**The effects of species behavioural responses to roads and life history traits on their
population level responses to roads**

by
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the requirements for the degree of

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Abstract

There is now a growing body of evidence that 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 mitigation will be effective at reducing/eliminating road related impacts on wildlife, it is important to have some validated theory that allows us to predict which species or species groups are most vulnerable to road effects at the population level, and the likely causes of those impacts, so that mitigation efforts can be tailored to those species. The overarching goal of my dissertation is to advance our understanding of the circumstances in which roads affect population persistence. In Chapter 1, I conducted extensive field surveys to quantify the relationships between road density and abundance for a wide range of mammal species in eastern Ontario. My results show that mammal species with lower reproductive rates, greater mobilities, and larger body sizes are more susceptible to negative road/traffic effects at the population level. In Chapter 2, I broadened the scope of the investigation by using a meta-analysis to combine empirical results of population level effects of roads from studies across the globe and on multiple taxa, to identify the species or species groups whose populations are most likely to be reduced by roads. These results confirm that wide-ranging large mammals with low reproductive rates are more susceptible to negative road effects at the population level. In addition, they indicate that birds with larger territories, all amphibians and reptiles, and species that do not avoid roads or are disturbed by traffic are susceptible to negative road effects. In Chapter 3, I used a simulation model to develop general hypotheses and predictions specifically of the circumstances leading to neutral and positive effects of roads on population abundance. My results suggest that there are many species and situations for which road mitigation is not

necessary. Taken together, my results demonstrate that priority for mitigation should be directed towards wide-ranging large mammals with low reproductive rates, birds with larger territories, and all amphibians and reptiles. More generally, mitigation should focus on species that do not avoid roads or are disturbed by traffic, and on all large species types.

Preface

Co-authorship Statement

My contributions to the research described in this thesis were: (1) I proposed and developed the research questions in corporation with Dr. Lenore Fahrig, and was primarily responsible for the design of the projects used to address these questions; (2) I carried out all field work for chapter 1; (3) I analysed all of the data; and (4) I wrote all first drafts of the chapters/manuscripts.

This thesis is formatted using the integrated thesis format and therefore each data chapter was formatted as an independent research article that has either been published in or was submitted to a peer-reviewed journal when this thesis was completed. There is some repetition in introductions and discussion, however I have cross-referenced between chapters to reduce repetition as much as possible. As indicated above, I performed the majority of the work described in this thesis. However, Dr. Lenore Fahrig contributed significantly during the conception and writing phases of the three chapters described herein.

I have permission from each publisher to reproduce published manuscripts in my thesis. I have also received permission from my co-author (Dr. Lenore Fahrig) to use the work in this thesis. A specific chapter that has been published elsewhere must be cited using the journal citation information provided below. However, to reference my thesis as a whole or an unpublished chapter, I recommend using the following citation:

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This dissertation is dedicated to the memory of my mother,
Deborah Anne Rytwinski (1953-2003)

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General Introduction

Increased land use by humans has led to habitat loss and fragmentation. Habitat loss has large, negative effects on biodiversity (Fahrig, 2003). Conflicting results however, have been reported on the effects of habitat fragmentation per se (the “breaking apart” of habitat independent of habitat loss) on biodiversity. Results of a literature review by Fahrig (2003) revealed that, when habitat fragmentation per se did have an effect on biodiversity, it was just as likely to be positive as negative.

One of the main causes of habitat fragmentation has been and continues to be the construction of roads. Over the last 100 years, North America’s landscapes have become increasingly fragmented by roads. For example, the network of paved roads in Canada has tripled from 100,000 km in 1959 to 300,000 km in 2001 (Forman et al., 2003). As road networks continue to increase worldwide, so too has the interest in their ecological effects. Over the past 12 years “road ecology” has emerged as a bona fide subdiscipline within ecology, as evidenced by road-ecology sessions at ecology conferences and transportation conferences, a dedicated biennial road-ecology scientific meeting (International Conference on Ecology and Transportation), the emergence of road-ecology research centers (e.g., Road Ecology Center, University of California at Davis; Center for Transportation and the Environment, North Carolina State University; Western Transportation Institute, Montana State University), and a textbook on road ecology (Forman et al., 2003). The main concern among conservationists and environmental planners is that roads and traffic may be reducing or even removing wildlife populations (Trombulak and Frissell, 2000; Forman et al., 2003). In a recent research agenda for road ecology, Roedenbeck et al. (2007) identify five relevant road ecology research questions that need to be addressed, the most pressing being: "Under what circumstances do roads affect

population persistence?" While there have been numerous studies on the effects of roads on wildlife movement and mortality, the important and crucial question is whether or not roads are having an impact on population viability. Roedenbeck et al. (2007) states that while there is a need for studies to evaluate the relationship between road density and wildlife population abundance and/or distribution, there is also a need to evaluate road effects at the landscape scale. Landscape-level studies that explicitly include the spatial patterns of the environment in a representation relevant to the organisms of question, and that address species-specific movement and abundance parameters are essential to extend fine-scale species environment relationships to the level of regional populations (Cushman, 2006).

The degree and direction to which habitat fragmentation by roads affects a population should depend on species traits. How a species responds to habitat fragmentation is assumed to be related to its ability to move through the landscape and persist in small patches (Etienne and Heesterbeek, 2001; Vos et al., 2001). Therefore, species characteristics (morphological, ecological and behavioural) interact with the landscape characteristics to affect viability of metapopulations (Hanski and Ovaskainen, 2000; Vos et al., 2001). For example, more mobile species are suggested to be less sensitive to habitat fragmentation (reviewed in Fahrig, 2007); however this theory does not take into consideration mortality of individuals in the matrix or "nonhabitat" areas of the landscape. To date, there are no studies investigating how species movement ranges and/or other life history traits affect the degree of species population-level responses to landscape fragmentation by roads. Several hypotheses have been proposed as explanations for road effects. These hypotheses fall into two main sets: (i) hypotheses based on species life history traits and (ii) hypotheses based on species behavioural 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). 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). Since species with large home ranges and low reproductive rates naturally occur at low densities, I 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).

The second set of hypotheses suggests that species behavioural responses to roads and traffic moderate the population-level effects of roads. Jaeger et al. (2005) proposed that there are three behavioural responses to roads and traffic: (i) avoidance of the road surface, (ii) avoidance of traffic disturbance (noise, lights, chemical emissions), and (iii) vehicle avoidance (described

as 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 behavioural response to roads is road attraction. 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).

In a review of the empirical literature on effects of roads on animal population abundance and distribution, we found 78 papers documenting effects of roads and/or traffic on animal abundance (Fahrig and Rytwinski, 2009). The number of documented negative effects outnumbered the number of positive effects by a factor of five and there were some clear differences among the groups. Amphibians and reptiles tended to show negative effects. Birds showed mainly negative or no effects, with a few positive effects for small birds and vultures. Small mammals generally showed either positive effects or no effect, mid-sized mammals showed either negative effects or no effect, and large mammals showed predominantly negative effects.

We synthesized this information with information on species attributes to develop predictions of the conditions that lead to positive or negative effects or no effects of roads on animal abundances (see Fig. 2 in Fahrig and Rytwinski, 2009). Although derived from the existing literature, these predictions still needed to be tested with independent data.

In my first data chapter, I investigated how life history traits affect mammal species responses to increasing road density using independent empirical data collected in eastern Ontario to address the question: *Is there an increasingly negative response of mammals to increasing road density as mammal movement ranges and body sizes increase and reproductive rates decrease?* Our literature review suggested that larger mammals (with larger movement ranges and lower reproductive rates) are more negatively affected by roads and that small mammals often show positive effects of roads. However, many of the studies in the review are compromised due to weaknesses in study design, particularly when the original purpose of the study was not to quantify the effects of roads. Two common issues are: 1) road density is often highly correlated with other land cover variables (e.g., urban area, forest amount); and 2) low variation in road density across landscapes, which reduces the apparent effect of road density. To address my first research question, I focused on the first set of hypotheses proposed as explanations for road effects and tested the predictions that the effects of roads on mammal populations should be increasingly negative with (1) decreasing reproductive rate, (2) increasing mobility, and (3) increasing body size. I did this by collecting relative abundances estimates for 17 mammal species over two field seasons (2008 and 2009) from landscapes ranging in road density using study designs that were not subject to common problems found in studies carried out at the landscape scale discussed above.

In Chapter 2, I addressed the research question: *What kind of species or species groups are most vulnerable to roads and traffic at the population level?* To address this question, I

conducted a meta-analysis using existing data from the literature that quantified the relationship between roads and/or traffic and population abundance of at least one species to determine species life history characteristics and behavioural responses to roads and/or traffic that make species or species groups prone to negative road and/or traffic effects. I did this by first converting the various estimates of the effects of roads and traffic on animal population abundance into a common measure (effect size), the Pearson correlation coefficient r . I then tested 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. I had initially hoped to include species-specific behavioural responses to roads and/or traffic as a moderator variable in the meta-analysis, however there was too little information available for too few species. Instead, I tabulated the species into behavioural response categories, in order of increasing predicted negative effects of roads and conducted a qualitative analysis of the tabulated results.

In Chapter 3, I constructed an individual-based simulation model of population dynamics to predict the combinations of life history traits and behavioural responses to roads that lead to neutral or positive effects of increasing road density on animal population abundance to address the question: *What circumstances lead to neutral and positive effects of roads on animal population abundance?* Several hypotheses linking roads to animal population abundance have been suggested, with possible outcomes across the full spectrum of negative, neutral and positive population-level effects. Although the majority of population-level responses to roads are negative, in our 2009 review paper we found that about 29% of responses were neutral and about 12% were positive. Following the addition of unpublished data from theses, and results of several recent studies, in the meta-analysis from my 2nd chapter the estimated proportion of

positive effects increased to about 24%. To date there are very few species for which quantitative data on both population-level responses to roads and/or traffic and behavioural responses to roads exist in the literature (only 17 species globally), and consequently, our understanding of how life history traits interact with particular behavioural responses to roads to affect species population-level responses to roads is limited. This prompted me to use an individual-based simulation model to improve prediction of the combinations of life history traits and behavioural responses to roads that lead to neutral and positive effects of roads on animal population abundance.

The three data chapters of my thesis are linked by their focus on advancing our understanding the circumstances in which roads affect population persistence, so that road mitigation measures can be tailored to those species whose populations are most at risk to negative population effects of roads. In Chapter 1, I conducted extensive field surveys to quantify the relationships between road density and abundance for a wide range of mammal species in eastern Ontario. In Chapter 2, I broadened the scope of the investigation by combining empirical results of population level effects of roads from studies across the globe and on multiple taxa, to identify the species or species groups whose populations are most likely to be reduced by roads, and the likely causes of those impacts. In Chapter 3, I used a simulation model to develop general hypotheses and predictions specifically of the circumstances leading to neutral and positive effects of roads on population abundance.

CHAPTER ONE

Reproductive rate and body size predict road impacts on mammal abundance

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Abstract

It has been hypothesized that mobile species should be more negatively affected by road mortality than less mobile species because they interact with roads more often, and that species with lower reproductive rates and longer generation times should be more susceptible to road effects because they will be less able to rebound quickly from population declines. Taken together, these hypotheses suggest that, in general, larger species should be more affected by road networks than smaller species because larger species generally have lower reproductive rates and longer generation times and are more mobile than smaller species. I tested these hypotheses by estimating relative abundances of 17 mammal species across landscapes ranging in road density within eastern Ontario, Canada. For each of the 13 species for which detectability was not related to road density, I quantified the relationship between road density and relative abundance. I then tested three cross-species predictions: that the slope of the relationship between road density and abundance should become increasingly negative with (1) decreasing annual reproductive rate; (2) increasing home range area (an indicator of movement range) and; (3) increasing body size. All three predictions were supported in univariate models, with R^2 values of 0.68, 0.50, and 0.52 respectively. The best overall model based on AICc contained both reproductive rate ($p=0.008$) and body size ($p=0.072$), and explained 77 percent of the variation in the slope of the relationship between road density and abundance. My results suggest that priority should be placed on mitigating road effects on large mammals with low reproductive rates.

Introduction

Over the last 100 years, North America's landscapes have become increasingly fragmented by roads. As road networks continue to increase worldwide, so too has the interest in their effects on wildlife populations (Trombulak and Frissell, 2000; Forman et al., 2003). In their research agenda for road ecology, Roedenbeck et al., (2007) identified five critical road ecology research questions that need to be addressed, the most pressing being: "Under what circumstances do roads affect population persistence?"

Several hypotheses have been suggested for predicting the types of species whose populations should be most negatively affected by roads. Species that make frequent, long-range movements over the landscape should be more negatively affected by roads because they interact with roads more often than do less mobile species (Carr and Fahrig, 2001; Gibbs and Shriver, 2002; Forman et al., 2003). Similarly, species with larger territories or home ranges should be more susceptible to road effects than those with smaller territories/home ranges. Species with lower reproductive rates and longer generation times (i.e., species having K-selected life histories), should also be more susceptible to road effects because they will be less able to rebound quickly from population declines (Gibbs and Shriver, 2002). Since species with large home ranges and low reproductive rates naturally occur at low densities, I also expect that species that naturally occur at low densities should be more susceptible to road effects.

These hypotheses can be summarized into two main mechanisms that should affect both the magnitude and direction of the road effect on mammals: (1) reproductive rate, which affects a species ability to rebound from low numbers resulting from road mortality and, (2) mobility (movement range and/or home range), which affects a species encounter rate with roads. Since

both mechanisms are related to a species natural density, as outlined above, density is indirectly captured in these two mechanisms. Taken together, these hypotheses also suggest that, in general, larger species should be more affected by road networks 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 small mammals, further strengthening the prediction that negative road effects should increase with increasing body size. 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; Fahrig and Rytwinski, 2009).

The purpose of this study was to test the predictions that the effects of roads on mammal populations should be increasingly negative with (1) decreasing reproductive rate, (2) increasing mobility, and (3) increasing body size. I did this by estimating relative abundances of 17 mammal species from landscapes ranging in road density within eastern Ontario, during three sampling periods: 2005, 2008, and 2009. For each of the 13 species for which detectability was not related to road density, I estimated the slope of the relationship between road density and relative abundance. I then tested for relationships between these slopes and reproductive rate, home range area as an indicator of mobility (Bowman et al., 2002), and body size.

Methods

In each of three field seasons (2005, 2008 and 2009) I targeted a particular set of mammal species representing a particular range of body sizes. In 2005 I targeted very small mammals (up to 22g), in 2008 I targeted mid-sized to large mammals (up to 9500g), and in 2009 I targeted the larger small mammals and smaller mid-sized mammals (up to 600g). To obtain abundance estimates of these different species across a large number of landscapes, I needed to use different sampling techniques for the different species groups. This resulted in a data set in which the relative abundance estimates for a single species within a single year are comparable across landscapes, but relative abundance estimates are not comparable across species or within species across years. However, since my objective was to evaluate effects of reproductive rate, mobility, and body size on the slope of the relationship between relative abundance and road density (not on abundance itself), I did not need absolute abundance estimates, or abundance estimates that are comparable across species; I only needed relative abundance estimates that are comparable within species across landscapes.

Surveys conducted during summer 2005 (as part of my MSc)

Site Selection

In 2005 I surveyed small mammals [*Peromyscus leucopus*, *Zapus hudsonius*, *Napaeozapus insignis*, *Blarina brevicauda*, *Tamias striatus*] in 14 forest patches selected such that they were centered in 14 landscapes that varied widely in road density (km/km^2). I defined each landscape as the area within a 2-km radius of each sampled patch (Fig. 1.1). This size of landscape was based on reported long-distance movements of small mammals. Such

Figure 1.1. Examples of two landscapes (the area inside the circles in each panel): (a) low road density and (b) high road density. Landscapes for the 2005 and 2009 sampling period were 2-km-radius areas around each of 14 and 24 forest patches, respectively. During 2005 and 2009, small mammals were sampled in a 100-m² grid and a 140-m² grid (respectively) in each patch. For the 2008 sampling period, landscapes were 3-km-radius areas around the center of each of the 29 sampling sites. The sample site is represented by a black dot, roads by lines, and forest cover by gray shading. Reprinted with permission from © 2011 Ecological Society of America.

reports are rare (Diffendorfer and Slade, 2002), but *Peromyscus* sp. has been reported to travel over 1 km in under a month (Murie and Murie, 1931; Howard, 1960; Bowman et al., 1999; Maier, 2002). In selecting the 14 sample patches, I attempted to maximize the variation in road density among the surrounding landscapes while controlling for landscape variables other than road density. I selected only rural landscapes, containing no urban development, and approximately 20-35% forest (Fig. 1.1). I chose 20-35% forest because it allowed the largest possible range of road density values, given the variation in forest cover and road densities in eastern Ontario. Landscapes also contained limited or no water (i.e., no rivers or lakes) and no railways, to avoid the possibility of additional barrier effects. I sampled forest patches that were located at least 3 km apart to minimize overlap of the landscapes. Sampled patches were all larger than 1 ha and of similar forest type (deciduous/mixed deciduous). Landscapes with lower and higher road densities were interspersed across the Ottawa region as much as possible to avoid possible confounding effects of regional trends (Fig. 1.2).

Mammal sampling

I sampled small mammals between 6 June and 29 July 2005 using footprint tracking tubes (Merriam, 1990). The proportion of tracking stations containing small mammal tracks has been shown to be a good estimate of relative abundance (Fahrig and Merriam, 1985; Brown et al., 1996; Drennan et al., 1998; Glennon et al., 2002).

I lined 30-cm lengths of 3.75 cm (inside diameter) plastic water pipe (PVC tubing) with a strip of white paper (28 x 7cm). To the center of each paper, I stapled a 6 x 6 cm square of waxed paper with a smear of powdered carbon black (decolourizing) and paraffin oil (Nams

Figure 1.2. Distribution of landscapes studied across eastern Ontario. Smaller circles represent the 2-km radius landscapes at the centers of which small mammals were sampled during summers of 2005 and 2009 (note that the smaller dotted circles correspond to those landscapes that were used for both the 2005 and 2009 sampling seasons), and larger circles represent the 3-km radius landscapes at the centers of which larger mammals were sampled during the summer of 2008. Gray-filled circles correspond to lower road density landscapes and white circles correspond to higher road density landscapes. All landscapes were in rural areas. Reprinted with permission from © 2011 Ecological Society of America.

and Gillis, 2002) in a ratio of 1:3 (by weight). Each sample patch contained a 10 x 10 grid of tubes at 10-m spacing. Tubes were not baited. I checked tubes weekly for tracks and replaced tubes with newly prepared papers weekly. Relative abundance was estimated as the total number of tracks found at the site over the eight week tracking period; the maximum possible value was 800 (i.e., 100 tubes for eight weeks at each site).

Sample Patch Characteristics

To assess whether local habitat variables differed among sampled patches, I carried out vegetation surveys in each patch from 13 July to 22 July 2005. For each patch, I estimated the number of woody tree species, density of shrub vegetation, percent cover of coarse woody debris (CWD), patch size, and patch shape (see Rytwinski and Fahrig (2007) for vegetation survey methods).

Surveys conducted during summer 2008

Site Selection

In 2008, I selected 29 landscapes within eastern Ontario to sample mid-sized and large mammals [*Mustela ermine*, *Tamiasciurus hudsonicus*, *Lepus americanus*, *Sylvilagus floridanus*, *Mephitis mephitis*, *Marmota monax*, *Martes pennant*, *Vulpes vulpes*, *Procyon lotor*, *Ursus americanus*]. Each landscape was centred on a sampling site containing a stream/creek and a forest patch greater than 6 ha within 150 m of each other. This was done to cover the reported habitat preferences for all target species. Landscapes were defined as the area within a 3-km radius of each sampling site. Since the home range sizes (and reported movement distances) of my target species range widely (e.g., in Ontario home range size for adult male and female short-

tailed weasels [*M. ermine*] are 21.3 ha and 8.3 ha respectively (Simms, 1979), compared to 4020 ha for adult female black bears [*U. americanus*; Maxie, 2009]), I could not select a landscape size that would encompass the entire home ranges of all species due to the logistical constraints of monitoring a large number of sites. I chose a 3-km radius (2826 ha) landscape to encompass the entire home range of the species with the second largest home range, the red fox (*V. vulpes*). I selected landscapes containing no urban development and similar forest amounts (approximately 20-35%) and forest types (deciduous/mixed deciduous), and varying as widely as possible in road density (km/km²). Landscapes were at least 2 km apart to minimize the chance of sampling the same individual at different sites. Landscapes with lower and higher road densities were interspersed across eastern Ontario as much as possible to avoid possible confounding effects of regional trends (Fig. 1.2).

Mammal Sampling

At each site, I placed three tubes, two enclosed track boxes and one semi-enclosed track box (described in next paragraph), to detect the presence of mammals at each site, near the center of each landscape (Fig. 1.3 and Fig. 1.4). All tubes and track boxes were placed at least 50 m apart. I placed one tube and one enclosed track box along the stream/creek edge, one tube and one semi-enclosed track box within 10m of the forest edge (inside the forest patch between the forest and the stream), and one tube and one enclosed track box farther than 100 m from all edges in the interior of the forest patch (Fig. 1.3).

