population structure and movements on freshwater turtles across a road-density gradient. *Landscape Ecology* 25, 791–801.
- Pupin, N.C., Gasparini, J.L., Bastos, R.P., Haddad, C.F.B., Prado, C.P.A., 2010. Reproductive biology of an endemic *Physalaemus* of the Brazilian Atlantic forest, and the trade-off between clutch and egg size in terrestrial breeders of the *P. signifier* group. *Herpetological Journal* 20, 147–156.
- R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>>.
- Riley, S.P.D., Pollinger, J.P., Sauvajot, R.M., York, E.C., Bromley, C., Fuller, T.K., Wayne, R.K., 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology* 15, 1733–1741.
- Rondinini, C., Doncaster, C.P., 2002. Roads as barriers to movement for hedgehogs. *Functional Ecology* 16, 504–509.
- Rosen, P.C., Lowe, C.H., 1994. Highway mortality of snakes in the Sonoran desert of Southern Arizona. *Biological Conservation* 68, 143–148.
- Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64, 672–684.
- Ruediger, W., 2001. High, wide, and handsome: designing more effective wildlife and fish crossings for roads and highways. In: Evink, G.L. (Ed.), *Proceedings of the 2001 International Conference on Ecology and Transportation*. North Carolina State University, Durham, NC.
- Rytwinski, T., Fahrig, L., 2007. Effect of road density on abundance of white-footed mice. *Landscape Ecology* 22, 1501–1512.
- Rytwinski, T., Fahrig, L., 2011. Reproductive rates and body size predict road impacts on mammal abundance. *Ecological Applications* 21, 589–600.
- Schindler, D.W., Walker, D., Davis, T., Westwood, R., 2006. Determining effects of an all weather logging road on winter woodland caribou habitat use in south-eastern Manitoba. *Rangifer* 17, 209–217.
- Schwarzkopf, L., 1994. Measuring trade-offs: a review of studies of costs of reproduction in lizards. In: Vitt, L.J., Pianka, E.R. (Eds.), *Lizard Ecology: Historical and Experimental Perspectives*. Princeton University Press, Princeton, NJ, pp. 7–30.
- Smith, D.J., 2004. Impacts of roads on ecological networks and integration of conservation and transportation planning: Florida as a case study. In: Jongman, R., Pungetti, G. (Eds.), *Ecological Networks and Greenways: Concept, Design, Implementation*. Cambridge University Press, Cambridge, UK, pp. 73–93.
- Steen, D.A. et al., 2006. Relative vulnerability of female turtles to road mortality. *Animal Conservation* 9, 269–273.
- Stewart, K.M., Bowyer, R.T., Kie, J.G., 2010. Spatial distributions of mule deer and North American elk: resources partitioning in a sage-steppe environment. *American Midland Naturalist* 163, 400–412.
- Sullivan, B.K., 1981. Observed differences in body temperature and associated behaviour of four snake species. *Journal of Herpetology* 15, 245–246.
- Summers, P.D., Cunningham, G.M., Fahrig, L., 2011. Are negative effects of roads on breeding birds caused by traffic noise? *Journal of Applied Ecology* 48, 1527–1534.
- Tanner, D., Perry, J., 2007. Road effects on abundance and fitness of Galápagos lava lizards (*Microlophus albemarlensis*). *Journal of Environmental Management* 85, 270–278.
- Taylor, B.D., Goldingay, R.L., 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. *Wildlife Research* 37, 320–331.
- Tinkle, D.W., Wilbur, H.M., Tilley, S.G., 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24, 55–74.
- Van Houtan, K.S., Pimm, S.L., Halley, J.M., Bierregaard Jr., R.O., Lovejoy, T.E., 2007. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters* 10, 219–229.
- Vance, M.D., Fahrig, L., Flather, C.H., 2003. Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology* 84, 2643–2653.
- Vetter, D., Hansbauer, M.M., Végvári, Z., Storch, I., 2011. Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. *Ecography* 34, 1–8.
- Viechtbauer, W., 2010. *Metafor: Meta-analysis Package for R*. R Package Version 1.5-0. <<http://www.R-project.org>>.
- Waller, J.S., Servheen, C., 2005. Effects of transportation infrastructure on grizzly bears in northwestern Montana. *Journal of Wildlife Management* 69, 985–1000.
- Watson, J.W., 1986. Range use by wintering rough-legged hawks in Southeastern Idaho. *Condor* 88, 256–258.
- Whittington, J., Clair St., C.C., Mercer, G., 2004. Path tortuosity and the permeability of roads and trails to wolf movement. *Ecology and Society* 9, 4, <<http://www.ecologyandsociety.org/vol9/iss1/art4/>>.
- Wilbur, H.M., 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. *The American Naturalist* 111, 43–68.
- With, K.A., King, A.W., 1999. Extinction threshold for species in fractal landscapes. *Conservation Biology* 13, 314–326.