I used enclosed track boxes to exploit the need of some mid-sized mammals to investigate confined spaces to locate food, den locations, and/or resting/shelter sites (Zielinski and Kucera, 1995; Foresman and Pearson, 1998; Loukmas et al., 2003; O'Connell et al., 2006). However, since other species may be reluctant to enter enclosed tracking boxes (Zielinski and

Figure 1.3. Set-up for each of the twenty-nine sites sampled during 2008. Six sampling devices were placed at each site: one tube and one enclosed track box were placed along a stream edge within 150 m of a forest patch > 6ha; one tube and one semi-enclosed track box were placed within 10 m of forest edge (inside the forest patch between the forest and the stream); and one tube and one enclosed track box were placed at least 100 m from all edges in the interior of the forest patch. All tubes and track boxes were placed 50 m apart. Key: enclosed tracking box ; semi-enclosed tracking box ; tracking tube . Reprinted with permission from © 2011 Ecological Society of America.

Figure 1.4. Examples of devices used to obtain mammal footprints: a) foot-prints of white-footed mouse (*Peromyscus leucopus*) on tracking paper from a 30-cm tracking tube with 3.75 cm inside diameter, used during 2005; b) enclosed tracking box (note raccoon (*Procyon lotor*) prints on paper); c) semi-enclosed tracking box; d) 50-cm tracking tube with 7.62 cm inside diameter. Types b-d, were used during 2008. Not shown are the 45-cm tubes with 7.62 cm and 10.16 cm inside diameter used in 2009. Reprinted with permission from © 2011 Ecological Society of America.

Kucera, 1995; Manley et al., 2006), I developed a modified open track plate (semi-enclosed) to promote visits from these species. I constructed enclosed tracking boxes (30 cm wide x 30 cm high x 85 cm long) from sheets of coroplast. Four wooden stakes 45cm long were hammered into the ground and tied with twine around the enclosed track plates to help provide stability (Fig. 1.4b). The tracking plate was composed of 1.6-mm thick polystyrene plastic sheets (29 x 81 cm) which were partially covered with brown butcher paper (contact paper) and placed inside the enclosed coroplast box. I aligned the contact paper at the center of the plastic sheet leaving about 13 cm of exposed plate at either end to which I painted a smear of powdered carbon black (decolourizing) and paraffin oil. The semi-enclosed tracking boxes were made from two 1.1 cm thick wood chip board sheets. The top sheet (1.0 x 1.0 m) was raised 35 cm above ground over a bottom sheet (0.8 x 0.8m) by four 45 cm long 5 x 5 cm wooden stakes that were screwed into the top sheet and then hammered into the ground alongside the bottom sheet (Fig. 1.4c). I constructed tracking plates from 1.6 mm thick polystyrene plastic sheets (0.8 x 0.8 m) which were partially covered with brown butcher paper (56 x 56 cm) and placed on the bottom sheet. The 12-cm exposed border around the perimeter of the tracking plate was then painted with the carbon black and paraffin oil mixture (1:3 ratio by weight). I constructed tracking tubes from 50 cm long plastic water pipes with 7.62 cm inside diameter. Tubes were lined with a strip of white paper (48 x 14 cm). At each end of the paper, a square piece of waxed paper (11 x 11 cm) was stapled and smeared with powdered carbon black and paraffin oil (1:3 ratio by weight). To prevent tubes from rolling on the ground, two 28 cm long, 5 x 5cm wooden stakes were placed under and perpendicular to the tube and secured by attaching 33-cm lengths of metal strapping around the tubes (Fig. 1.4d).

Track stations had a lure of mink gland and salmon oil (1:1 mixture) presented in a non-reward manner (Loukmas et al., 2003), to entice visitation by short-tailed weasels (*Mustela erminea*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*) and fisher (*Martes pennanti*). I chose a lure with no reward over bait to reduce the chance of the same individual revisiting track stations every week. The lure mixture was placed inside a housing capsule constructed from galvanized plumbing supplies attached to the roof of each track station. Lure capsules released the lure scent without allowing the animal to ingest the lure.

Tracking began 2 June 2008 and continued for 11 consecutive weeks, ending 22 August 2008. Tracking stations were checked once a week for a total of 11 checks. During weekly checks, the butcher paper was collected and replaced and the tracking stations were repainted and fresh lure was added. Tracks were identified using Rezendes (1999) and compared to the Carleton University footprint library. Relative abundance was taken as the number of weeks that a mammal species tracks were identified at each sample site.

Local Site Characteristics

I carried out vegetation surveys from 28 July to 15 August 2008, based on vegetation associations of target species, *Mustela erminea*, *Mephitis mephitis*, *Procyon lotor* and *Martes pennanti* (Pedlar et al., 1997; Larivières and Messier, 1998; Gehring and Swihart, 2003; Zielinski et al., 2004; Baldwin et al., 2006; Zielinski et al., 2006). Four 10 x 10 m plots were created 25 m from the two tracking boxes in the forest patch in each cardinal direction. Within each of the eight 10 x 10 m plots, all trees and snags (dead standing trees) ≥ 10 cm diameter were identified and their diameter at breast height (DBH) recorded. Tree and snag density was measured as the combined total of all trees (or snags) from the eight plots divided by the area sampled. Average

tree and snag DBH was the sum of all tree (or snag) DBHs for the eight plots, divided by the total number of trees (or snags). Within each of the eight 10-m² plots, the lengths of all fallen dead and down CWD ≥ 10 cm diameter were recorded. The average length of CWD was the sum of all lengths recorded from the eight plots, divided by the total number of CWD. At each 10 x 10 m plot, one tree within the forest stand was randomly selected and its height was determined using a clinometer. Average canopy height was the average height of the eight trees from the eight plots. Canopy cover was measured by walking the perimeter of the 10-m² plots and stopping at 2-m intervals to record 20 'hit' or 'miss' readings using an ocular tube for the presence or absence of canopy cover sighted (James and Shugart, 1970). Percent canopy cover was the percentage of the 160 sightings that were 'hits'.

A 3 x 3 m plot was sampled for woody and herbaceous vegetation at the center of each 10 x 10 m plot. The number of woody and herbaceous stems was counted (separately) and separated into height intervals: 0.5 to <1 m, 1 to <2 m, and >2 m with <10 cm DBH, the latter for woody stems only. Stem density was estimated for woody and herbaceous vegetation within each height interval as the number of stems for all 3 x 3 m plots divided by the total area sampled (i.e., 24- m² area). Percent ground cover was estimated in a 1 x 1 m ground cover frame placed in the center of each 10 x 10 m sampling plot. Percent ground cover was averaged over the eight 1-m² sampling plots in each site. The number of potential dens was estimated by walking a 30 x 10 m plot 5m from each of the two tracking boxes, in each cardinal direction and recording the number of ground dens (holes in ground with openings ≥ 5 cm diameter), CWD that were ≥ 30 cm DBH at their maximum diameter, snags that were ≥ 30 cm DBH, brush piles, and rock piles. The total number of potential dens for a site was the number of all potential dens from the eight 30 x 10 m walked plots.

Surveys conducted during summer 2009

Site Selection

In 2009, I surveyed small mammals and smaller mid-sized mammals [*Peromyscus leucopus*, *Zapus hudsonius*, *Napaeozapus insignis*, *Blarina brevicauda*, *Clethrionomys gapperi*, *Mustela ermine*, *Tamias striatus*, *Tamiasciurus hudsonicus*, *Sciurus carolinensis*, *Procyon lotor*] in 24 forest patches selected such that they were centered in 24 landscapes that varied in road density (km/km^2), using the same criteria for landscape and site selection as in 2005 (above; Fig. 1.2) with the exception that sampled patches were all larger than 4 ha.

Mammal sampling

I conducted sampling between 1 June 2009 and 24 July 2009 using a combination of tracking tubes and semi-enclosed tracking boxes (all unbaited). Forty-five-cm lengths of tracking tubes were used in two different diameters (7.62 cm and 10.16 cm inside diameter) and lined with paper containing a square of carbon black-coated waxed paper. As in 2008, I included semi-enclosed tracking boxes (same construction as described 2008, but smaller; top and bottom chipboard sheets were 40 x 40 cm) to promote visits from species that may be reluctant to enter confined spaces (e.g., arboreal species such as *Sciurus carolinensis*). Each focal patch contained a 7 x 7 grid of tubes and boxes at 20-m spacing (seven lines with seven tracking stations per line). Each line consisted of one semi-enclosed box, and either three 7.62-cm (inside diameter) tubes and three 10.16-cm (inside diameter) tubes or four 7.62-cm (inside diameter) tubes and two 10.16-cm (inside diameter) tubes. This resulted in a total of twenty-five 7.62-cm tubes, seventeen 10.16-cm tubes and seven boxes per grid (Fig. 1.5).

Figure 1.5. Set-up of each of the twenty-four sites sampled during 2009. Each focal patch contained a 7 x 7 grid of tubes and boxes at 20-m spacing (7 lines with 7 tracking stations per line). All tracking stations were placed at least 10 m from any forest edge. Each line consisted of one semi-enclosed box, and either three 7.62-cm (inside diameter) tubes and three 10.16-cm (inside diameter) tubes (lines A, C, and E) or four 7.62-cm (inside diameter) tubes and two 10.16-cm (inside diameter) tubes (lines B, D, F, and G). Key: semi-enclosed tracking box ; 7.62cm tracking tube ; 10.16cm tracking tube . Reprinted with permission from © 2011 Ecological Society of America.

I checked tubes and boxes weekly for tracks and replaced tracking papers weekly. Relative abundance was estimated as the total number of tracks found at the site over the eight week tracking period; the maximum possible value was 392 (i.e., 49 tracking stations for eight weeks at each site). Tracking procedures for all three years followed guidelines from the Canadian Council on Animal Care (CCAC) and were approved by the Carleton University Animal Care Committee.

Sample Patch Characteristics

I carried out vegetation surveys on each sample patch from 16 July to 11 August 2009. Habitat variables measured were selected based on vegetation associations of target small mammal species (Dueser and Shugart, 1978; Zollner and Crane, 2003; Lee 2004; and Holloway and Malcolm, 2006). At each sample patch, I randomly chose six points within the sampling grid and centered a 10 x 10 m plot over each point. I measured average tree and snag DBH, tree and snag density, canopy cover, and woody and herbaceous stem density as in 2008 except that I used 2 x 2 m plots for woody and herbaceous stem density; and percent of ground covered by coarse woody debris as in Rytwinski and Fahrig (2007).

GIS Analyses (2005, 2008 and 2009 surveys)

I calculated road density as the total length of all road types within each landscape divided by the total area of the landscape (km/km^2), based on digital maps of public roads from the National Road Network of Canada vector road datasets for Ontario (Natural Resource Canada, 2003). All road types were included: one and two-lane municipal and county roads (unpaved and paved), and secondary and divided highways (paved). Road width ranged from ~4.5 m for one-lane gravel roads to ~10 m for two-lane secondary highways (paved surface

width). Traffic volume varied across road types from ~25 to ~20,000 average annual daily (24-h) traffic (AADT), though detailed traffic volume data are not available for all roads within my study area. Road verges were usually grasses and shrubs. Amount of forest within each landscape was obtained from digital 1:50,000 Natural Resources Canada topographic maps. GIS analyses were conducted using ArcView 3.2 (ESRI, Redlands, California, USA).

Statistical Analysis

Confounding variables

Before estimating the relationship between road density and abundance of each species, I first wanted to rule out the possibility of confounding vegetation and other habitat variables, by determining whether the local habitat characteristics were correlated with road density. I conducted Spearman Rho correlations to determine the association between each local habitat variable and road density. I intended to include in further analyses any variable that showed a significant correlation with road density.

I also wished to rule out the possibility that any relationship I found between the effect of road density and my predictor variables (reproductive rate, home range size and body size) was due to a correlation between detection probability and road density, where detection probability is defined as the probability of detecting at least one individual during a particular sampling occasion, given the species is present in the area (MacKenzie et al., 2002). This could occur if, for example, nearby roads increase or reduce the likelihood of an animal entering a tracking station. Therefore, I wanted to limit my analysis to species for which detection probability is clearly not affected by road density.

The objective of the detectability analysis was, for each species-year combination, to determine whether a model that assumes a relationship between road density and detectability fit my data better than a model that assumes no relationship between road density and detectability. To be as conservative as possible, I eliminated any species-year combination where the first model was selected over the second, regardless of model strength or significance and/or error associated with model parameters. I used a model developed by Royle and Nichols (2003) which accommodates heterogeneity in a species detection probability at a site as a result of variation in abundance. The model uses maximum likelihood estimation to find the most likely values for the two key parameters, λ (mean abundance across sites) and r (species detection probability). Assumptions are that abundance follows a given probability distribution (e.g., a Poisson distribution), and that the probability of detecting a species at a site is related to its detection probability and its abundance at the site.

I evaluated two models for detection probability for each species-year combination: (1) a model assuming a linear road density effect on detection probability (r) and (2) a model assuming constant r (no relationship between road density and r); in both cases I assumed a Poisson distribution. I determined the relative support for each model (i.e. model fit) using Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson, 2002). As stated above, to be as conservative as possible, any species-year combination in which the road-density-effect model was selected as the better model (lower AICc) was removed from the analyses below, regardless of model strength, error associated with model parameters, or the difference between the AICc values (ΔAICc).

Reproductive rate, species mobility, and body size

Reproductive rate, mobility and body size were taken from the literature for the 13 species for which detectability was not related to road density. Reproductive rate was the mean number of offspring per litter multiplied by the maximum reported number of litters per year; the values were taken from sources as close to my study region as possible (see Appendix A for values and sources). The most common measures of species mobility are dispersal distance (or movement range) and home range area. Bowman et al. (2002) found that mammal dispersal distance and home range area are significantly linearly related ($R^2 = 0.74$), even after the effects of body size were removed ($R^2 = 0.50$). Since for my species I had more confidence in the values available for home range area than the values available for dispersal distance, I used mean (of the two sexes) home range area as my measure of species mobility, taken from studies as close to my region as possible. If more than one study was close in proximity to my study region, I calculated the mean across studies weighted by study sample size (see Appendix A for values and sources). Body size (Appendix A) was the average body size of the two sexes in grams. All values for body size were taken from Eder (2002).

Road effect vs. predictor(s)

I first standardized the relative abundance values for each of the 13 species (within year) and the road density values to z-scores (see Appendix B for raw data). I then performed separate simple linear regressions of each species' standardized relative abundance on standardized road density to obtain the standardized coefficients and standard errors of the coefficients from each regression. To perform a single analysis on species for which I had more than one year of

sampling data, I included year as a factor, to account for differences in sampling methodology and overall abundance between years (see Appendix C).

I then tested the three cross-species predictions that the slope of the relationship between abundance and road density should become increasingly negative with decreasing reproductive rate, increasing home range area, and increasing body size, by performing three separate weighted regressions of the log-transformed standardized coefficient+2 for each species (response variable) on the log-transformed predictor variables (i.e., reproductive rate, home range area, and average body size). Before taking logs of the standardized coefficients I had to add a constant (here, 2) to all values, since I could not take logs of negative values. All variables were log-transformed to meet model assumptions. Each regression was weighted by the inverse of the standard error of the regression coefficients (of abundance on road density). Since the three predictor variables were correlated, I also fit multiple regression models to determine whether I could detect independent effects of predictor variables while controlling for the presence of the others. The detectability analyses were conducted using the Rmark 1.9.3 package (Laake and Rexstad, 2008) in R (R Development Core Team, 2009), and all other statistical procedures were conducted using PASW Statistics 18 (SPSS Inc., 2010).

Results

None of the possible confounding vegetation and habitat variables that I measured showed a significant correlation with road density (see Appendix D for correlations and Appendix E for raw data); therefore, they were not included in further analyses. Seventeen mammal species were tracked during the combined sampling periods, ranging in size from the white-footed mouse (*Peromyscus leucopus*) and the meadow jumping mouse (*Zapus hudsonius*)

at 20 g to the black bear (*Ursus americanus*) at 155,000 g. The road-density-effect model of detection probability was selected as a better model than the no-road-density-effect model for 4 of the 17 species (see Appendix F): *Tamias striatus* (eastern chipmunk), *Sylvilagus floridanus* (eastern cottontail rabbit), *Ursus americanus* (black bear), and *Clethrionomys gapperi* (southern red-backed vole). One of these species, *T. striatus*, was surveyed in more than one year, and the road-density-effect model was the better model in both years based on AICc values. I therefore excluded these four species from further analyses, leaving thirteen mammal species to test my predictions.

Across the 13 species, as expected, reproductive rate and mean home range area were negatively correlated (Spearman's $\rho = -0.549$; $p=0.026$), and average body size was positively correlated with mean home range area (Spearman's $\rho = 0.893$; $p<0.001$) and negatively correlated with reproductive rate (Spearman's $\rho = -0.521$; $p=0.034$). As predicted, there was a significant cross-species positive relationship between reproductive rate and the slope of the relationship between abundance and road density (Table 1.1; Fig. 1.6a: $F= 22.90$, $df = 1, 11$; $p=0.001$, $R^2 = 0.68$); species with lower reproductive rates showed a more negative response to increasing road density. Mean home range area was negatively related to the slope of the relationship between abundance and road density (Table 1.1; Fig. 1.6b: $F= 10.93$, $df = 1, 11$; $p= 0.007$, $R^2 = 0.50$); species with larger home ranges showed a more negative response to increasing road density. There was a significant negative relationship between the body size and the slope of the relationship between abundance and road density (Table 1.1; Fig. 1.6c: $F= 11.66$, $df = 1, 11$; $p= 0.006$, $R^2= 0.52$); larger species showed a more negative response to increasing road density. Based on model fit, the species trait that best explained variation in the coefficients

Table 1.1. Model summaries of cross-species relationships between the slope of the relationship between abundance and road density (log [regression coefficient + 2]; see Appendix C) and predictors log (reproductive rate), log (home range area), and log (body size). Each regression is weighted by the inverse of the standard errors of slope coefficients from single-species regressions of abundance on standardized road density; Appendix C: Table C1. AICc is Akaike's information criterion corrected for small sample size. Sample size = 13 mammal species. Note: 2 was added to the response variable (standardized regression coefficient) to make all values positive, so that I could take logs. Reprinted with permission from © 2011 Ecological Society of America.

Model	Model R ²	Predictor	β	SE	F	df	p-value	AICc
1	0.68	log (reproductive rate)	0.135	0.028	22.90	1, 11	0.001	-49.96
2	0.50	log (mean home range area)	-0.020	0.006	10.93	1, 11	0.007	-44.30
3	0.52	log (average body size)	-0.023	0.007	11.66	1, 11	0.006	-44.72
4	0.75	log (reproductive rate)	0.102	0.033	9.80	1, 10	0.011	-48.80
		log (mean home range area)	-0.009	0.005	2.81	1, 10	0.125	
5	0.77	log (reproductive rate)	0.101	0.030	11.00	1, 10	0.008	-50.02
		log (average body size)	-0.012	0.006	4.04	1, 10	0.072	

(a)

(b)

(c)

Figure 1.6. Linear regressions of the log (regression coefficient + 2) - from single-species regressions of standardized relative abundance on standardized road density – on: (a) log (reproductive rate) ($F = 22.90$, $df = 1, 11$; $p = 0.001$, $R^2 = 0.68$); (b) log (mean home range area) ($F = 10.93$, $df = 1, 11$; $p = 0.007$, $R^2 = 0.50$); and (c) log (average body size) ($F = 11.66$, $df = 1, 11$; $p = 0.006$, $R^2 = 0.52$). Each regression is weighted by the inverse of the standard errors of the coefficients; thicker dots correspond to data points with lower standard errors (Appendix C - Table C1). Note: 2 was added to the response variable (standardized regression coefficient) to make all values positive, so that I could take logs. Reprinted with permission from © 2011 Ecological Society of America.

relating mammal abundance to road density was reproductive rate (Table 1.1; AICc = -49.96 compared to -44.72 and -44.30 for average body size and mean home range area respectively). A model including both reproductive rate and body size (the two species traits with the lowest AICc values and the least correlated) had an R^2 of 0.77 and the lowest AICc value (Table 1.1), with reproductive rate being significantly positively related to the slope of abundance vs. road density ($F= 11.00$, $df=1, 10$, $p=0.008$) and body size being marginally significantly negatively related to the slope of abundance vs. road density ($F= 4.04$, $df=1, 10$, $p=0.072$).

Discussion

This is the first direct test of the hypotheses that the negative effect of road density at the population level decreases with reproductive rate, increases with movement range, and increases with body size. The results support my predictions (Table 1.1; Fig. 1.6a-c). In my study, the common negative correlation between forest cover and road density (e.g., Houlahan and Findlay, 2003; Roedenbeck and Köhler, 2006) was avoided through my experimental design, and none of the habitat variables I measured was correlated with road density (Appendix D). In addition, my results were not affected by species detection probabilities because I limited my analyses to species for which detection probability was not related to road density (Appendix F). Note that if I include the three species for which the difference in AICc for the road-density-effect model of detection probability relative to the no-road-density-effect model of detection probability was very small ($\Delta AICc < 2$), my results did not change substantially: the direction of all relationships remained the same; for reproductive rate the R^2 increased to 0.69 from 0.68; for home range size the R^2 dropped to 0.49 from 0.50; for body size the R^2 dropped to 0.47 from 0.52 (see Appendix G); and the model including both reproductive rate and body size, had an R^2 that increased slightly to 79 from 77 and still had the lowest AICc value of all the models.

My results provide strong support for the hypothesis that species with lower reproductive rates are more negatively affected by road density than are species with higher reproductive rates. Reproductive rate was the best predictor of population-level response to roads, explaining nearly 70% of the variation in the coefficients relating mammal abundance to road density (Table 1.1; Fig 1.6a). The effect of reproductive rate remained strong in the model that included both reproductive rate and home range size, and in the model that contained both reproductive rate and body size (Table 1.1). Therefore, reproductive rate appears to have an effect on species response to roads, independent of its correlations with movement range and other life history attributes that are correlated with body size.

Although this is the first test of the hypothesis that the negative effect of road density at the population level decreases with mammal reproductive rate, several previous studies - both theoretical and empirical - have found similar strong effects of reproductive rate on species response to habitat loss: species with lower reproductive rates require more habitat for population persistence than species with higher reproductive rates. For example, modeling studies suggest that reproductive rate has a larger effect than dispersal rate/ability on the amount of habitat required for population persistence (With and King, 1999; Fahrig, 2001). Vance et al. (2003) found a negative cross-species relationship between reproductive rate and the amount of forest in a landscape required for a 50% probability of presence of forest bird species. Similarly, Holland et al. (2005) found a strong cross-species negative relationship between reproductive rate of 12 species of longhorned beetles and the minimum habitat amount required for species presence, and this relationship was stronger than the effect of movement rate.

My results are less clear for the hypothesized positive cross-species relationship between movement range and road impacts. In a univariate model, home range size explained 50% of the

variation in species response to road density, but this was the weakest of the three univariate models (Table 1.1). Interestingly however, when either body size or home range area was combined in a model with reproductive rate, the model explained an additional 7 to 9 % variation in comparison to the model with reproductive rate alone (Table 1.1). Since average body size and mean home range area were highly correlated ($\rho = 0.893$) and body size and reproductive rate were only moderately correlated ($\rho = -0.521$), the additional explained variance suggests that there is an added effect of mobility on top of the effect of reproductive rate. When comparing model fit however, the difference in AICc values between the combined models including either body size or home range area and reproductive rate, and the univariate model with reproductive rate alone, was very small; the combined model including body size and reproductive rate improved model fit slightly (lower AICc) over the model including reproductive rate alone ($\Delta\text{AICc} < 1$), while the AICc of the combined model with home range area and reproductive rate increased slightly compared to the model including reproductive rate alone ($\Delta\text{AICc} \sim 1$) (Table 1.1). Although this is the first direct test of this hypothesis, as for reproductive rate (above), there are analogous results in the habitat loss literature. Some modelling studies (Casagrandi and Gatto, 1999; Fahrig, 2001; Flather and Bevers, 2002) and some empirical studies (Gibbs, 1998; León-Cortés et al., 2003; 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 current study this increased risk results from increased road mortality rather than decreased habitat amount, but the mechanism linking the landscape change (road density or habitat loss) to movement range is the same, i.e., increased risk of mortality.

I had expected that body size would be the best predictor of mammal species responses to increasing road density because, through its correlations with reproductive rate and mobility, in a sense it "represents" all of the main mechanisms. However, in my dataset, while body size was highly correlated with home range size, it was only moderately correlated with reproductive rate. Essentially, this allowed us to at least partially separate the effects of reproductive rate and mobility and to make conclusions about their relative importance on the effect of roads. I found evidence for both mechanisms, but the effect of reproductive rate was stronger than the effect of mobility.

In my analysis, 23% of the variation in the coefficients relating mammal abundance to road density was not explained by my predictor variables. Some of this variation is most likely explained by differences among species in their behavioural responses to roads and traffic (Jaeger et al., 2005; Fahrig and Rytwinski, 2009). For example, species that are either attracted to roads or do not avoid roads, and that show low car avoidance (e.g. slow-moving species that are unable to avoid cars) are particularly vulnerable to road mortality (van Langevelde and Jaarsma, 2005). This combination of factors is most likely responsible for the frequent negative effects of roads and traffic on abundances of amphibians and reptiles (Fahrig and Rytwinski, 2009). Some turtles use roads and roadsides as nesting sites (Haxton, 2000; Aresco, 2005; Steen et al., 2007) and some snakes have been reported to come to the road surface to bask during the day or to thermoregulate at night (Sullivan, 1981; Rosen and Lowe, 1994). This proximity to roads and the slow movement of these species across roads leaves them vulnerable to very high road mortality rates (Hels and Buchwald, 2001; Bouchard et al., 2009). Other species may avoid roads at a distance, due to traffic disturbances (noise, lights, and chemical emissions), a response that is commonly thought to explain the reduced abundances of birds near high-traffic roads (Reijnen et

al., 1996; Forman et al., 2002; Rheindt, 2003). Such species, while less likely to be killed on roads, are susceptible to habitat loss, as habitat quality within the vicinity of roads is reduced; the higher the traffic amount on the road, the more habitat is effectively lost to the species. In general, the degree to which behavioural responses to roads and traffic either obscure or reinforce the relationships between the road effect and reproductive rate, movement range, and body size will depend on how the behavioural responses are related to these three predictor variables.

In conclusion, I found strong support for the hypothesis that species with lower reproductive rates are more susceptible to negative road effects than species with higher reproductive rates, and moderate support for the hypothesis that more mobile species are more susceptible than less mobile species to negative road effects. My results suggest that priority should be placed on mitigating road effects on larger mammals with lower reproductive rates.

CHAPTER TWO

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

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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. I 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 behavioural responses to roads and/or traffic that make species or species groups prone to negative road and/or traffic effects. I 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, my 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.

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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 behavioural 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, I 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; Fahrig and Rytwinski, 2009).

The second set of hypotheses suggests that species behavioural 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, (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 behaviours 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 behavioural 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).

Methods

Search and selection of studies for meta-analysis

I 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 I 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. I limited my 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, I 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, I attempted a thorough search, including data available in theses.

Database and data extraction

I divided the studies into six categories, based on study design (Table 2.1). 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 authors 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

Table 2.1. The six categories of study design for studies of the effects of roads and traffic on animal abundance. For each category, examples of response and predictor variables are provided along with the associated corrected sample size used for effect size weighting in the meta-analysis. C=continuous variable; D= dichotomous variable. Reprinted with permission from © 2012 Elsevier.

Study Design	Examples of:		Corrected Sample Size
	Responses	Predictors	
1. Landscape or region	species abundance C	road density (km/km ²) C traffic density (Σ AADT km/km ²) C	# of landscapes or regions
	species density C	road density (km/km ²) C traffic density (Σ AADT km/km ²) C	# of landscapes or regions
		total length of roads (km) C	# of landscapes or regions
2. Home range/territory area	mean road density(km/km ²) C mean traffic density (Σ AADT km/km ²) C	home ranges vs. study area D	# home ranges (individuals) + 1 (study area)
		home range areas vs. random areas D present plots vs. absent plots D present plots vs. random plots D	# home ranges/present plots (individuals) + 1 (1 for all random/absent areas)
	mean length of roads C	home ranges vs. study area D	# home ranges (individuals) + 1 (study area)
		home range areas vs. random areas D present plots vs. absent plots D	# home ranges/present plots (individuals) + 1 (1 for all random/absent areas)
3. Plot size	mean road density C	present plots vs. random plots D present plots vs. absent plots D present plots vs. all plots sampled D	# of individuals (or # of spatially independent present plots) + 1 (1 for all random/absent plots)
	mean traffic density C	present plots vs. absent plots D	# of individuals (or # of spatially independent present plots) + 1 (1 for all absent plots)
	mean distance to a road C	present plots vs. random plots D present plots vs. absent plots D	# of individuals (or # of spatially independent present plots) + 1 (1 for all random/absent plots)
	species density C	road category 1 vs. road category 2 D	# of spatially independent sampling plots * # of roads

Table 2.1. Continued

Study Design	Examples of:		Corrected Sample Size
	Responses	Predictors	
4. Distance from road (multiple distances)	species abundance C	distance from road C	# of distance from road intervals sampled that are assumed spatially independent * # of roads sampled or # of spatially independent sampling locations
	fecal density (droppings/pellets/scat etc.) C	distance from road C	# of distance from road intervals sampled that are assumed spatially independent * # of roads sampled or # of spatially independent sampling locations
	# of territories (occupied nest boxes) C	distance from road C	# of distance from road intervals sampled* # of roads sampled or # sampling locations
	species density (density of nests) C	distance from road C	# of distance from road intervals sampled* # of roads sampled or # sampling locations
	species density (density within ponds)	distance from road C	# of ponds
	mean % of GPS locations C	distance from road C (buffer zones)	# of individuals
	mean # of GPS fixes per individual C	distance from road C (buffer zones)	# of individuals
	density of GPS locations C	distance from road C (buffer zones)	# of individuals
5. Distance from road (near vs. far)	mean species abundance C	near vs. far D	# of spatially independent sampling locations *2 (2 for the number of distance categories – near vs. far) or 1 if not spatially independent
	mean species density C	near vs. far D	# of spatially independent sampling locations *2 (2 for the number of distance categories – near vs. far)
6. Road presence/absence	mean species abundance C	presence or absence of road D	# of spatially independent sampling locations

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, I 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, I 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, I averaged estimates across years and/or habitat types; however, if study design varied across years or habitats, I 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, I 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, I included the estimates from each road type, unless one road type was a subset of another, in which case I selected the road category that included the most road types.

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 I 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), I first calculated the standardized mean difference;

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

where $\overline{X}_{G1}$ and $\overline{X}_{G2}$ 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),

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

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

$$r = \frac{ES_{sm}}{\sqrt{(ES_{sm})^2 + \frac{1}{p(1-p)}}} \quad \text{where } p = \text{proportion of the total sample in one of the two groups.} \quad (4)$$

As suggested by Hedges and Olkin (1985), I transformed correlation coefficients using

$$\text{Fisher's } z\text{-transform, } ES_z r = 0.5 \log_e \left[\frac{1+r}{1-r} \right].$$

Adjustments prior to analysis

After obtaining the z -transformed r value for each effect ($ES_z r$), 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, I worked from the assumption that I should attribute one data point to each spatially-independent sample in each data set. I 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 I 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, I 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 I 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 spatially independent sampling locations.

After determining the adjusted sample size of each study (n) I 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 H for study and species lists, effect sizes, adjusted sample sizes, and study design categories for each study.

Data analysis

My main objective was to determine species characteristics and behavioural responses to roads and/or traffic that make species prone to negative road and/or traffic effects. I 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 behavioural 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 I 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, I used the median of these ranges. Details on species values and information sources are in Appendix I.

Information on species behavioural 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 behavioural 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, I 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 my 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, I 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 differences 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, I performed a mixed effects model including taxon (at the class level). Amphibians and reptiles were combined due to the small sample size for reptiles. I 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, I 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 I expected life history traits to be inter-correlated, I removed highly redundant traits, while maximizing the number of complete datasets (Table 2.2). 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

Table 2.2. 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). Reprinted with permission from © 2012 Elsevier.

	Reproductive rate	Mobility	Body mass	Body length	Age at sexual maturity
<i>(a)</i>					
Reproductive rate	120	-0.737	-0.763		
Mobility	<0.0001	114	0.879		
Body mass	<0.0001	<0.0001	126		
Body length	<0.0001	<0.0001	<0.0001		
Age at sexual maturity	<0.0001	<0.0001	<0.0001	<0.0001	
<i>(b)</i>					
Reproductive rate	247	-0.286	-0.246		
Mobility	<0.0001	171	0.549		
Body mass	<0.0001	<0.0001	252		
Body length	<0.0001	<0.0001	<0.0001		
Age at sexual maturity	<0.0001	<0.0001	<0.0001	<0.0001	
<i>(c)</i>					
Reproductive rate	55	0.133			
Mobility	<0.0001	53			
Body mass	<0.0001	<0.0001			
Body length	<0.0001	<0.0001			
Age at sexual maturity	<0.0001	<0.0001	<0.0001	<0.0001	

Table 2.2.Continued

	Reproductive rate	Mobility	Body length	Age at sexual maturity
<i>(d)</i>				
Reproductive rate	22	0.155	0.689	0.617
Mobility	0.492	22	0.146	-0.297
Body length	<0.0001	0.517	22	0.753
Age at sexual maturity	0.002	0.179	<0.0001	22

characteristics than reproductive rate, and there were fewer datasets containing information on age at sexual maturity than reproductive rate, I removed age at sexual maturity as an explanatory variable from analyses. I 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, I 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, I 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, I 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, I 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 I 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.

I had initially hoped to include species-specific behavioural 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, I tabulated the species in the six behavioural 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, I assumed species had no vehicle avoidance unless there was quantitative evidence suggesting otherwise. It is also important to note that behavioural 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 behavioural response category.

Results

Review statistics

I 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 H).

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 my 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 (Fig. 2.1).

The effects of roads and/or traffic on animal abundance varied by taxonomic class (heterogeneity of the model $Q_M = 21.64$, $p < 0.0001$, $n = 455$ 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. 2.2). 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. 2.2). 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.

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 2.2). After removing the redundant life history characteristics from each database (i.e., body

Figure 2.1. Funnel plot of asymmetry for the meta-analysis of the effect of roads and/or traffic on animal population abundance including all datasets ($n = 455$). The individual observed effect sizes are plotted as a function of sample size to visually assess publication bias. The potential for publication bias was determined to be low since a typical funnel plot was produced with greater scatter in studies based on small sample sizes and a lack of significant relationship between the magnitude of effect size and sample size ($r = -0.010$, $p = 0.837$, $n = 455$). Reprinted with permission from © 2012 Elsevier.

Figure 2.2. Weighted-mean effect sizes (ES_r) for each animal class derived from a mixed effects meta-analytical model. Error bars indicate 95% confidence intervals. Reprinted with permission from © 2012 Elsevier.

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.

Mammals

Reproductive rate, species mobility, and body mass were related to population-level effects of roads for mammals in univariate models (Fig. 2.3 a; Table 2.3; $Q_M = 7.90$, $p = 0.0049$; $Q_M = 10.12$, $p = 0.0015$; $Q_M = 11.16$, $p = 0.0008$, $n = 108$ respectively). As predicted, species with lower reproductive rates, higher mobility, and larger body sizes showed more negative responses to roads and/or traffic (Fig. 2.3 a; Table 2.3). Since the magnitude of population-level responses to road effects was not significantly different among datasets using different study designs or road categories, I 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; Table 2.3). 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; Table 2.4). However, all 3 models had substantial support, with $\Delta AICc$ less than 2 and models including combinations of 2 or more of these traits did not improve model fit (Table 2.4).

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; Table 2.5). As predicted, more mobile birds (larger territory sizes) showed a more negative response to roads and/or traffic (Fig. 2.3 b). The magnitude of population-level

(a) Mammals

(b) Birds

(c) Amphibians + reptiles

(d) Amphibians only

(e) Anurans only

Figure 2.3. Weighted-mean effect sizes (ES_r) 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. Reprinted with permission from © 2012 Elsevier.

Table 2.3. Mean Fisher's z-transformed effect sizes (ES_{Zr}) and back-transformed effect-sizes (ES_r) with statistical significance of moderators for mammal species. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_{Zr}	ES_r	CI (lb)	CI (ub)	p (ES_{Zr})	Q_E^a	Q_M^b	p(Q_M)	n
Reproductive rate	0.161	0.160	0.049	0.274	0.0049	1146.71	7.90	0.0049	108
Mobility	-0.045	-0.045	-0.073	-0.017	0.0015	1188.96	10.12	0.0015	108
Body Mass	-0.064	-0.064	-0.101	-0.026	0.0008	1165.27	11.16	0.0008	108
Taxon (Order)						1119.80	16.79	0.0790	108
<i>Artiodactyla</i>	-0.319	-0.309	-0.635	-0.003	0.0476				21
<i>Carnivora</i>	-0.246	-0.241	-0.494	0.003	0.0524				33
<i>Didelphimorphia</i>	0.022	0.022	-0.747	0.792	0.9545				3
<i>Diprotodontia</i>	-0.154	-0.153	-1.485	1.176	0.8203				1
<i>Erinaceomorpha</i>	-0.169	-0.167	-1.542	1.205	0.8098				1
<i>Lagomorpha</i>	-0.158	-0.156	-0.951	0.635	0.6966				3
<i>Pholidota</i>	-1.333	-0.870	-2.806	0.140	0.0761				1
<i>Primates</i>	-1.004	-0.763	-1.832	-0.176	0.0174				3
<i>Proboscidae</i>	-0.090	-0.090	-1.213	1.034	0.8755				2
<i>Rodentia</i>	0.185	0.183	-0.043	0.412	0.1118				37
<i>Soricomorpha</i>	0.090	0.090	-0.689	0.868	0.8210				3
Study Design						1136.66	2.29	0.6830	108
<i>Landscape or region</i>	-0.086	-0.085	-0.376	0.204	0.5628				24
<i>Home range area</i>	-0.115	-0.114	-0.453	0.223	0.5058				18
<i>Plot size</i>	-0.074	-0.074	-0.456	0.309	0.7053				14
<i>Distance from road (multiple distances)</i>	-0.298	-0.290	-0.599	0.002	0.0514				27
<i>Distance from road (near vs. far)</i>	0.012	0.012	-0.271	0.295	0.9341				25
Road Category						1219.78	6.07	0.1081	108
<i>4-lane divided highways</i>	0.286	0.278	-0.065	0.637	0.1101				16
<i>2-lane paved roads</i>	-0.133	-0.132	-0.396	0.131	0.3242				28
<i>1-lane paved or gravel/dirt roads</i>	-0.237	-0.233	-0.542	0.068	0.1281				24
<i>all or multiple road types</i>	-0.190	-0.188	-0.414	0.035	0.0974				40

^a Residual heterogeneity.

^b Between groups/model heterogeneity.

Table 2.4. Model on the influence of the life history traits found to explain variation in effect sizes (population-level responses to road and/or effects) for mammal species. All moderator variables were log transformed. AICc = the Akaike information criterion corrected for small sample size; K = number of parameters in model; n = number of datasets; $\Delta\text{AICc} = \text{AICc}_i - \text{AICc}_{\min}$. Reprinted with permission from © 2012 Elsevier.

Model	AICc	K	n	ΔAICc
Reproductive rate + Mobility + Body mass	289.81	7	108	18.10
Reproductive rate + Mobility	280.98	6	108	9.27
Reproductive rate + Body mass	279.56	6	108	7.84
Mobility + Body mass	281.77	6	108	10.06
Reproductive rate	272.60	5	108	0.88
Mobility	273.37	5	108	1.66
Body mass	271.71	5	108	0.00

Table 2.5. Mean Fisher's z-transformed effect sizes (ES_{Zr}) and back-transformed effect-sizes (ES_r) with statistical significance of moderators for bird species. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_{Zr}	ES_r	CI (lb)	CI (ub)	p (ES_{Zr})	Q_E^a	Q_M^b	p(Q_M)	n
Reproductive rate	-0.001	-0.001	-0.068	0.066	0.9759	336.75	0.00	0.9759	169
Mobility	-0.022	-0.022	-0.044	-0.001	0.0395	324.15	4.24	0.0395	169
Body Mass	-0.016	-0.016	-0.045	0.013	0.2856	332.65	1.14	0.2856	169
Taxon (Order)						293.80	29.89	0.0009	169
<i>Charadriiformes</i>	-2.139	-0.973	-2.940	-1.338	<0.0001				1
<i>Ciconiiformes</i>	0.029	0.029	-0.662	0.720	0.9344				1
<i>Columbiformes</i>	0.060	0.060	-0.375	0.495	0.7866				2
<i>Coraciiformes</i>	0.113	0.113	-0.453	0.679	0.6954				1
<i>Falconiformes</i>	0.063	0.063	-0.305	0.430	0.7384				3
<i>Galliformes</i>	-0.141	-0.140	-0.613	0.331	0.5574				2
<i>Gaviiformes</i>	-0.216	-0.213	-0.549	0.117	0.2037				1
<i>Gruiformes</i>	-0.040	-0.040	-0.543	0.463	0.8761				1
<i>Passeriformes</i>	-0.032	-0.032	-0.073	0.009	0.1289				147
<i>Piciformes</i>	0.053	0.053	-0.104	0.211	0.5089				8
<i>Strigiformes</i>	-0.083	-0.083	-0.369	0.203	0.5695				2
Study Design						257.55	39.75	<0.0001	169
<i>Home range area</i>	-0.556	-0.505	-0.734	-0.378	<0.0001				3
<i>Plot size</i>	-0.030	-0.030	-0.096	0.036	0.3754				59
<i>Distance from road (multiple distances)</i>	-0.261	-0.255	-0.486	-0.036	0.0232				14
<i>Distance from road (near vs. far)</i>	0.001	0.001	-0.040	0.043	0.9493				93
Road Category						239.91	66.01	<0.0001	169
<i>4-lane divided highways</i>	-0.066	-0.066	-0.154	0.023	0.1444				47
<i>2-lane paved roads</i>	-0.031	-0.031	-0.097	0.034	0.3477				41
<i>1-lane paved or gravel/dirt roads</i>	0.019	0.019	-0.028	0.067	0.4187				77
<i>all or multiple road types</i>	-0.810	-0.670	-1.005	-0.615	<0.0001				4

^a Residual heterogeneity.

^b Between groups/model heterogeneity.

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; Table 2.5). 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 2.6 a). I therefore subdivided the datasets by study design only, and to increase sample size, I 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. $n = 62$). I then tested the effect of mobility within this group, after removing the single dataset from the order Charadriiformes to control for among-taxon heterogeneity (Table 2.5). 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 J Table J1).

Amphibians and reptiles (combined)

For amphibians + reptiles, the magnitude of effect sizes did not vary among taxa ($Q_M = 4.69$, $p = 0.1956$, $n = 50$; Table 2.7); and none of the life history characteristics were related to the population-level effects of roads (Fig. 2.3 c; Table 2.7; reproductive rate: $Q_M = 2.04$, $p = 0.1531$; mobility: $Q_M = 2.82$, $p = 0.0929$; 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; Table 2.7) and these two moderators were not independent (Table 2.6 b). Since the sample sizes in the road category levels were too

Table 2.6. 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 Table 2.1): 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. Reprinted with permission from © 2012 Elsevier.

	Road Category				Total
	1	2	3	4	
<i>(a)</i>					
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				
<i>(b)</i>					
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				

Table 2.7. Mean Fisher's z-transformed effect sizes (ES_{Zr}) and back-transformed effect-sizes (ES_r) with statistical significance of moderators for amphibian and reptile species. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_{Zr}	ES_r	CI (lb)	CI (ub)	p (ES_{Zr})	Q_E^a	Q_M^b	p(Q_M)	n
Reproductive rate	0.040	0.040	-0.015	0.096	0.1531	391.96	2.04	0.1531	50
Mobility	0.037	0.037	-0.006	0.081	0.0929	335.21	2.82	0.0929	50
Body Length	-0.016	-0.016	-0.174	0.142	0.8420	388.27	0.04	0.8420	50
Age at Sexual Maturity	0.069	0.069	-0.154	0.292	0.5453	366.69	0.37	0.5453	50
Taxon (Order)						354.45	4.69	0.1956	50
<i>Anura</i>	-0.192	-0.190	-0.390	0.005	0.0565				22
<i>Caudata</i>	-0.470	-0.438	-0.760	-0.179	0.0015				13
<i>Squamata</i>	-0.574	-0.518	-0.958	-0.189	0.0034				6
<i>Testudines</i>	-0.198	-0.195	-0.562	0.166	0.2862				9
Study Design						287.93	18.08	0.0012	50
<i>Landscape or region</i>	-0.088	-0.088	-0.316	0.140	0.4490				13
<i>Home range area</i>	-0.372	-0.355	-0.652	-0.091	0.0094				9
<i>Plot size</i>	-0.240	-0.235	-0.458	-0.021	0.0317				18
<i>Distance from road</i> <i>(multiple distances)</i>	-0.974	-0.750	-1.329	-0.619	<0.0001				7
<i>Road presence/absence</i>	-0.129	-0.128	-0.668	0.411	0.6400				3
Road Category						302.38	11.89	0.0078	50
<i>4-lane divided</i> <i>highways</i>	-0.564	-0.511	-1.223	0.094	0.0931				2
<i>2-lane paved roads</i>	-0.755	-0.638	-1.066	-0.445	<0.0001				9
<i>1-lane paved or</i> <i>gravel/dirt roads</i>	-0.366	-0.350	-0.739	0.008	0.0549				6
<i>all or multiple road</i> <i>types</i>	-0.162	-0.160	-0.321	-0.002	0.0467				33

^a Residual heterogeneity.

^b Between groups/model heterogeneity.

small to allow meaningful tests of life history characteristics within sub-groups, and since study design and road category shared similar information, I removed road category from further analyses. For the study design moderator, I 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 J Table J2).

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. 2.3 d; Table 2.8; $Q_M = 4.15$, $p = 0.0416$, $n = 35$). 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; Table 2.8). 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; Table 2.8). For anurans only (anurans was the larger subgroup), reproductive rate, body length, and age at sexual maturity all explained variation in the magnitude of population-level effects of roads in univariate models (Fig. 2.3 e; Table 2.9; $Q_M = 5.71$, $p = 0.0169$; $Q_M = 4.34$, $p = 0.0371$; $Q_M = 4.72$, $p = 0.0297$, $n = 22$ respectively). Anuran species with lower

Table 2.8. Mean Fisher's z-transformed effect sizes (ES_{Zr}) and back-transformed effect-sizes (ES_r) with statistical significance of moderators for amphibian species only. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_{Zr}	ES_r	CI (lb)	CI (ub)	p (ES_{Zr})	Q_E^a	Q_M^b	p(Q_M)	n
Reproductive rate	0.080	0.080	0.003	0.157	0.0416	118.50	4.15	0.0416	35
Mobility	0.023	0.023	-0.020	0.065	0.2959	129.42	1.09	0.2959	35
Body Length	-0.101	-0.100	-0.359	0.158	0.4444	132.90	0.59	0.4444	35
Age at Sexual Maturity	0.019	0.019	-0.440	0.478	0.9365	132.57	0.01	0.9365	35
Taxon (Order)						124.95	3.78	0.0518	35
<i>Anura</i>	-0.196	-0.193	-0.350	-0.041	0.0130				22
<i>Caudata</i>	-0.474	-0.441	-0.708	-0.240	<0.0001				13
Study Design						122.27	6.28	0.1791	35
<i>Landscape or region</i>	-0.156	-0.154	-0.393	0.082	0.1987				10
<i>Home range area</i>	-0.542	-0.494	-0.876	-0.207	0.0015				5
<i>Plot size</i>	-0.217	-0.214	-0.438	0.005	0.0548				14
<i>Distance from road</i> <i>(multiple distances)</i>	-0.606	-0.541	-1.036	-0.176	0.0058				3
<i>Road presence/absence</i>	-0.129	-0.128	-0.628	0.371	0.6134				3
Road Category						123.55	3.90	0.2723	35
<i>4-lane divided</i> <i>highways</i>	-0.251	-0.245	-0.997	0.496	0.5108				1
<i>2-lane paved roads</i>	-0.515	-0.474	-0.824	-0.205	0.0011				6
<i>1-lane paved or</i> <i>gravel/dirt roads</i>	-0.414	-0.392	-0.788	-0.040	0.0302				5
<i>all or multiple road</i> <i>types</i>	-0.188	-0.185	-0.353	-0.022	0.0268				23

^a Residual heterogeneity.

^b Between groups/model heterogeneity.

Table 2.9. Mean Fisher's z-transformed effect sizes (ES_{Zr}) and back-transformed effect-sizes (ES_r) with statistical significance of moderators for amphibian species from the order Anura only. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_{Zr}	ES_r	CI (lb)	CI (ub)	p (ES_{Zr})	Q_E^a	Q_M^b	p(Q_M)	n
Reproductive rate	0.109	0.108	0.020	0.198	0.0169	26.10	5.71	0.0169	22
Mobility	0.007	0.007	-0.050	0.064	0.8090	33.65	0.06	0.8090	22
Body Length	0.182	0.180	0.011	0.352	0.0371	27.28	4.34	0.0371	22
Age at Sexual Maturity	0.320	0.310	0.031	0.609	0.0297	27.26	4.72	0.0297	22
Study Design						30.93	1.40	0.7062	22
<i>Landscape or region</i>	-0.156	-0.155	-0.299	-0.014	0.0319				9
<i>Home range area</i>	-0.180	-0.178	-0.455	0.095	0.1988				2
<i>Plot size</i>	-0.245	-0.240	-0.375	-0.115	0.0002				10
<i>Distance from road</i> <i>(multiple distances)</i>	-0.338	-0.326	-0.683	0.007	0.0545				1
Road Category						33.73	0.15	0.6977	22
<i>2-lane paved roads</i>	-0.249	-0.244	-0.457	-0.042	0.0186				4
<i>all or multiple road</i> <i>types</i>	-0.204	-0.201	-0.298	-0.110	<0.0001				18

^a Residual heterogeneity.

^b Between groups/model heterogeneity.

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. 2.3 e; Table 2.9). Since the magnitude of the population-level response to road effects did not vary with study design or road category for anurans, I 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; Table 2.9). 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) (Table 2.10). Models including combinations of 2 or more traits did not improve model fit (Table 2.10; see Table 2.2 d for correlations between anuran traits).

Analysis of behavioural responses to roads

I found 17 species for which data on both population-level responses to roads and/or traffic and behavioural responses to roads existed (11 mammals, 2 birds, 3 reptiles, and 1 amphibian) (Table 2.11). Qualitatively, results did not follow my predictions that the negative effects of roads on animal abundance will increase with increasing order of behavioural 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 2.11). While the vehicle avoidance response category showed the strongest negative effect of roads/traffic on animal abundance, there was only one species, woodland

Table 2.10. Model on the influence of the life history traits found to explain variation in effect sizes (population-level responses to road and/or effects) for anuran species. All moderator variables were log transformed. AICc = the Akaike information criterion corrected for small sample size; K = number of parameters in model; n= number of datasets; $\Delta AICc = AICc_i - AICc_{min}$. Reprinted with permission from © 2012 Elsevier.

Model	AICc	K	n	$\Delta AICc$
Reproductive rate + Body Length + Age at Sexual Maturity	12.37	7	22	12.97
Reproductive rate + Body Length	7.60	6	22	8.20
Reproductive rate + Age at Sexual Maturity	5.45	6	22	6.05
Body Length + Age at Sexual Maturity	5.02	6	22	5.62
Reproductive rate	1.80	5	22	2.40
Body Length	1.72	5	22	2.33
Age at Sexual Maturity	-0.60	5	22	0.00

Table 2.11. 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. Reprinted with permission from © 2012 Elsevier.

Behavioural Response	Reference	Effect Size (<i>r</i>)
no data		
<i>Rangifer tarandus</i> (woodland caribou)	Curatolo and Murphy 1986	-0.293
* <i>Peromyscus leucopus</i> (white-footed mouse)	McGregor et al. (2008)	0.145
* <i>Tamias striatus</i> (eastern chipmunk)	Ford and Fahrig (2008); McGregor et al. (2008)	-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> (Grey 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

Table 2.11. Continued

Behavioural Response	Reference	Effect Size (<i>r</i>)
<i>Rangifer tarandus</i> (woodland caribou)	James and Stewart-Smith (2000); Dyer et al. (2001); Schindler et al. (2006)	-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)	McLelland and Shackleton (1988); Mace et al. (1996); Gibeau (2000); Chruszcz et al. (2003); Waller and Servheen (2005)	-0.230
<i>Rana pipiens</i> (northern leopard frog)	Bouchard et al. (2009)	-0.189
<i>Corvus corax</i> (common raven)	Knight and Kawashima (1993)	-0.042
<i>Milvus migrans</i> (black kite)	Meunier et al. (2000)	0.073

caribou (*Rangifer tarandus*) which was reported to show this behaviour, and this same species was also documented to avoid roads from a distance due to traffic disturbance.

Discussion

Mammals and life history attributes

My 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 3 models were essentially indistinguishable in terms of model support, due to the high correlations among the life history variables (Table 2.2 a; Table 2.4).

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. My ability to isolate the effect of reproductive rate in my 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 ($r > 0.7$; Table 2.2 a). Note that the results for mammals in this meta-analysis do not depend on the inclusion of the empirical results from my 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 J Table J3). 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.

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. 2.3 b; Table 2.5), 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 I controlled for differences in study design (Appendix J Table J1). 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 K). 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.

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. 2.2), 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 my 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 salamanders (Caudata) and snakes (Squamata) showed the strongest negative effects (Table 2.7). In general my results confirm the notion that amphibians and reptiles are particularly vulnerable to road effects.

Reptiles and life history attributes

Due to the small number of studies on the effects of roads on reptile populations, I 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, 1993; Congdon et al., 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, 1993; Congdon et al., 1994). While I was 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.

Amphibians and life history attributes

I 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. 2.3 d; Table 2.8). 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 (Table 2.8). 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 8 species), anurans: mean reproductive rate = 2923.3 (range = 650 - 8000, n = 22 datasets of 9 species)). I 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. 2.3 e; Table 2.9). Of the three species traits, age at sexual maturity showed the strongest model fit (Table 2.10) although the traits were strongly inter-correlated (Table 2.2 d). I 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 Salthe, 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, my 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.

Behavioural 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 behavioural responses to roads

and traffic (Jaeger et al., 2005; Fahrig and Rytwinski, 2009). Qualitatively, my 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 behavioural 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 Stewart-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*), grey wolves (*Canis lupus*), cougars (*Puma concolor*), black bears (*Ursus americanus*)) (Table 2.11). I found that the vehicle avoidance response showed the strongest negative population-level response to roads out of all behavioural 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.

I 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 behavioural response category. I 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 behaviour 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 behavioural responses on the population-level effects of roads. To do so would require more studies of the behavioural responses to roads for more of the species in Appendix I. Such behavioural 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 blackbird)), and (4) most amphibian and reptiles species with particular attention to squamates (i.e., snakes) and caudate species (i.e., salamanders and newts).

In conclusion, my 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. I 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. My 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, my 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, my 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.

CHAPTER THREE

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

This chapter formed the basis for the following publication:

Rytwinski, T., Fahrig, L. Why are some animal populations unaffected or positively affected by roads? *Oecologia*.

Abstract

In reviews of the empirical literature on effects of roads on animal population abundance and distribution we found that most effects are negative; however, there are also many neutral and positive responses (Fahrig and Rytwinski, 2009; Rytwinski and Fahrig, 2012). Here I use an individual-based simulation model to (1) confirm predictions from the existing literature of the combinations of life history traits and behavioural responses to roads that lead to negative effects of roads on animal population abundance, and (2) improve prediction of the combinations of life history traits and behavioural responses to roads that lead to neutral and positive effects of roads on animal population abundance. The simulations predict that populations of species with small territories and movement ranges, and high reproductive rates, i.e. many small mammals and birds, should not be reduced by roads. Contrary to previous suggestions, the results also predict that populations of species that obtain a resource from roads (e.g., vultures) do not increase with increasing road density. In addition, my simulations support the predation release hypothesis for positive road effects on prey, whereby abundance of a prey species increased with increasing road density due to reduced predation by generalist road-affected predators; moreover, the simulations suggest that this mechanism can produce positive responses for both small and large prey species. Interestingly, the simulations predict an optimal road density for the large prey species if it avoids roads or traffic emissions, suggesting that, unlike the effects of road mortality, the effects of habitat loss and subdivision due to roads are only evident at high road densities. Overall, the simulation results suggest that there are many species for which road mitigation is not necessary; mitigation efforts should be tailored to the species that show negative population responses to roads.

Introduction

In a review of the empirical literature on effects of roads on animal population abundance and distribution, we found that most, about 59%, of such effects are negative (Fahrig and Rytwinski, 2009). The negative effects of roads on population abundance and distribution are thought to be mainly due to road mortality, population fragmentation, and traffic disturbance, and they are largely concentrated on amphibians and reptiles, large mammal species with low reproductive rates and large home ranges, and more mobile birds (Rytwinski and Fahrig 2011, 2012). In addition, populations of species that avoid roads from a distance due to traffic disturbance (e.g., noise, lights) and species that show no ability to avoid oncoming traffic on roads, therefore suffering high road mortality, are more likely to be negatively affected by roads (Jaeger et al., 2005; Rytwinski and Fahrig, 2012).

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

There are several possible explanations for neutral and positive effects of roads on wildlife populations. First, populations of species that avoid going onto roads but are not disturbed by road traffic, have small territory sizes, and have high reproductive rates should show weak or no effect of roads since traffic mortality should be low and viable populations should be able to exist within areas bounded by roads. This combination of conditions has been suggested as an explanation for observed lack of effect or weak effects on small mammals (Garland and Bradley,

1984; McGregor et al., 2008). Second, as suggested by Jaeger et al. (2005), populations of some species may be unaffected by roads if they are able to avoid being killed by oncoming vehicles. Third, populations of animals that are attracted to roads for a resource (e.g., carrion-feeders such as ravens and some raptor species) and are able to avoid oncoming vehicles should show a net positive effect of roads (Knight and Kawashima, 1993; Meunier et al., 2000). Finally, roads could indirectly produce a net increase in abundance of species whose main predators show negative population-level responses to roads, through predation release. This has been suggested as a possible cause for the observed positive effects of roads on populations of several small mammal species (Johnson and Collinge, 2004; Rytwinski and Fahrig, 2007; Fahrig and Rytwinski, 2009) and the white-tailed deer (*Odocoileus virginianus*) (Munro et al., *in press*).

Several of the potential explanations for effects of roads on animal abundance (above) involve specific behavioural responses to roads or to individual vehicles. To date there are very few species for which there are quantitative data on such behavioural responses to roads (only 17 species globally – see Rytwinski and Fahrig, 2012), and consequently, hypotheses predicting species responses to roads based on behavioural responses are not empirically testable. In addition, the predation release hypothesis for positive road effects on prey has been proposed but not quantitatively evaluated. In this study I use an individual-based simulation model to study the circumstances - life history traits, behavioural responses to roads, and predation pressure - leading to negative, positive and neutral effects of roads on animal abundance. I first confirm that the model is able to derive the known relationships between life history attributes and negative population level responses to roads. I then focus mainly on the conditions leading to neutral and positive effects of roads on animal population abundance. My purpose is to derive a set of predictions that could be tested in future empirical work.

Methods

Overview

I developed a stochastic, individual-based, spatially-explicit simulation model using the Netlogo modeling environment (Wilensky, 1999). The model simulated the dynamics of a hypothetical animal population in a landscape with a given road density. The landscape was scaled to represent an area of dimensions 7.5 by 7.5 km, to allow realistic representation of a range of species with different territory sizes and movement ranges (below). A second version of the model represented the population dynamics of a prey species under predation by generalist predators. I conducted simulation experiments in which each behavioural response to roads and traffic was set at one of two extremes, either 0 or 100% (with the exception of traffic mortality described below). Species type was characterized by a set of life history traits chosen to represent either a typical small species (small territory size, small movement range, and high reproductive rate) and a typical large species (large territory size, large movement range, and low reproductive rate).

Six experiments were run for each species type (small and large), in landscapes with different road densities to develop predictions of how the species type interacts with the following behavioural responses to roads, as road density increases: (1) road attraction + vehicle avoidance (e.g., vultures), (2) road attraction + no vehicle avoidance (e.g., turtles, snakes), (3) vehicle avoidance only (e.g., caribou), (4) traffic disturbance avoidance (e.g., grizzly bear, elk), (5) road surface avoidance (e.g., some small mammals), and (6) no avoidance (traffic mortality) (e.g., amphibians) (see Table 3.1 and 3.2 for model parameters; see Table 3.3 for definitions of behavioural responses to roads). In the predation-effect version of the model, the generalist predators (individual predators from an unspecified number of species) were assumed in all

experiments to be large species types (large territory size, large movement range, and low reproductive rate) that were negatively affected by roads. There were two prey species types (in separate simulations), a small prey species (small territory size, small movement range, and high reproductive rate) and a large prey species (large territory size, large movement range, and low reproductive rate). The same six experiments as outlined for the single-species version were run for each prey species type (small and large) at the eight different road densities (Table 3.2).

Model description

The simulated landscape comprised a 2-dimensional uniformly gridded landscape of 751 x 751 square cells, each representing a 10m x 10m area. This landscape size (~56 km²) was large enough to allow for a population (up to 37 individuals) of a large animal with realistic territory size and movement distance values, but small enough to keep the maximum population size of the small animal with small territory size computationally manageable (< 282,000 individuals). There were two kinds of cells, habitat and roads; roads were 1 cell (10m) wide.

The model proceeded in time steps equivalent to years (or generations). Each run continued until the population size reached a steady state (i.e., the population varied by less than 5% from year to year for at least 10 years), the population went extinct, or 100 years, whichever came first.

Submodels

The model includes three submodels – reproduction, movement, and density limit – applied in this order to each individual in each time step (Fig. 3.1). Each submodel is completed for all individuals before the next submodel begins.

Table 3.1. Parameter values held constant among simulation runs. Road attraction zone was the distance from which a road-attracted individual was attracted to a road i.e., if a road-attracted individual is within a road attraction zone, it is moved to the center of the nearest road cell.

Attracted-benefit (B) applied to those individuals that are attracted to a road, and that are reproducers in the current time step, and avoid oncoming vehicles. These individuals receive a benefit from the road in the form of extra offspring; the number of extra offspring is a proportion, B , of its nominal reproductive output.

Parameters	Values
Landscape size	751 x 751 cells (~56 km ²)
Time steps in simulation	100 or until stable or extinct
Maximum cell occupancy	1 individual per cell
Road attraction zone	within 4 cells of a road
Attracted-benefit, B (proportion of reproductive output)	1
Traffic density (vehicles/cell)	3
Traffic disturbance zone (# of cells road from):	
if movement distance = 1.5	avoid road from 1 cell away
if movement distance = 500	avoid road from 45 cells away

Table 3.2. Parameters that varied among the simulation experiments. The same experiments with the same parameter values were run for the single-species and predation-effect simulations, with the exception that the nominal reproductive rates differed (predation-effect rates are in brackets); this was necessary to allow population persistence in the predation-effect model (see text). T = probability of an animal avoiding the road from a distance due to traffic disturbance, determined by the avoidance parameter k ; C = probability that an animal on a road can avoid oncoming vehicles, determined by the avoidance parameter k ; M = probability of an animal being killed on the road given it attempted to cross, determined by the mortality parameter d (0, 2.5, or 200, corresponded to 0% , 88%, and 100% probabilities (respectively)); A = probability of an animal being attracted to a road from a given distance; and R = probability of an animal avoiding moving onto or across roads, in the event that its randomly selected movement trajectory would have taken it onto or across a road (0 or 1 corresponded to 0% and 100% probabilities respectively). Note for the predation-effect version, the generalist predators were large species (reproductive rate = 35; movement distance = 500; territory size = 15,000) showing no road avoidance behaviours and high traffic mortality in all experiments.

Experiments	Species type	Life History Trait			Avoidance Behaviour					Number of roads
		Reproductive rate	Movement distance	Territory size	T (k)	C (k)	M (d)	A	R	
1. road attraction + vehicle avoidance	small	32 (55)	1.5	2	0	200	2.5	1	0	0 to 14 (by 2)
	large	1 (35)	500	15000	0	200	2.5	1	0	0 to 14 (by 2)
2. road attraction + no vehicle avoidance	small	32 (55)	1.5	2	0	0	2.5	1	0	0 to 14 (by 2)
	large	1 (35)	500	15000	0	0	2.5	1	0	0 to 14 (by 2)
3. vehicle avoidance	small	32 (55)	1.5	2	0	200	2.5	0	0	0 to 14 (by 2)
	large	1 (35)	500	15000	0	200	2.5	0	0	0 to 14 (by 2)

Table 3.2. Continued

Experiments	Species type	Life History Trait			Avoidance Behaviour					Number of roads
		Reproductive rate	Movement distance	Territory size	$T(k)$	$C(k)$	$M(d)$	A	R	
4. traffic disturbance avoidance	small	32 (55)	1.5	2	200	0	2.5	0	0	0 to 14 (by 2)
	large	1 (35)	500	15000	200	0	2.5	0	0	0 to 14 (by 2)
5. road surface avoidance	small	32 (55)	1.5	2	0	0	2.5	0	1	0 to 14 (by 2)
	large	1 (35)	500	15000	0	0	2.5	0	1	0 to 14 (by 2)
6. no avoidance	small	32 (55)	1.5	2	0	0	2.5	0	0	0 to 14 (by 2)
	large	1 (35)	500	15000	0	0	2.5	0	0	0 to 14 (by 2)

Table 3.3. Definitions of the behavioural scenarios used in the six experiments and how roads and traffic were expected to impact population size/persistence for each. Traffic mortality = enhanced mortality due to collisions with vehicles; resource inaccessibility = less access to food, mates, habitat etc. (barrier effect); habitat loss = less habitat available for breeding, foraging etc.); population subdivision = populations become fragmented into smaller, partially isolated local populations that are more vulnerable to extinction.

Behavioural Responses	Definition	Expected road and traffic impacts
1. road attraction + vehicle avoidance	Animals are attracted to a road for a resource (e.g., for food, a nesting site, a mate, or thermoregulation). Once on the road, animals can avoid oncoming vehicles, resulting in some individuals returning to the original side of the road and others crossing the road.	no negative road effects increased resources
2. road attraction + no vehicle avoidance	Animals are attracted to a road for a resource (e.g., for food, a nesting site, a mate, or thermoregulation). Once on the road, animals cannot avoid oncoming vehicles.	traffic mortality
3. vehicle avoidance	Animals can avoid oncoming vehicles, resulting in some individuals returning to the original side of the road and others crossing the road.	no negative road effects
4. traffic disturbance avoidance	Animals avoid roads from a distance due to traffic disturbance (e.g., lights, noise, chemical emissions).	resource inaccessibility habitat loss population subdivision
5. road surface avoidance	Animals avoid going onto the road surface itself.	resource inaccessibility population subdivision
6. no avoidance	Animals move onto roads irrespective of traffic.	traffic mortality

Setup

An individual simulation run begins by placing the roads in the landscape (if roads are present), followed by assigning the remaining grid cells to habitat. The spatial pattern of the landscape is constant throughout the simulation run. I increased the number of roads from 0 to 14 in increments of 2, corresponding to a road density range of 0 to 1.86 km/km² (Table 3.2). This covers the range of road densities where negative effects on wildlife populations have been observed (e.g., van Dyke et al., 1986; Mech et al., 1988; Mladenoff et al., 1995; Rytwinski and Fahrig, 2011). In addition, at the maximum road density of 14 roads, the resulting loss of habitat was less than two percent, allowing us to be confident that effects of road density would not be a result of direct habitat loss. Roads were straight and formed a grid pattern, with an equal number of horizontal and vertical roads extending the entire width of the landscape. Parallel roads were equidistant from one another.

Once the landscape was generated, in the single-species model version 1000 individuals were distributed randomly across habitat i.e., individuals did not start the simulation on a road. In the predation-effect simulations, 1000 prey and 50 generalist predators were distributed randomly across habitat.

Reproduction

At the beginning of each time step, each individual produces a number of offspring determined by the nominal reproductive rate, a constant value applied to all individuals in all time steps for a model run. In the current runs, nominal reproductive rate was either high (32 offspring) or low (1 offspring), representing small and large (respectively) generic species (Table 3.2). These values were determined experimentally to ensure that under all other parameter combinations (Table 3.2) at least a few individuals survived for the entire simulation. In the

predation-effect version, the reproductive rate of the predators was held constant at 35 for all predators and runs. This is higher than the rate for the large animal in the single-species simulations (Table 3.2), which was necessary to ensure some predators survived at higher road densities. As a result, the nominal reproductive rate for the large prey species was also 35 and the small prey species was higher at 55 (Table 3.2).

The total number of individuals is not allowed to exceed the maximum capacity of the landscape as determined from the territory size (natural density) (Fig. 3.1). This is determined by dividing the number of habitat cells in the landscape by the territory size (number of cells per individual). In the current runs, territory size was either small (2 cells per individual or 200m² (maximum population size = 282,000 individuals)) or large (15,000 cells per individual or 1.5km² (maximum population size = 37 individuals)), representing small and large (respectively) generic species (Table 3.2). If the potential number of individuals prior to reproduction, based on the nominal reproductive rate (i.e., potential number of individuals = current number of individuals x nominal reproductive rate), was greater than the maximum population size, the reproductive rate was adjusted (actual reproductive rate = (potential number of individuals – maximum population size) / current number of individuals). All individuals can reproduce.

For one experiment (road attraction + vehicle avoidance) the number of individuals can exceed the maximum capacity of the landscape prior to reproduction as a result of receiving a benefit from the road in the form of extra offspring at the end of the previous generation (year) (see the movement submodel below). To ensure that the population does not exceed the maximum population size prior to movement in the current generation, excess individuals are killed off randomly if the number of individuals in the landscape exceeds the maximum population size (Fig. 3.1).

Figure 3.1. Model flow chart.

Movement

Net movement per individual per time step is modeled one individual at a time (Fig. 3.2). A random movement angle is selected between 0 and 360°. Nominal movement distance is a constant applied to all individuals in all time steps. In the current runs, nominal movement distance was either small (1.5 cells = 15m) or large (500 cells = 5km), representing the small and large (respectively) generic species (Table 3.2). When a moving individual encounters the border of the landscape, it re-enters the landscape on the opposite side and continues moving in the same direction (wrapped grid). Actual movement distance is determined by the combination of nominal movement distance and the species behavioural response to roads and traffic.

There are five parameters determining behavioural responses to roads and traffic, and traffic mortality (Figs. 3.2 and 3.3):

1. Traffic disturbance avoidance

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

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

where k is the avoidance parameter, and V is the traffic density. k determines the probability of an animal avoiding the road from a distance (below) at a given traffic density (Appendix L Fig. L1a). In the current simulations I held traffic density constant at 3 vehicles per 10m road cell for all model runs, and k , was either 0 or 200, corresponding to 0% and 100% probabilities (respectively) of avoiding the road (Appendix L Fig. L1a and Table 3.1 and 3.2).

The avoidance distance is a function of the animal's nominal movement distance so that larger road-avoiding animals avoid the road from farther away than do smaller road-avoiding animals (Fig. 3.4). Given the dimensions of the landscape and the road densities I investigated,

the maximum avoidance distance possible in the current runs was 450m, which is consistent with distances reported for large species such as woodland caribou (250m – Dyer et al., 2001), grizzly bears (500m – Waller and Servheen, 2005); and moose (≥ 500 m – Laurian et al., 2008). If at the beginning of a simulation an individual is closer to a road than its avoidance distance, it is moved to the nearest cell out of the disturbance zone before the simulation begins. If a traffic disturbance avoiding individual's nominal movement end point would place it on or across a road, or inside a disturbance zone, the individual moves in its current direction until it reaches the disturbance zone.

2. Road Attraction

A, the probability of an animal being attracted to a road (e.g., for food, a nesting site, a mate, or thermoregulation) was set at either 0 (no road attraction) or 1 (100% road attraction) (Table 3.2), and the road attraction zone for those attracted was set at 4 cells (Table 3.1). I made this simplifying assumption because road attraction zones are generally unknown. It is known that perceptual range in animals are highly variable depending on both the species (Zollner, 2000; Mech and Zollner, 2002; Forero-Medina and Vieira, 2009) and the particular context (Yeomans, 1995; Zollner and Lima, 1999; Schooley and Wiens, 2003; Olden et al., 2004; Flaherty et al., 2008; Forero-Medina and Vieira, 2009; Prevedello et al., 2011). If a road-attracted individual is within a road attraction zone, it is moved to the center of the nearest road cell and the vehicle avoidance submodel (below) is then applied.

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

Figure 3.2. Flow chart of the movement submodel.

Figure 3.3. Illustration of traffic disturbance avoidance, *T*, road surface avoidance, *R*, road attraction *A*, vehicle avoidance *C* and the probability of animals killed on the road, *M*.

Figure 3.4. Illustration of a traffic disturbance zone. Animals that avoid traffic disturbance due to vehicle lights, emissions, noise or pollution, avoid the habitat near roads from a certain distance away from the road(s). In the current simulations I assumed that the large species avoided the roads from 45 grid cells away (450m) and the small species type avoided the roads from 1 grid cell away (10m).

“normal” reproductive output. In the current runs B was set at 1 for all model runs, so reproductive output was doubled for animals receiving the benefit.

3. Road surface avoidance

R is the probability of an animal avoiding moving onto a road, in the event that its randomly selected movement trajectory would have taken it onto the road. Road surface avoidance occurs in species, such as some small mammals (Ford and Fahrig, 2008; McGregor et al., 2008), that are unlikely to move onto exposed surfaces such as roads (probably to avoid predation), but are not repulsed by traffic disturbance itself. In the current runs, the probability of avoiding the road surface was either 0 (no surface avoidance) or 1 (100% surface avoidance) (Table 3.2). If an individual avoids the road surface, it is moved back to the habitat cell adjacent to the road on the side from which it came (Fig. 3.2).

4. Vehicle avoidance

C , the probability that an animal on a road avoids oncoming vehicles, is a function of traffic density and is estimated using the same equation as for traffic disturbance avoidance (above), replacing T with C . k is the avoidance parameter and V is the traffic density. k is the probability of an animal avoiding vehicles(s) at a given traffic density (Appendix L Fig. L1a). In the current runs I held traffic density constant at 3 vehicles per road cell, and k was either 0 or 200, corresponding to 0% and 100% probabilities, respectively, of avoiding oncoming vehicles (Tables 3.1 and 3.2). If an individual on a road shows vehicle avoidance, 70% of the time, it is returned to the habitat cell adjacent to the road on the side of the road it came from (Fig. 3.2); otherwise it moves to the habitat cell adjacent to the road on the opposite side of the road (i.e., it crosses the road). I therefore assumed that animals frightened by vehicles are more likely to

return to a familiar location than move to an unfamiliar one, unless they are close to the unfamiliar side.

5. Road (traffic) mortality

M , the probability of an animal being killed on the road given it attempted to cross, is a function of traffic density and is estimated using the same equation as for traffic disturbance avoidance (above), replacing T with M . d is the mortality parameter and V is the traffic density. d is the probability of an animal being killed at a given traffic density (Appendix L Fig. L1b). In the current runs traffic density was held constant at 3 vehicles per road cell and d was either 0 or 2.5, corresponding to probabilities of road mortality of 0% and 88% respectively (Table 3.1 and 3.2). I used an upper limit of 88% to ensure that in all parameter combinations at least a few individuals would survive.

Density limit

In addition to the maximum population size for the landscape, as determined from the territory size (see reproduction submodel above), the density of species that avoid roads in each habitat block is not allowed to exceed a maximum, given the number of territories available in the block. For individuals that avoid roads from a distance (traffic disturbance avoidance; above), the effective block area is reduced to exclude the parts of the block within the traffic avoidance zone. In addition, for all current model runs, the maximum number of individuals per cell was at 1 individual per 10m x 10m cell (Table 3.1; Fig. 3.1).

Predation effect

The predation release hypothesis (above) does not invoke a paired predator-prey dynamic. Rather, it hypothesizes that release from predation pressure in landscapes with high

road density may compensate or even over-compensate for road mortality on a prey species. Therefore, I did not model a paired predator-prey dynamic; rather, I modelled generalist predators (from an unspecified number of species). The population of predators is not dependent on the prey population abundance.

The predation-effect version of the model contains individual generalist predators and a prey species (Table 3.2). In the current runs the predators were modeled as large species (large territory size, large movement range, and low reproductive rate) that should be negatively affected by road mortality i.e., showing no road avoidance behaviour. These characteristics were held constant for all predators for all experiments. The reproductive rate of the predators was 35. This is higher than the rate for the large animal in the single-species simulations (Table 3.2), which was necessary to ensure that some predator individuals survived at higher road densities. Two prey species types were modeled in separate runs, a large prey species (e.g., deer, moose) and a small prey species (e.g., small mammal, bird) (Table 3.2). Reproductive rate for the small prey species was 55 and for the large prey species was 35 (Table 3.2). After the movement submodel is applied to both predators and prey, individual predators create circular territories (15,000 cells in the current runs), within which all prey are eaten (Fig. 3.1).

Number of simulation runs

The total number of runs possible was limited because of the large spatial extent represented by the model, resulting in very large population sizes for many of the runs for the small species types. Some runs took longer than two months to run on high performance computers (1. Dell Precision T7500 – 2x Intel (R) Xeon (R) 2.67 GHz, total RAM 48GB; and 2. Beowulf Cluster - 64 nodes 4x 2.2GHz Opteron Cores w/8 GB RAM per node – 3 nodes with 12x 2.53 GHz Intel Xeron E5649 w/24 GB RAM per node), thus restricting me to 1 replicate per

parameter combination (above). I checked the impact of this by running up to 100 replicates for selected parameter combinations that ran more quickly, and found that model results did not qualitatively vary, with the exception of the large prey species runs. Thus for the large prey species runs, I ran 50 replicates per parameter combination. In all, 192 simulations were run. The outcome of each run was recorded as the mean abundance over the last 10 generations (zero if the population went extinct) (see Appendix M for simulated abundance data).

Results

Small species types

There was no behavioural response to roads scenarios predicted to result in a negative effect of increasing road density on the abundance of a small species type in either the single-species or predation-effect runs (Fig. 3.5). In single-species runs the abundance of the small species type was predicted to be unaffected by increasing road density for all behavioural response scenarios; the proportion of the maximum number of individuals observed remained near 1 as road density increased (Fig. 3.5a). In the presence of generalist predators that were negatively affected by increasing road density, the small prey species type was positively affected by increasing road density for all behavioural response scenarios; the proportions of the maximum number of individuals observed increased from 0 to >0.9 when the number of roads in the landscape exceeded 2 (Fig. 3.5b).

Large species types

Neutral effects of roads on the large species occurred in single-species runs when it was able to avoid oncoming vehicles and it either (i) showed no road or traffic disturbance avoidance

or (ii) was attracted to the road for a resource (Fig. 3.6a). In predation-effect scenarios, these scenarios led to positive effects of roads on the abundance of the large prey species (Fig. 3.6b). In addition, the abundance of large prey species that either (i) avoided roads from a distance due to traffic or (ii) avoided the road surface, increased with increasing road density until an optimum, above which it decreased (Fig. 3.6d). In all other scenarios the large species type was predicted to decrease in abundance with increasing road density (Fig. 3.6 c, e and f).

Discussion

The results support several previously suggested hypotheses to explain neutral or positive effects of roads on animal abundance. First, small species that avoid going onto roads but are not disturbed by road traffic are predicted to be unaffected by increasing road density (Fig. 3.5a). These conditions likely explain the observed lack of effect or weak effects for many small mammals and small birds. Second, the abundance of both a large and small species is predicted to be unaffected by roads if the species can avoid oncoming vehicles (Fig. 3.5a and 3.6a). These conditions might explain the lack of effect or weak effects of roads on some large and small mammal populations; however, despite many anecdotal observations, to my knowledge there are no studies that quantify vehicle avoidance behaviour in animals. Third, increasing road density is predicted to produce a net increase in abundance of small prey species whose generalist predators are negatively affected by road mortality (Fig. 3.5b), supporting the predation release hypothesis for observed positive effects of roads on populations of several small mammal species (Johnson and Collinge, 2004; Rytwinski and Fahrig, 2007; Fahrig and Rytwinski, 2009). Interestingly, my model also predicts a positive effect of roads on a large prey species in the presence of road mortality-affected predators, when the large prey species is able to avoid

Figure 3.5. Simulated predictions of the relative abundance - plotted as the proportion of the maximum number of individuals observed - of the small species types as a function of increasing road density, for different assumed behavioural responses to roads. Small species types had small territory sizes/high natural densities, small movement ranges, and high reproductive rates. (a) single-species version with no predators in the model; (b) predation-effect version, where the small species was prey for road mortality-affected large generalist predators.

Figure 3.6. Simulated predictions of the relative abundance - plotted as the proportion of the maximum number of individuals observed - of large species types as a function of increasing road density, for different assumed behavioural responses to roads. Large species types had large territory sizes/low natural densities, large movement ranges, and low reproductive rates. Predictions are separated into columns for results from the single-species runs with no predation in the model (large single species) (a, c, and e), and the predation-effect runs (large prey species).

oncoming vehicles (Fig. 3.6b), which may explain an observed positive effect of road density on abundance of white-tailed deer (Munro et al., *in press*).

Based on my simulation results I propose several new hypotheses to explain neutral or positive effects of roads on animal abundance. The single-species simulations predict that species with small territories and movement ranges and high reproductive rates are generally unaffected by roads, with all behavioural scenarios predicting neutral effects (Fig. 3.5a). Furthermore, there were no circumstances predicted to lead to negative effects of roads on this species type. These results suggest that the combination of high reproductive output, low mobility, and small territory sizes (high density) render populations resilient to effects of traffic mortality, resource inaccessibility and population subdivision as road density increases in the landscape. Such small animals can maintain viable populations within the habitat blocks surrounded by roads. It is possible that negative effects of roads on this species type might have been observed if the number of roads were increased further, especially for species that show no avoidance behaviour towards roads or traffic and therefore should suffer from high traffic mortality, and/or species that avoid traffic disturbance from a distance and therefore should suffer from high habitat loss and resource inaccessibility. As Forman et al. (2003) noted, road networks can vary greatly in density, with urban centers typically having a road density of about 40 km/km², suburban areas about 10 km/km², and rural agricultural landscapes having a road density of about 2 km/km². I designed my simulated landscapes to reflect the latter, and as such believe my predictions are valid for landscapes having road densities <2 km/km².

Since there are many documented negative effects of roads on abundance of amphibians and reptiles (reviewed in Rytwinski and Fahrig 2012), the "small animal type" in my simulations clearly does not represent these species well. The model must be missing important elements of

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

Roads are generally predicted to negatively affect populations of the large species types (Fig. 3.6 c, e and f), as expected *a priori* (e.g., Mladenoff et al., 1995; Mech et al., 1988, Mace et

al., 1996; Newmark et al., 1996; Reijnen et al., 1996; Dyer et al., 2001; Roedenbeck and Köhler, 2006). However, there are situations in which there is either a positive predicted effect (see above), no effect, or a hump-shaped predicted effect of roads on large species. Populations of species that do not avoid roads or traffic emissions (e.g., noise) and are able to avoid oncoming vehicles when attempting to cross roads are predicted to be unaffected by roads (Fig. 3.6a), as suggested by Jaeger et al. (2005). One could interpret this as indicating an imperative for studies quantifying vehicle avoidance behaviour in animals, so that road mitigation projects can be directed to species that are unable to avoid oncoming vehicles. However, I suggest that such studies may be unnecessary, since the presence of road-killed animals indirectly indicates an inability (or at least a lack of perfect ability) to avoid oncoming vehicles. This tends to support the current intuitive practice of planning mitigation for large species that are found killed on roads (e.g., Florida Panther (*Puma concolor coryi*), black bear (*Ursus americanus*), key deer (*Odocoileus virginianus clavium*) (Florida); grizzly bear (*Ursus arctos horribilis*), wolf (*Canis lupus*), wolverine (*Gulo gulo*) (Banff National Park Canada); large ungulates (British Columbia) (Evink, 1996; Leeson, 1996; Sielecki, 2007), particularly when there is sufficient information on population size to estimate the per capita road mortality rate (e.g., Florida Panther, Maehr et al., 1991; key deer, Calvo and Silvy, 1996).

The simulations do not support the idea that a species, either large or small, that is attracted to the road for a resource and able to avoid oncoming vehicles should show a positive population-level response to roads; rather, the simulations predict a neutral effect in these cases (Fig. 3.5a and 3.6a). In my model, it seems that the territory size of the species limits the extent to which the added resources near roads can increase the population, as the populations of both the large and small species types were predicted to remain close to the maximum capacity for the

landscape even as road density increased. If true, this suggests that the apparent positive effects of road attraction on animal abundance (e.g., vultures and raptors - Knight and Kawashima, 1993; Meunier et al., 2000; Benítez-López et al., 2010) may be illusory in some cases; it may actually represent increased time spent within the portion of habitat near to roads, and a benefit at the individual level i.e., extra offspring to the individuals near roads, rather than a positive effect of roads on the overall population, which would require an increase in the number of territories. On the other hand, food availability has been identified as the most important determinant of home-range size and shape in birds (Rolando, 2002), with home ranges often being smaller when resource density is higher (Zabel et al., 1995). Therefore, it may be possible that landscape containing higher road densities can support a larger number of smaller territories of a particular species. To my knowledge however, to date there are no studies showing smaller territory sizes near roads for animals such as birds of prey which are attracted to roads.

Interestingly, the simulations predict an optimal road density for the large prey species type that avoids the road or traffic emissions (Fig. 3.6d). For these species road mortality is low due to their road/traffic avoidance. As road density increases, the benefit of reduced predation can outweigh the habitat loss/resource inaccessibility associated with roads and traffic avoidance. However, above an intermediate road density these negative road effects prevail. This indicates that, unlike the effects of road mortality, the effects of habitat loss and subdivision due to roads are only evident at high road densities. This is supported by previous simulations where by traffic mortality had a much stronger effect on animal population persistence than did road avoidance alone (Jaeger and Fahrig, 2004). In addition, Jaeger and Fahrig (2004) found that road mortality decreased persistence time, whereas road avoidance led to longer persistence times in most simulated cases. This result is also supported by some empirical studies of large species

showing road density thresholds, above which the species is absent from the landscape. For example, numerous studies have found that wolves are absent from areas with road densities exceeding 0.6 km/km^2 (> 4 roads in my model) (Thiel, 1985; Mech et al., 1988; Mladenoff et al., 1995), most likely due to road mortality (Fuller, 1989). For species such as elk (*Cervus elaphus*), which avoid roads from a distance (Rowland et al., 2000; Gagnon et al., 2007; Dodd et al., 2007; Stewart et al., 2010), and are therefore affected by habitat loss and resource inaccessibility rather than mortality, much higher road density thresholds have been reported e.g., 3.2 km/km^2 for a 25% decline in usable elk habitat (Lyon, 1983).

The comparisons reported here represent extreme contrasts in life history and behavioural responses to roads. Due to the realistic spatial extent of the model, computing demands were heavy, and so I was not logistically able to simulate all combinations of full gradients of all the parameters. Many real combinations are missing from my runs. For example, the short-tailed weasel (*Mustela erminea*) has a relatively large home range (13 ha) for its small body size (75 g) (Ontario, Canada; Simms, 1979; Eder, 2002) compared to the similar sized eastern chipmunk (*Tamias striatus*) with a home range size of 0.1 ha (Yerger, 1953); thus it is neither a typical small species nor a typical large species type. However, even with the restricted set of parameter combinations that I evaluated, several new working hypotheses emerged (above), representing generalized conditions of the circumstances which lead to neutral and positive road effects. The model could be used in future to develop predictions for particular species population-level responses to road density.

This study represents the first to develop general hypotheses and predictions specifically of the circumstances leading to neutral and positive effects of roads on population abundance. My results suggest that there are many situations where road mitigation is not necessary (18 of

24 scenarios predicted neutral or positive effects of roads). However, many of these (10 of 18) depend on generalist predators whose populations are negatively affected by road mortality. This implies priority for mitigating road effects should be directed towards the predators of small mammals and birds rather than the small mammals and birds themselves. Although these species were predicted to benefit from reduced predation, they were also predicted to be largely unaffected by roads even in the absence of predation, suggesting again that mitigation for these species is unnecessary. In contrast, for large prey species, if mitigation is directed towards their predators, increased predation may result in negative road effects on the large prey; therefore road mitigation should be directed towards all large species types. For large species that are mainly affected by roads through road mortality, mitigation should be mainly directed towards preventing animals from moving onto roads through complete fencing of the road and wildlife crossing structures in key movement areas. For birds, mitigating for road mortality would require installation of tall structures along roads that encourage or force birds to fly above the height of traffic. For the larger mammals that are disturbed by traffic, road effects can be mitigated by measures aimed at reducing road and traffic density in the landscape. In addition, engineering solutions to reducing traffic noise, e.g., changes to pavement or tires, could partially mitigate the disturbance effects. However, since many of the species that have been reported to avoid roads from a distance, have been reported to nevertheless cross roads in certain locations and thus potentially suffer from road mortality, providing complete fencing in combination with wildlife crossing structures in key movement areas would also be beneficial.

In conclusion, my simulations suggest that species with small territories and movement ranges and high reproductive rates are not negatively affected by roads. The results also suggest, contrary to previous suggestions, that populations of species that obtain resources from a road

are nevertheless not positively affected by increasing road density. In addition, my results support the predation release hypothesis for positive road effects on populations of both small and large prey species types. Interestingly, the simulations predict an optimal road density for large prey species that avoid roads or traffic emissions and have predators that are negatively affected by roads. Therefore, unlike the effects of road mortality, the effects of habitat loss and subdivision due to roads are only evident at high road densities. Overall, the simulation results suggest that there are many species for which road mitigation is not necessary; mitigation efforts should be tailored to the species, such as large predators, that show negative population-level responses to roads.

General Discussion

There is now a growing body of evidence that 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 becoming common in new highway construction projects (Beckmann and Hilty, 2010). Roedenbeck et al. (2007) suggest that maximizing the impact of road research in the decision-making process requires that the questions addressed by road ecologists be directly relevant to the practical issues of road planning and construction. To ensure mitigation will be effective at reducing/eliminating road related impacts on wildlife, it is important to have some validated theory that allows us to predict which species or species groups are most vulnerable to road effects at the population level, and the likely causes of those impacts, so that mitigation efforts can be tailored to those species. As such, the focus of my thesis was to directly address the most critical road ecology research question identified by Roedenbeck et al. (2007) in their research agenda for road ecology: "Under what circumstances do roads affect population persistence?"

Results from my dissertation contribute to road effects theory by identifying the main factors/circumstances, specifically the life history traits and/or behavioural factors by in which roads affect animal populations: 1) at the class level, mammals with lower reproductive rates, greater mobilities, and larger body sizes are more susceptible to negative road/traffic effects at the population level than smaller mammals with higher reproductive rates and lower mobilities (Chapter 1 and 2); more mobile birds are more susceptible to negative road and/or traffic effects than less mobile birds (Chapter 2); and amphibians and reptiles are generally vulnerable to negative road effects (Chapter 2); 2) more generally, populations of species with small territories and movement ranges and high reproductive rates should not be reduced by roads

(Chapter 3); 3) populations of species with large territories and movement ranges and low reproductive rates, that are attracted to roads for a resource, or that move onto roads irrespective of traffic are strongly susceptible to traffic mortality at the population level (Chapter 2 and 3), unless they are able to avoid oncoming vehicles (Chapter 3); 4) populations of species with large territories and movement ranges and low reproductive rates, that are disturbed by traffic (Chapter 2 and 3) or avoid the road surface (Chapter 3), are more vulnerable to negative road effects (resource inaccessibility, habitat loss, population subdivision), unless these species have predators that are negatively affected by roads, in which case, an optimal road density was predicted from simulations, whereby the abundance of large prey species, increased with increasing road density until an optimum, above which it decreased (Chapter 3); 5) contrary to previous suggestions, populations of species that obtain a resource from roads are nevertheless not positively affected by increasing road density (Chapter 3); and 6) populations of both small and large prey species types can be positively affected by roads, supporting the predation release hypothesis (Chapter 3).

The main finding in Chapter 1 was that mammal species with lower reproductive rates, greater mobilities, and larger body sizes are more susceptible to negative road effects at the population level. A number of hypotheses based on species life history traits have been proposed as explanations for road effects (outlined in general introduction), but this was the first study to test the effects of species traits on mammal responses to roads at the population level. Of particular importance was the finding that reproductive rate - which affects a species ability to rebound from low numbers resulting from road mortality - was the best predictor of population-level response to roads (Table 1.1; Fig 1.6a). Similar strong effects of reproductive rate on species response to habitat loss have been reported in both the theoretical and empirical literature

(With and King, 1999; Fahrig, 2001; Vance et al., 2003; Holland et al., 2005), however, to my knowledge, I am the first to provide strong support for the hypothesis that species with lower reproductive rates are more negatively affected by road density than are species with higher reproductive rates. Results from Chapter 1 imply that priority should be placed on mitigating road effects on larger mammals with lower reproductive rates.

The next question to address was whether a similar pattern is found when synthesizing the results across a set of studies conducted under a variety of circumstances and whether this pattern was similar for other taxa. When broadening the scope of the investigation into road and/or traffic effects on mammal populations in Chapter 2 (i.e., 34 studies from 12 countries including 84 species) the meta-analysis provides further support for Chapter 1 results that populations of mammals with lower reproductive rates, greater mobilities, and larger body sizes are most vulnerable to the negative effects of roads and/or traffic. Results from this chapter confirm that priority for road mitigation should be directed towards larger mammal species with low reproductive rates and large home ranges.

Some of the life history traits found to explain population level responses to roads for mammals were also found to explain animal responses to roads and/or traffic for other taxa. For birds, species mobility - which affects a species encounter rate with roads - was the only life history trait that explained variability in the magnitude of population-level responses to roads (Fig. 2.3 b; Table 2.5), indicating that more mobile bird species are more susceptible than less mobile species to negative road effects. Although support for this hypothesis was weak, this result 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). This

result suggests that priority should be placed on mitigating road effects on bird species with larger territories.

I also found that of the taxonomic classes in the meta-analysis, amphibians and reptiles were the most negatively affected by roads and/or traffic (Fig. 2.2), 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). Of particular interest is that similar to mammals, reproductive rate was the main predictor of amphibian population level responses to roads (Fig. 2.3 d; Table 2.8). Similarly, when looking at anurans only, age at sexual maturity (which was highly correlated with reproductive rate $r > 0.6$; Table 2.2) showed the strongest model fit - species with shorter ages at sexual maturity were more negatively affected by roads and/or traffic (Fig. 2.3 e; Table 2.9). Taken together, these results suggest that in general, reproductive rate and/or age at sexual maturity are likely good indicators of species' susceptibility to road effects. Contrary to mammals however, both reptiles and amphibians display indeterminate growth, in which reproductive rate increases with body size and thus with age. For amphibians and reptiles, indeterminate growth, in combination with their need to access multiple required resources in the landscape (Wilbur, 1980; Gibbons, 1986; Hecnar and M'Closkey, 1996) and/or high movements rates associated with foraging and mate searching (King and Duvall, 1990), likely contributes to their susceptibility as a group to road effects. In general my results confirm the notion that amphibians and reptiles are particularly vulnerable to road effects and as such these results imply that priority for mitigation should be directed towards all amphibians and reptiles.

I had initially hoped to include species-specific behavioural 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 (11 mammals, 2 birds, 3 reptiles, and 1 amphibian) (Table

2.1.1). Qualitatively, my 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 behavioural responses to roads. These results imply that priority for mitigating road effects should be directed towards species that do not avoid roads or are disturbed by traffic.

From our review paper (Fahrig and Rytwinski, 2009) and the results from chapter 2, it was observed that although the majority of population-level responses to roads are negative, there were also many species whose populations have been shown to be unaffected or even to increase in response to roads. In response to these observations, Chapter 3 represents the first study to develop general hypotheses and predictions specifically of the circumstances leading to neutral and positive effects of roads on population abundance. My results suggest that there are many situations where road mitigation is not necessary (18 of 24 scenarios predicted neutral or positive effects of roads). However, many of these (10 of 18) depend on generalist predators whose populations are negatively affected by road mortality. This implies that priority for mitigating road effects should be directed towards the predators of small mammals and birds rather than the small mammals and birds themselves. For large prey species (e.g., large herbivores), if mitigation is directed towards their predators, increased predation may result in negative road effects on the large prey; therefore road mitigation should be directed towards all large species types.

A valid question proposed by Bissonette and Rosa (2009) asks: Can we even speak of a group response (e.g., “small mammals”) when results from several studies show species specific responses? This is a question that road ecologists do not appear to have settled among themselves, and yet, some consensus would appear to be necessary. Therefore, an important

question to now address is: Taken together, do the results from my dissertation provide enough evidence to move forward and mitigate road effects for those species groups identified herein as being most vulnerable to road/traffic effects? Below I address this question for each taxon separately in attempt to provide some clarity.

Mammals

I am confident that results from all three chapters of my dissertation have provided enough evidence to recommend that priority for road mitigation should be directed towards all larger mammal species with low reproductive rates, large home ranges, and low natural densities. The negative effects of roads on these species populations appear to be mainly due to road mortality, and traffic disturbance (resource inaccessibility, habitat loss, population subdivision) (Table 2.11 and Fig. 3.6 c-f). Results from my simulations suggest that no road mitigation should be necessary for those species able to avoid oncoming vehicles (Fig. 3.6 a and b); however, to date, there are only anecdotal observations of species showing this behaviour, therefore I recommend we assume no species are able to perfectly avoid vehicles every time they encounter them and mitigate for all mammals with low reproductive rates, large home ranges, and low natural densities, placing priority on predators. Furthermore, unless there is evidence to suggest road mitigation is necessary for a particular small mammal species i.e., a species of conservation concern, results from this dissertation and the empirical literature to date, suggest no road mitigation measures should be needed for smaller mammals.

Amphibians and Reptiles

I believe there is enough evidence to recommend priority for road mitigation should be directed towards all amphibians and reptiles. Although only Chapter 2 directly relates to these groups, results clearly show that these two classes are particularly vulnerable to roads/traffic

effects, with negative effects appearing to be mainly due to road mortality and road avoidance (resource inaccessibility, subpopulation subdivision) (Table 2.11). This information, in combination with the fact that they have the highest threat status of all terrestrial vertebrates, with significantly more species at risk than either mammals or birds (IUCN, 2010), suggests that priority for mitigation is necessary for these classes as a whole. Therefore I suggest that there is enough evidence to warrant that projects now be focused on mitigating road effects for these two groups. With that said, there are however a few interesting questions that could still be addressed. As mentioned above, reptiles and amphibians are unique to other vertebrates in this dissertation, in that they display indeterminate growth. I suggest that further study investigating the effects of roads on amphibian and reptile fecundity deserves attention in future in order to better understand how indeterminate growth affects species responses to roads and/or traffic.

Birds

I believe results from Chapter 2 and 3 provide sufficient evidence to suggest that priority should be placed on mitigating road effects on bird species with larger territories. With that said, results from my thesis have also highlighted some important areas where further study is needed in order to better understand the circumstances in which roads/traffic affect bird populations. For example, are there other potentially important causal mechanisms underlying how life history traits may affect species responses to roads not included in my Chapter 2 and 3 analyses? 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, may be 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 K), suggesting that more studies on a wider range of bird orders are needed. 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. For birds, species that spend more time on the ground (e.g., ground nesters, ground-dwelling species) or those that are unable to move themselves off the ground quickly (low agility) will likely be more susceptible to colliding with vehicles. For example, Jacobson (2005) suggested that ground-dwelling birds are at greater risk of vehicle collisions because they spend longer time on the road surface, and often have a shallow escape flight trajectory. Furthermore, birds with high wing loading (e.g., female owls) were suggested to be more vulnerable to being struck by vehicles because of lower agility due to higher weight (in Kociolek and Clevenger, 2011). In addition, species requiring multiple habitat types to complete their life cycle in close proximity (i.e., landscape complementation), as in the case of some woodland birds and wintering waterbirds (Petit, 1989; Kloskowski et al., 2009), will likely be more sensitive to road impacts. Therefore species traits such as nesting height, wing loading, and the number of habitat (cover) types required to complete life cycle may be necessary traits to investigate in future work.

Further study is also required to better understand the effects of roads/traffic on populations of small birds in particular. Contrary to small mammals, negative population level effects of roads/traffic have been reported in the empirical literature for some small bird species (e.g., Reijnen et al., 1996; Forman et al., 2002; Peris and Pescador, 2004). Despite this, there was no behavioural response to roads scenarios predicted to result in a negative effect of increasing road density on the abundance of a small species type in my simulations (Fig. 3.5). There are some potential reasons for this inconsistency. First, some of the empirical studies of road effects on birds were designed such that the effects of distance from the road and distance from habitat edge are confounded, which means that apparent road effects could be partly or even mainly

because of habitat edge effects on birds. This problem is recognized by some authors (e.g., Delgado et al., 2007; Summers et al., 2011), and as such, for some studies it may not be possible to state conclusively that the negative effects of roads are real due to weakness in study design. Second, as stated above, my model maybe missing important elements of these species life histories that would make them susceptible to roads (e.g., nesting height, wing loading, and the number of habitat (cover) types needed to complete life cycle). Third, characteristics of the road, other than the number of them in a landscape, will likely affect species responses to roads (Jaeger et al., 2005). For example, a species that avoids roads from distance due to traffic disturbance (e.g., traffic noise - as is commonly assumed for many birds species), while less likely to be killed on roads, are susceptible to habitat loss, as habitat quality within the vicinity of the road is reduced; the higher the traffic amount on the road, the more habitat is effectively lost to the species. Therefore, future work could involve using my simulation model to study trade-offs between traffic volume and the relative effects of different road impacts (i.e., mortality, habitat loss etc.). Fourth, the comparisons reported in my simulations represent extreme contrasts in life history and behavioural responses to roads. Due to the realistic spatial extent of the model, computing demands were heavy, and so I was not logistically able to simulate all combinations of full gradients of all the parameters. Many real combinations are missing from my runs. For example, the White-throated sparrow (*Zonotrichia albicollis*) - which has been found to be negatively affected by roads (Summers, 2009) - has a relatively low reproductive rate (4 offspring per year) for its small body size compared to the similar sized Song sparrow (*Melospiza melodia*) - which has been found to be positively affected by roads (Summers, 2009) - with a higher reproductive rate (12 offspring per year). Thus the White-throated sparrow is neither a typical small species nor a typical large species type. As such, the simulation model

could be used in future to develop predictions for species which have different combinations of life histories than those simulated in chapter 3.

When planning and designing road mitigation measures, we should be aiming to provide full mitigation of all road impacts, for as many species or species groups as possible. Here is what I would consider the ideal road mitigation design for an existing road to fully mitigate all road impacts for all the road affected species groups identified above. To prevent road mortality, mitigation should be mainly directed towards preventing animals from moving onto roads through complete fencing of the road and providing wildlife crossing structures (ecopassages) in key movement areas. To prevent large mammals from going onto roads, fencing with an apron buried below ground to keep digging animals from going under the fence should be used (Clevenger and Ford, 2010). Such fences, if constructed with solid material such as cement or a less dense material such as wood, would also act as a noise barrier for reducing traffic noise for those species affected by traffic disturbance (Jacobson, 2005). Additionally, due to the solid nature of the fence, this would prevent smaller species such as amphibians and reptiles affected by road mortality from going onto the road. For highly mobile birds, mitigating road mortality would require installation of structures along roads that encourage or force birds to fly above the height of traffic, for example, installing diversion poles to the top of the fence (Jacobson, 2005). For those species mainly affected by roads through traffic disturbance, mitigation should be mainly directed at reducing road and traffic density in the landscape, and reducing traffic noise. In addition to constructing the fence to act as a noise barrier, engineering solutions to reduce traffic noise, e.g., changes to pavement or tires, could help to mitigate the disturbance effects. In order to increase permeability of the road corridor for those species that avoid the road surface, and to off-set the imposed complete movement barrier of the mitigation fencing, wildlife

crossing structures would need to be placed in key movement areas. To accommodate larger mammals, wildlife overpasses designed to restore habitat continuity from one side to the other should be used and be closed to the public (Clevenger and Ford, 2010). In order to ensure connectivity for amphibians and reptiles, extended stream crossings should be placed wherever streams or wetlands intersect with roads (Clevenger et al., 2001; Huijser and McGowen, 2010). Extended stream crossings 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. To maximize the effectiveness, such underpasses should be constructed large enough to also allow movement of larger mammals.

Having identified those species groups for which there is sufficient evidence that their populations are negatively affected by roads and/or traffic, and the likely causes of those impacts, I suggest the focus now needs to be shifted towards addressing other pressing questions raised in the Rauischholzhausen agenda (Roedenbeck et al., 2007) such as: (1) What is the relative importance of road effects versus other impacts on population persistence? In order to develop efficient and effective mitigation strategies for road affected species, it is important to know whether roads contribute substantially to the decline of a particular animal population relative to other impacts (Roedenbeck et al., 2007). For example, Eigenbrod et al. (2008) studied the relative importance of forest amount versus traffic density on amphibian populations and found that traffic density has at least as large a negative effect on anurans as does deforestation. This information will be useful in identifying those species or species groups where immediate priority for mitigation is necessary. (2) Under what circumstances can road effects be mitigated? In a review of the use and effectiveness of wildlife crossing structures, van der Ree et al. (2007) noted that most measures designed to increase the permeability of roads for wildlife were

successful at the level of the individual animal; however there was insufficient information and analysis in the majority of studies to evaluate whether the viability of the population has increased to an acceptable level. As suggested by van der Ree et al. (2007), research needs to focus more explicitly on quantifying the effectiveness of mitigation measures rather than their use alone.

In conclusion, my dissertation has made significant contributions to the field of landscape and road ecology. In particular, results from my dissertation contribute to road effects theory by clarifying key patterns of the circumstances in which roads affect animal populations. In addition, I have identified those species or species groups most vulnerable to road effects at the population level, and the likely causes of those impacts, so that mitigation efforts can now be tailored to those species.

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Appendix A. Reproductive rate, average body size, and mean home range area of mammal species used in this study (Chapter 1).

Table A1. Reproductive rate and average body size of the 17 mammal species tracked during 2005, 2008, and 2009. Reproductive rate was measured as the mean number of offspring per litter multiplied by the maximum reported number of litters per year. Most values for reproductive rate were taken from Eder (2002). However, when not stated in Eder (2002), values were taken from other sources as close to my study region as possible. Body size was measured as the average body size for both sexes in grams. All values for body size were taken from Eder (2002). Note: maximum reported number of litters per year could not be found in the literature for *Clethrionomys gapperi*; however, this species was not included in the road effect vs predictor analyses since the road-density-effect model fit the data better than the no-road density-effect model (Appendix F – Table F1). Reprinted with permission from © 2011 Ecological Society of America.

Species	Reproductive Rate			Reproductive rate	Average Body Size (g)
	Mean litter size	Max # litters/year	Source		
<i>Peromyscus leucopus</i>	5.0	2	Eder 2002	10.0	20.0
<i>Zapus hudsonius</i>	5.5	2	Eder 2002	11.0	20.0
<i>Napaeozapus insignis</i>	4.5	1	Eder 2002	4.5	21.5
<i>Blarina brevicauda</i>	6.0	2	Blair 1940b	12.0	21.5
<i>Clethrionomys gapperi</i>	5.0	n/a	n/a	n/a	27.5
<i>Mustela erminea</i>	8.0	1	King 1983	8.0	75.0
<i>Tamias striatus</i>	4.0	2	Smith and Smith 1972	8.0	102.5
<i>Tamiasciurus hudsonicus</i>	4.5	1	Eder 2002	4.5	195.0
<i>Sciurus carolinensis</i>	4.5	1	Eder 2002	4.5	555.0
<i>Sylvilagus floridanus</i>	5.0	4.5	Chapman et al. 1977	22.5	1200.0

Table A1. Continued

Species	Reproductive Rate				Average Body Size (g)
	Mean litter size	Max # litters/year	Source	Reproductive rate	
<i>Lepus americanus</i>	4.0	3	Eder 2002	12.0	1250.0
<i>Mephitis mephitis</i>	6.0	1	Wade-Smith and Verts 1982	6.0	3050.0
<i>Marmota monax</i>	4.5	1	Eder 2002	4.5	3600.0
<i>Martes pennanti</i>	2.5	1	Eder 2002	2.5	3750.0
<i>Vulpes vulpes</i>	5.5	1	Eder 2002	5.5	5200.0
<i>Procyon lotor</i>	4.5	1	Eder 2002	4.5	9500.0
<i>Ursus americanus</i>	3.0	1	Eder 2002	3.0	155000.0

Table A2. Mean home range area of the 17 mammal species tracked during 2005, 2008, and 2009 measured as the average area (ha) for the two sexes. If more than one study was close in proximity to my study region, I calculated a weighted mean home range area by weighting each study by its sample size. Total sample size refers to the combined sample sizes from all sources used. Reprinted with permission from © 2011 Ecological Society of America.

Species	Mean Home Range Area			
	Mean home range area (ha)	Total Sample Size	Source	Study location
<i>Peromyscus leucopus</i>	0.6	73	Smith and Speller 1970 Wegner 1995	eastern Ontario eastern Ontario
<i>Zapus hudsonius</i>	0.4	50	Blair 1940a	southern Michigan
<i>Napaeozapus insignis</i>	1.1	32	Blair 1941	northern Michigan
<i>Blarina brevicauda</i>	0.4	7	Blair 1941	northern Michigan
<i>Clethrionomys gapperi</i>	0.3	7	Blair 1941	northern Michigan
<i>Mustela erminea</i>	13.1	33	Simms 1979 Robitaille and Raymond 1995	southern Ontario southern Quebec
<i>Tamias striatus</i>	0.1	32	Yerger 1953	central New York
<i>Tamiasciurus hudsonicus</i>	2.2	13	Layne 1954	central New York
<i>Sciurus carolinensis</i>	20.3	13	Bridges 2002	central Ontario
<i>Sylvilagus floridanus</i>	1.3	19	Trent and Rongstad 1974	southwestern Wisconsin
<i>Lepus americanus</i>	5.9	27	O'Farrell 1965 Rongstad 1971	Alaska Minnesota
<i>Mephitis mephitis</i>	294.7	26	Storm 1972	northern, Illinois
<i>Marmota monax</i>	6.4	15	Ferron and Ouellett 1989	southeastern Quebec
<i>Martes pennanti</i>	655.0	26	Koen et al. 2007	eastern Ontario
<i>Vulpes vulpes</i>	900.0	34	Voigt and Macdonald 1984	southwestern Ontario
<i>Procyon lotor</i>	391.0	30	Rosatte et al. 2010	eastern Ontario
<i>Ursus americanus</i>	4020.0	23	Maxie 2009	Algonquin Provincial Park, Ontario

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Appendix B. Raw relative abundance data for the 17 mammal species tracked during 2005, 2008, and 2009, and road density values.

Table B1. Relative abundance data from the 2005 tracking period. Tracking began 6 June 2005 and was carried out in focal patches at the center of each landscape for eight consecutive weeks ending 29 July 2005. Landscapes correspond to landscape names with numbers in brackets corresponding to original site identifications. Percent forest is the total amount of forest within each of the 2-km radius landscapes. Relative abundance was estimated as the total number of tracks found at the site over the eight week tracking period. Road density values were calculated as the total length of all road types within each landscape divided by the total area of the landscape (km/km^2). PL: *Peromyscus leucopus*, ZH: *Zapus hudsonius*, NI: *Napaeozapus insignis*, BB: *Blarina brevicauda*, TS: *Tamias scurius*.

Landscape	Road Density (km/km^2)	% Forest	PL	ZH	NI	BB	TS
1 (24)	0.42	36	7	0	0	2	0
2 (47)	0.46	26	10	3	1	3	0
3 (22)	0.49	28	11	2	2	0	0
4 (2)	0.63	18	25	0	3	6	0
5 (12)	0.68	25	18	1	1	28	1
6 (10)	0.76	18	0	3	1	0	0
7 (25)	0.85	33	28	0	5	34	0
8 (27)	1.24	18	26	4	1	0	0
9 (36)	1.25	28	28	0	1	24	0
10 (38)	1.29	23	23	1	0	49	0
11 (31)	1.32	20	72	0	0	10	0
12 (35)	1.42	27	54	0	0	2	3
13 (33)	1.45	38	13	2	3	3	0
14 (43)	1.62	20	30	12	0	15	16

Table B2. Relative abundance data from the 2008 tracking period. Tracking began 2 June 2008 and continued for eleven consecutive weeks, ending 22 August 2008. Relative abundance was taken as the number of weeks that a mammal species tracks were identified at each sample site. Landscapes correspond to landscape names with numbers in brackets corresponding to original site identifications. Each landscape was centred on a sampling site containing a stream/creek and a forest patch greater than 6ha within 150m of each other, where tracking took place. Road density values were calculated as the total length of all road types within each landscape divided by the total area of the landscape (km/km^2). Percent forest is the total amount of forest within each of the 3-km radius landscapes. ME: *Mustela ermine*, TH: *Tamiasciurus hudsonicus*, LA: *Lepus americanus*, SF: *Sylvilagus floridanus*, MM: *Mephitis mephitis*, Mm: *Marmota monax*, MP: *Martes pennanti*, VV: *Vulpes vulpes*, Pl: *Procyon lotor*, UA: *Ursus americanus*.

Landscape	Road Density (km/km^2)	% Forest	ME	TH	LA	SF	MM	Mm	MP	VV	Pl	UA
1 (160)	0.73	23.8	1	2	0	0	1	0	1	0	9	0
2 (3496)	0.75	33.6	0	4	0	0	0	0	0	0	9	0
3 (252)	0.76	20.2	0	3	0	0	2	1	2	0	10	0
4 (355)	0.79	24.2	0	2	0	0	2	0	0	0	10	0
5 (3327)	0.86	34.7	0	4	0	0	1	0	1	0	8	0
6 (2263)	0.88	29.9	0	1	0	0	0	0	0	0	11	0
7 (2293)	0.89	34.4	0	1	0	0	0	0	1	0	9	2
8 (1276)	0.94	30.5	0	0	0	0	0	0	0	0	11	0
9 (2679)	1.27	25.3	0	1	0	0	1	0	0	0	8	0
10 (2733)	1.02	27.2	0	0	0	0	0	0	4	0	4	0
11 (2032)	1.08	22.3	0	0	0	0	5	1	5	0	11	0
12 (1651)	1.13	32.7	0	2	0	0	0	1	0	0	11	0
13 (940)	1.16	20.6	2	0	0	0	0	0	0	2	9	0
14 (3130)	1.18	22.0	0	0	0	0	0	0	3	0	7	0
15 (1232)	1.19	31.0	0	2	0	0	2	0	0	0	8	0

Table B2. Continued

Landscape	Road Density (km/km²)	% Forest	ME	TH	LA	SF	MM	Mm	MP	VV	PI	UA
16 (2071)	1.19	25.6	3	1	0	0	0	0	0	0	10	0
17 (2957)	1.19	25.3	0	0	1	1	0	0	0	0	5	0
18 (1151)	1.21	29.0	0	2	0	0	1	0	0	0	11	0
19 (1901)	1.36	22.2	2	1	0	0	3	2	1	0	8	0
20 (246)	1.25	20.9	0	2	0	0	0	0	2	0	11	0
21 (1767)	1.45	20.4	0	3	0	0	0	0	0	0	9	0
22 (1919)	1.28	32.5	0	3	0	0	0	0	0	0	6	0
23 (933)	1.29	30.4	1	1	0	0	0	0	0	0	2	0
24 (196)	1.30	20.3	0	3	0	2	3	1	2	0	7	0
25 (321)	1.59	26.5	0	2	0	0	0	0	0	0	10	0
26 (1775)	1.34	21.8	1	0	0	2	0	0	0	0	8	0
27 (136)	1.34	34.1	0	2	0	0	0	0	0	0	9	0
28 (202)	1.48	1.36	0	4	0	0	0	0	0	0	6	0
29 (3046)	1.58	31.7	1	1	0	0	1	0	0	0	11	0

Table B3. Relative abundance data from the 2009 tracking period. Tracking began 1 June and was carried out in focal patches at the center of each landscape for eight consecutive weeks ending 24 July 2009. Relative abundance was estimated as the total number of tracks found at the site over the eight week tracking period. Landscapes correspond to landscape names with numbers in brackets corresponding to original site identifications. Road density values were calculated as the total length of all road types within each landscape divided by the total area of the landscape (km/km^2). Percent forest is the total amount of forest within each of the 2-km radius landscapes. PL: *Peromyscus leucopus*, ZH: *Zapus hudsonius*, NI: *Napaeozapus insignis*, BB: *Blarina brevicauda*, CG: *Clethrionomys gapperi*, ME: *Mustela ermine*, TS: *Tamias striatus*, TH: *Tamiasciurus hudsonicus*, SC: *Sciurus carolinensis*, Pl: *Procyon lotor*.

Landscape	Road Density (km/km^2)	% Forest	PL	ZH	NI	BB	CG	ME	TS	TH	SC	Pl
1 (275)	0.41	27.0	32	7	1	0	0	0	37	29	0	3
2 (47)	0.46	26.0	57	6	0	1	3	0	7	1	1	2
3 (314)	0.46	29.7	48	1	0	5	3	3	136	39	3	24
4 (22)	0.49	28.0	28	3	1	3	1	3	23	5	1	11
5 (4702)	0.59	30.0	59	0	1	0	0	1	49	19	2	16
6 (3085)	0.66	21.3	10	1	0	1	3	0	10	2	2	8
7 (294)	0.74	21.3	68	2	0	10	8	3	34	73	2	8
8 (290)	0.75	21.5	75	0	0	3	2	1	84	7	1	18
9 (1500)	0.76	29.5	131	3	1	0	1	0	1	1	0	11
10 (4892)	0.76	23.3	89	2	0	3	4	0	7	12	3	9
11 (403)	0.80	21.7	31	0	1	0	1	0	121	11	1	19
12 (3274)	0.85	29.1	36	4	2	2	3	0	18	4	0	8
13 (2679)	1.27	25.3	70	3	0	6	3	0	15	7	1	7
14 (31)	1.32	20.0	54	4	3	5	9	1	4	4	0	5

Table B3. Continued

Landscape	Road Density (km/km²)	% Forest	PL	ZH	NI	BB	CG	ME	TS	TH	SC	PI
15 (1775)	1.34	21.8	44	3	2	5	1	1	2	14	5	8
16 (1901)	1.36	22.2	25	1	0	1	0	0	6	23	2	0
17 (1767)	1.45	20.4	44	4	3	7	6	1	4	7	1	1
18 (336)	1.48	25.2	21	1	1	0	1	1	63	2	0	7
19 (321)	1.59	26.5	42	0	0	0	0	0	81	28	1	15
20 (396)	1.59	21.9	144	12	1	14	5	0	42	28	1	17
21 (1481)	1.64	27.2	82	3	0	1	0	1	16	10	0	7
22 (6207)	1.72	27.4	59	3	0	2	1	2	11	10	2	10
23 (308)	1.75	22.9	59	3	0	1	1	3	14	3	0	11
24 (240)	1.95	29.9	75	2	1	2	1	0	3	4	1	4

Appendix C. Model summaries and parameter estimates from the linear regressions of relative abundance on road density.

Table C1. For each of seventeen mammal species tracked during 2005, 2008, and 2009: parameter estimates (standardized regression coefficient (β) and its standard error (SE)) from the simple linear regression of relative abundance on road density for each year separately, and R^2 value. Sample sizes (number of landscapes) are 14, 29, and 24 for species surveyed in 2005, 2008, and 2009 respectively. For species with more than one year of data, I included year as a factor variable to account for variation in sampling methodology and overall abundance between years (Year + Year rows). Reprinted with permission from © 2011 Ecological Society of America.

Species	Year	Linear Regression Analysis		
		β	SE	R^2
<i>Peromyscus leucopus</i>	2005	0.571	0.237	0.326
	2009	0.183	0.210	0.033
	2005+2009	0.323	0.160	0.104
<i>Zapus hudsonius</i>	2005	0.355	0.270	0.126
	2009	0.092	0.212	0.008
	2005+2009	0.187	0.166	0.035
<i>Napaeozapus insignis</i>	2005	-0.245	0.280	0.060
	2009	0.105	0.212	0.011
	2005+2009	-0.021	0.169	0.000
<i>Blarina brevicauda</i>	2005	0.207	0.282	0.043
	2009	0.136	0.211	0.018
	2005+2009	0.161	0.167	0.026
<i>Clethrionomys gapperi</i>	2009	-0.065	0.213	0.004
<i>Mustela erminea</i>	2008	0.159	0.190	0.025
	2009	-0.047	0.213	0.002
	2008+2009	0.066	0.141	0.004
<i>Tamias striatus</i>	2005	0.475	0.254	0.225
	2009	-0.280	0.205	0.079
	2005+2009	-0.008	0.169	0.000
<i>Tamiasciurus hudsonicus</i>	2008	-0.069	0.192	0.005
	2009	-0.188	0.209	0.035

Table C1. Continued

Species	Year	Linear Regression Analysis		
		β	SE	R^2
	2008+2009	-0.123	0.140	0.015
<i>Sylvilagus floridanus</i>	2008	0.188	0.189	0.035
<i>Sciurus carolinensis</i>	2009	-0.137	0.211	0.019
<i>Lepus americanus</i>	2008	0.028	0.192	0.001
<i>Mephitis mephitis</i>	2008	-0.104	0.191	0.011
<i>Marmota monax</i>	2008	0.019	0.192	0.000
<i>Martes pennanti</i>	2008	-0.210	0.188	0.044
<i>Vulpes vulpes</i>	2008	0.004	0.192	0.000
<i>Procyon lotor</i>	2008	-0.169	0.190	0.029
	2009	-0.224	0.208	0.050
	2008+2009	-0.194	0.139	0.038
<i>Ursus americanus</i>	2008	-0.207	0.188	0.043

Appendix D. Correlations between habitat variables and road density for each sampling year.

Table D1. Correlations between habitat variables and road density. Sample sizes are 14, 29, and 24 for variables measured in 2005, 2008 and 2009 respectively. Reprinted with permission from © 2011 Ecological Society of America.

Habitat Variables	Spearman's rho	p-value
Patch Size (ha), 2005	$\rho = -0.046$	$p = 0.876$
Patch Shape, 2005 (Perimeter-to-area ratio)	$\rho = 0.300$	$p = 0.180$
# Tree Species, 2005	$\rho = -0.130$	$p = 0.637$
Shrub Density, 2005	$\rho = 0.217$	$p = 0.457$
Percent CWD, 2005	$\rho = -0.218$	$p = 0.455$
Tree Density, 2008	$\rho = 0.084$	$p = 0.666$
Snag Density, 2008	$\rho = 0.280$	$p = 0.141$
Average Tree DBH, 2008	$\rho = -0.180$	$p = 0.576$
Average Snag DBH, 2008	$\rho = 0.085$	$p = 0.662$
Average CWD Length (cm), 2008	$\rho = 0.052$	$p = 0.788$
Average Canopy Height (m), 2008	$\rho = 0.018$	$p = 0.927$
Percent Canopy Cover, 2008	$\rho = -0.076$	$p = 0.695$
Woody Stem Density, 2008 0.5 - <1m	$\rho = 0.153$	$p = 0.430$
Woody Stem Density, 2008 1 - <2m	$\rho = 0.176$	$p = 0.360$

Table D1. Continued

Habitat Variables	Spearman's rho	p-value
Woody Stem Density, 2008 ≥2m	$\rho = 0.004$	$p = 0.985$
Herbaceous Stem Density, 2008 0.5 - <1m	$\rho = 0.240$	$p = 0.210$
Herbaceous Stem Density, 2008 1 - <2m	$\rho = 0.202$	$p = 0.293$
Average Percent Ground Cover, 2008	$\rho = -0.189$	$p = 0.325$
Number of Potential Dens, 2008	$\rho = 0.158$	$p = 0.412$
Patch Size (ha), 2009	$\rho = 0.170$	$p = 0.427$
Average Tree DBH, 2009	$\rho = -0.213$	$p = 0.317$
Average Snag DBH, 2009	$\rho = -0.016$	$p = 0.942$
Tree Density, 2009	$\rho = 0.002$	$p = 0.991$
Snag Density, 2009	$\rho = 0.277$	$p = 0.191$
# Tree Species, 2009	$\rho = -0.275$	$p = 0.193$
Percent CWD, 2009	$\rho = 0.204$	$p = 0.340$
Percent Canopy Cover, 2009	$\rho = -0.324$	$p = 0.122$
Woody Stem Density, 2009 0.5 - <1m	$\rho = -0.048$	$p = 0.823$
Woody Stem Density, 2009 1 - <2m	$\rho = 0.039$	$p = 0.857$
Woody Stem Density, 2009 ≥2m	$\rho = -0.127$	$p = 0.555$

Table D1. Continued

Habitat Variables	Spearman's rho	p-value
Herbaceous Stem Density, 2009 0.5 - <1m	$\rho = 0.389$	$p = 0.061$
Herbaceous Stem Density, 2009 1 - <2m	$\rho = 0.275$	$p = 0.193$

Appendix E. Raw data for local (sample patch) characteristics for 2008 and 2009.

Table E1. Vegetation summary data for sample patches within each landscape in 2008. Sample patch names correspond to landscape original site identifications. Vegetation surveys were carried in each sample patch from 28 July to 15 August 2008. Four 10 x 10 m plots were created 25 m from the two tracking boxes in the forest patch in each cardinal direction. Tree and snag (DEN) density was measured as the combined total of all trees (or snags) from the eight plots divided by the area sampled. Average tree and snag diameter at breast height (DBH) was the sum of all tree (or snag) DBHs for the eight plots, divided by the total number of trees (or snags). The average length of coarse woody debris ≥ 10 cm (CWD) was the sum of all lengths recorded from the eight 10-m² plots, divided by the total number of CWD diameter. Average canopy height was the average height of the eight trees from the eight plots (height determined for 1 tree from each plot using a clinometer). Canopy cover was measured by walking the perimeter of the 10-m² plots and stopping at 2-m intervals to record 20 'hit' or 'miss' readings using an ocular tube for the presence or absence of canopy cover sighted (James and Shugart, 1970). Percent canopy cover was the percentage of the 160 sightings that were 'hits'. Stem density was estimated for woody and herbaceous vegetation within each height interval as the number of stems for all eight 3 x 3 m plots (3-m² plots located at the center of each 10-m² plot) divided by the total area sampled (i.e., 24-m² area). Percent ground cover was averaged over eight 1-m² sampling plots (1-m² plots placed in the center of each 10-m² plot) in each site. The number of potential dens was estimated by walking a 30 x 10 m plot 5m from each of the two tracking boxes, in each cardinal direction and recording the number of ground dens (holes in ground with openings ≥ 5 cm diameter), CWD that were ≥ 30 cm DBH at their maximum diameter,

snags that were ≥ 30 cm DBH, brush piles, and rock piles. The total number of potential dens for a site was the number of all potential dens from the eight 30 x 10 m walked plots. Note see Rytwinski (2006) for raw data for sample patch characteristics for 2005.

Sample Patch	Patch Size (ha)	Tree DEN	Snag DEN	Avg Tree DBH (cm)	Avg Snag DBH (cm)	Avg Length CWD (cm)	Avg Canopy Height (m)	% Canopy Cover	Woody DEN (m)			Herb DEN (m)		Avg % Ground Cover	# of Dens
									0.5-<1	1-<2	≥ 2	0.5-<1	1-<2		
3130	177.7	0.50	0.16	15.8	27.2	445.5	17.2	58.8	0.83	0.33	1.08	18.25	17.67	87.9	76
1276	47.9	0.20	0.00	26.5	0.0	754.8	20.1	55.6	0.21	0.00	0.00	9.46	0.50	56.3	51
2293	55.2	0.41	0.11	19.4	17.1	444.7	14.3	61.9	0.21	0.13	0.17	11.17	65.21	73.4	36
252	26.2	0.21	0.03	36.4	12.5	742.0	11.9	56.9	0.75	1.46	2.17	2.71	0.21	42.8	45
2733	25.2	0.46	0.06	21.1	25.8	345.1	16.2	51.9	0.75	0.54	0.88	4.88	0.00	51.5	32
355	10.9	0.63	0.03	18.6	30.4	250.0	13.2	53.8	1.00	1.00	2.50	4.00	2.04	66.3	56
1151	6.8	0.51	0.11	21.8	20.4	79.8	11.7	46.3	0.21	0.25	0.29	2.38	0.79	63.1	65
2679	13.9	0.54	0.13	21.7	23.3	493.2	17.2	80.0	0.25	0.54	1.33	3.79	0.00	22.8	87
2263	119.2	0.25	0.08	24.7	21.7	416.4	15.6	87.5	0.71	0.17	0.96	2.58	0.33	65.3	113
1651	13.2	0.86	0.08	15.8	25.6	446.9	15.4	65.0	1.63	1.17	1.67	3.17	1.21	45.9	27
160	14.7	0.65	0.30	18.1	18.0	495.2	8.9	61.3	1.46	0.92	0.63	5.13	13.04	81.3	22
2957	30.5	0.55	0.01	20.1	28.5	543.6	16.8	70.0	1.08	2.04	1.67	2.25	0.21	50.6	44
1775	24.6	0.61	0.11	22.9	21.2	463.8	15.7	58.1	2.33	1.17	1.88	4.54	0.79	46.4	81
3327	9.8	0.53	0.04	16.5	13.2	391.0	16.7	71.9	0.50	0.33	2.08	0.00	0.00	37.4	36
3496	130.1	0.36	0.05	22.0	30.6	460.9	23.7	71.3	0.29	0.42	0.58	0.13	0.00	47.8	40
1901	7.2	0.91	0.06	15.4	16.5	485.0	14.4	71.9	1.88	0.54	0.54	592.79	12.50	34.6	93
321	16.0	0.24	0.08	20.6	31.9	475.5	16.7	69.4	0.75	0.54	2.04	0.08	0.04	31.9	35
202	58.4	0.40	0.15	15.2	26.2	444.6	13.9	23.1	2.08	1.58	1.92	22.00	5.04	81.3	47
246	30.8	0.98	0.35	17.4	19.1	515.5	17.1	88.1	1.38	0.83	0.63	7.42	5.88	42.8	67
940	38.2	0.46	0.08	22.3	29.3	406.8	11.7	68.8	0.38	0.13	0.42	1.13	0.00	41.9	90
1767	22.5	0.65	0.15	20.0	18.8	421.6	18.3	83.1	0.96	0.79	0.71	6.38	1.46	42.5	68

Table E2. Continued

Sample Patch	Patch Size (ha)	Tree DEN	Snag DEN	Avg Tree DBH (cm)	Avg Snag DBH (cm)	Avg Length CWD (cm)	Avg Canopy Height (m)	% Canopy Cover	Woody DEN (m)			Herb DEN (m)		Avg % Ground Cover	# of Dens
									0.5-<1	1-<2	≥2	0.5-<1	1-<2		
933	6.2	0.49	0.10	18.9	16.6	550.2	11.4	63.1	0.17	0.25	0.83	0.08	0.00	31.9	81
1232	26.7	0.43	0.03	20.7	28.6	698.2	19.4	83.8	0.58	0.75	0.83	0.58	0.00	21.5	69
2032	32.9	0.30	0.08	21.4	18.4	617.8	15.3	58.8	1.13	1.50	2.83	11.58	11.71	83.8	26
136	23.1	0.39	0.04	20.4	15.1	327.4	8.2	50.6	1.92	2.17	2.08	7.54	2.50	55.6	22
196	71.5	0.85	0.29	24.0	16.7	542.8	16.9	60.0	0.38	0.33	0.00	6.13	0.83	17.5	90
2071	19.3	0.65	0.08	21.2	19.1	591.2	17.3	36.9	1.46	3.00	3.46	4.00	9.46	71.3	21
1919	7.8	0.43	0.03	14.7	14.4	541.7	15.5	81.3	0.29	0.67	2.29	2.79	7.63	56.3	33
3046	9.9	0.30	0.11	27.5	30.9	541.8	17.9	61.9	0.17	0.38	0.58	15.04	20.00	64.0	52

Table E2. Vegetation summary data for sample patches within each landscape in 2009. Sample patch names correspond to landscape original site identifications. Vegetation surveys were carried in each sample patch from 16 July to 11 August 2009. At each sample patch, 6 six points within the sampling grid were randomly chosen and a 10 x 10 m plot was centered over each point. I measured average tree and snag diameter at breast height (DBH), tree and snag (DEN) density, percent canopy cover, and woody and herbaceous stem density as in 2008 (described above in Table E1) except that I used 2 x 2 m plots for woody and herbaceous stem density. Percent of ground covered by coarse woody debris (CWD) was measured along five 10 m transects at each sample patch (see Rytwinski and Fahrig (2007) for further detail).

Sample Patch	Patch Size (ha)	Avg Tree DBH (cm)	Avg Snag DBH (cm)	Tree DEN	Snag DEN	# Tree Species	% Canopy Cover	% CWD Cover	Woody DEN (m)			Herb DEN (m)	
									0.5 - <1	≥1 - <2	≥2	0.5 - <1	≥1 - <2
275	28.3	19.37	17.28	0.67	0.07	6	88.33	2.85	1.83	0.50	1.33	32.92	5.33
47	21.12	19.37	16.43	0.67	0.05	6	80.00	3.10	5.75	0.50	1.25	13.00	0.00
314	21.1	21.15	19.75	0.65	0.07	7	84.17	9.07	12.42	0.75	2.42	28.00	0.00
22	16.18	21.45	16.95	0.52	0.22	11	75.00	7.12	17.83	1.75	2.08	10.67	0.17
4702	6.5	19.74	12.60	0.98	0.20	5	90.83	14.81	2.50	0.08	0.42	11.50	0.00
3085	13.4	20.60	32.98	0.45	0.10	6	80.00	8.40	8.25	0.67	1.67	63.33	0.00
294	27.0	16.91	15.04	0.93	0.13	8	81.67	8.68	8.00	0.33	1.42	15.33	0.00
290	27.5	22.41	13.52	0.82	0.08	7	79.17	6.04	5.67	0.33	1.17	26.83	0.00
1500	17.6	16.85	17.08	0.83	0.10	7	84.17	8.18	2.67	0.33	1.25	28.00	0.00
4892	26.6	22.06	17.92	0.60	0.22	7	80.83	12.80	4.58	1.00	2.08	62.92	0.08
403	10.9	16.43	15.73	0.78	0.07	7	83.33	6.58	7.42	0.25	2.25	32.17	0.00
3274	6.0	23.40	16.50	0.40	0.02	4	89.17	9.63	6.08	1.83	3.50	10.83	0.00
2679	13.9	20.34	19.90	0.82	0.08	6	85.83	17.75	10.08	0.83	1.92	30.58	0.00
31	27.46	18.11	19.84	0.35	0.12	5	57.50	9.80	11.58	1.75	2.08	10.67	0.17

Table E2. Continued

Sample Patch	Patch Size (ha)	Avg Tree DBH (cm)	Avg Snag DBH (cm)	Tree DEN	Snag DEN	# Tree Species	% Canopy Cover	% CWD Cover	Woody DEN (m)			Herb DEN (m)	
									0.5 - <1	≥1 - <2	≥2	0.5 - <1	≥1 - <2
1775	24.6	22.92	17.42	0.83	0.18	8	75.00	19.53	4.75	0.25	1.00	47.25	0.00
1901	7.2	16.47	12.25	1.10	0.10	4	80.00	6.28	6.67	0.92	1.33	55.00	0.08
1767	22.5	18.46	13.71	0.73	0.17	3	80.00	13.65	7.42	0.33	0.83	55.75	0.25
336	18.8	17.24	12.98	0.97	0.07	5	81.67	12.78	2.08	0.00	1.67	7.67	0.00
321	16.02	15.74	18.26	0.65	0.12	4	84.17	5.30	8.75	0.42	1.58	32.00	0.00
396	11.5	20.10	17.14	0.67	0.08	7	80.00	13.33	14.83	0.67	1.00	157.00	0.67
1481	20.8	17.57	18.58	0.45	0.20	6	75.00	14.53	7.92	1.42	1.50	38.67	0.08
6207	14.6	18.51	15.06	0.97	0.12	8	86.67	5.63	6.58	0.50	1.00	25.75	0.00
308	22.6	17.59	13.33	0.78	0.18	5	75.00	5.05	1.33	0.25	1.00	72.00	0.42
240	16.3	23.06	22.46	0.32	0.18	6	70.00	10.37	5.42	3.67	2.75	134.67	0.50

Literature Cited for Appendix E

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Appendix F. Detection probability analysis results.

Table F1. Parameter estimates (r = species detection probability, λ = mean abundance across all sites) from the Royle and Nichols (2003) model, the Akaike information criterion corrected for small sample size (AICc), and the difference between AICc values (Δ AICc) and the model coefficients, for the no-road-density-effect model β_0 (constant detection probability in relation to road density ($r(\cdot)\lambda(\cdot)$), and the road-density-effect model β_0 and β_1 (linear change in detection probability with road density $r(RD)\lambda(\cdot)$). Species with boldface type were removed from the road effect vs. predictor(s) (i.e., reproductive rate, home range area and body size) analyses because the road-density-effect model fit the data better than the no-road density-effect model. Reprinted with permission from © 2011 Ecological Society of America.

Species	Year	Detection Probability Analysis						
		Models	r	λ	AICc	Δ AICc	β_0	β_1
<i>Peromyscus leucopus</i>	2005	$r(\cdot)\lambda(\cdot)$	0.689	2.225	89.88	0.00	0.797	
		$r(RD)\lambda(\cdot)$	0.714	2.106	92.84	2.96	0.343	0.575
	2009	$r(\cdot)\lambda(\cdot)$	0.000	0.000	33161.80	0.00	-24.924	
		$r(RD)\lambda(\cdot)$	0.000	0.000	33164.43	2.63	-38.911	14.377
<i>Zapus hudsonius</i>	2005	$r(\cdot)\lambda(\cdot)$	0.000	17061.181	19346.81	0.00	-11.764	
		$r(RD)\lambda(\cdot)$	0.000	70287.280	19350.12	3.31	-13.724	0.554
	2009	$r(\cdot)\lambda(\cdot)$	0.000	0.000	33161.80	0.00	-17.765	
		$r(RD)\lambda(\cdot)$	0.000	0.000	33164.43	2.63	-18.426	0.491
<i>Napaeozapus insignis</i>	2005	$r(\cdot)\lambda(\cdot)$	0.000	179591.390	19346.81	0.00	-14.580	
		$r(RD)\lambda(\cdot)$	0.000	83500.724	19350.12	3.31	-12.700	-1.206
	2009	$r(\cdot)\lambda(\cdot)$	0.038	2.606	123.27	0.00	-3.237	
		$r(RD)\lambda(\cdot)$	0.038	2.552	125.66	2.40	-3.530	0.284
<i>Blarina brevicauda</i>	2005	$r(\cdot)\lambda(\cdot)$	0.406	1.678	124.42	0.00	-0.382	
		$r(RD)\lambda(\cdot)$	0.406	1.678	127.73	3.31	-0.349	-0.032

Table F1. Continued

Species	Year	Detection Probability Analysis						
		Models	r	λ	AICc	Δ AICc	β_0	β_1
<i>Clethrionomys gapperi</i>	2009	r(.) λ (.)	0.172	1.816	213.07	0.00	-1.574	
		r(RD) λ (.)	0.173	1.799	215.68	2.61	-1.486	-0.069
<i>Tamias striatus</i>	2009	r(RD) λ (.)	0.069	3.554	205.30	0.00	-2.119	-0.450
		r(.) λ (.)	0.000	0.000	33161.80	32956.50	-22.313	
<i>Mustela erminea</i>	2005	r(RD) λ (.)	0.134	0.227	35.92	0.00	-4.612	2.769
		r(.) λ (.)	0.270	0.170	36.19	0.27	-0.996	
	2009	r(RD) λ (.)	0.313	3.797	218.56	0.00	0.160	-0.871
		r(.) λ (.)	0.342	3.442	220.79	2.23	-0.656	
	2008	r(.) λ (.)	0.071	0.496	95.94	0.00	-2.578	
		r(RD) λ (.)	0.057	0.586	97.99	2.05	-4.177	1.187
	2009	r(.) λ (.)	0.066	1.655	131.28	0.00	-2.645	
		r(RD) λ (.)	0.069	1.577	133.73	2.45	-2.320	-0.252
<i>Tamiasciurus hudsonicus</i>	2008	r(.) λ (.)	0.028	5.757	270.56	0.00	-3.559	
		r(RD) λ (.)	0.027	5.832	272.92	2.36	-3.293	-0.244
	2009	r(.) λ (.)	0.215	3.920	253.82	0.00	-1.295	
		r(RD) λ (.)	0.207	4.087	255.25	1.44	-0.928	-0.380
<i>Sciurus carolinensis</i>	2009	r(.) λ (.)	0.019	8.247	163.86	0.00	-3.938	
		r(RD) λ (.)	0.012	12.612	165.22	1.36	-3.866	-0.483
<i>Lepus americanus</i>	2008	r(.) λ (.)	0.000	71870.036	40069.44	0.00	-16.394	
		r(RD) λ (.)	0.000	125604.280	40071.94	2.50	-17.827	0.322
<i>Sylvilagus floridanus</i>	2008	r(RD) λ (.)	0.025	0.249	49.82	0.00	-17.342	11.835
		r(.) λ (.)	0.101	0.155	50.50	0.68	-2.182	
<i>Mephitis mephitis</i>	2008	r(.) λ (.)	0.105	0.682	153.93	0.00	-2.143	
		r(RD) λ (.)	0.102	0.696	156.39	2.45	-1.885	-0.251
<i>Marmota monax</i>	2008	r(.) λ (.)	0.020	0.943	63.64	0.00	-3.886	
		r(RD) λ (.)	0.021	0.910	66.11	2.48	-4.194	0.299
<i>Martes pennanti</i>	2008	r(.) λ (.)	0.131	0.547	149.17	0.00	-1.891	
		r(RD) λ (.)	0.120	0.579	151.62	2.45	-1.499	-0.425

Table F1. Continued

Species	Year	Detection Probability Analysis						
		Models	r	λ	AICc	Δ AICc	β_0	β_1
<i>Vulpes vulpes</i>	2008	r(.) λ (.)	0.150	0.042	23.32	0.00	-1.732	
		r(RD) λ (.)	0.012	0.056	25.14	1.82	-609.545	524.016
<i>Procyon lotor</i>	2008	r(.) λ (.)	0.297	5.102	321.13	0.00	-0.863	
		r(RD) λ (.)	0.292	5.184	323.07	1.94	-0.421	-0.403
	2009	r(.) λ (.)	0.206	4.000	258.62	0.00	-1.350	
		r(RD) λ (.)	0.194	4.250	260.08	1.46	-1.030	-0.365
<i>Ursus americanus</i>	2008	r(RD) λ (.)	0.000	0.149	23.20	0.00	324.750	-366.631
		r(.) λ (.)	0.150	0.042	23.32	0.12	-1.732	

Literature Cited for Appendix F

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence counts. *Ecology* 84:777-790.

Appendix G. Linear regression of the log-transformed standardized coefficient (response variable) - from single-species regressions of standardized relative abundance on standardized road density for 16 mammal species (including three species that were originally removed from analyses because the road-density-effect model fit the data better than the no-road density-effect model (*Clethrionomys gapperi*, *Tamias striatus*, *Ursus americanus*)) – on the log-transformed predictor variables (i.e., reproductive rate, home range area, and average body size).

(a)

(b)

(c)

Figure G1. Linear regressions of the log (regression coefficient + 2) - from single-species regressions of standardized relative abundance on standardized road density – on: (a) log (reproductive rate) ($F= 30.81$, $df = 1, 14$; $p< 0.001$, $R^2 = 0.69$); (b) log (mean home range area) ($F= 13.65$, $df = 1, 14$; $p= 0.002$, $R^2 = 0.49$); and (c) log (average body size) ($F= 12.16$, $df = 1, 14$; $p= 0.004$, $R^2 = 0.47$) for 16 mammal species tracked in eastern Ontario (including three species that were originally removed from analyses because the road-density-effect model fit the data better than the no-road density-effect model) . Each regression is weighted by the inverse of the standard errors of the coefficients; thicker dots correspond to data points with lower standard errors (Appendix C - Table C1). Note: 2 was added to the response variable (standardized regression coefficient) to make all values positive, so that I could take logs. Reprinted with permission from © 2011 Ecological Society of America.

Appendix H. Studies, species lists, effect sizes, adjusted sample sizes, and study design categories used in meta-analysis.

Table H1. Mammal species used in meta-analysis with calculated effect sizes and adjusted sample sizes used for effect size weighting (N). Note: study design number refers to the six effects of roads and traffic on animal abundance categories in Table 2.1. Reprinted with permission from © 2012 Elsevier.

Study Reference	Species Name	ESr	Adjusted N	Study Design
Adam and Geis (1983)	<i>Microtus californicus</i>	0.057	18	5
Adam and Geis (1983)	<i>Microtus californicus</i>	-0.441	18	5
Adam and Geis (1983)	<i>Peromyscus maniculatus</i>	0.050	76	5
Adam and Geis (1983)	<i>Peromyscus maniculatus</i>	0.094	76	5
Adam and Geis (1983)	<i>Peromyscus maniculatus</i>	-0.077	18	5
Adam and Geis (1983)	<i>Peromyscus maniculatus</i>	0.113	18	5
Adam and Geis (1983)	<i>Peromyscus maniculatus</i>	0.087	70	5
Adam and Geis (1983)	<i>Peromyscus maniculatus</i>	0.050	70	5
Adam and Geis (1983)	<i>Ochrotomys nuttalli</i>	-0.049	100	5
Adam and Geis (1983)	<i>Ochrotomys nuttalli</i>	0.070	100	5
Adam and Geis (1983)	<i>Peromyscus leucopus</i>	0.062	100	5
Adam and Geis (1983)	<i>Peromyscus leucopus</i>	0.090	100	5
Adam and Geis (1983)	<i>Microtus ochrogaster</i>	-0.070	76	5
Adam and Geis (1983)	<i>Microtus ochrogaster</i>	0.090	76	5
Adam and Geis (1983)	<i>Reithrodontomys humulis</i>	0.060	100	5
Adam and Geis (1983)	<i>Reithrodontomys humulis</i>	-0.050	100	5
Adam and Geis (1983)	<i>Microtus pennsylvanicus</i>	0.060	100	5
Adam and Geis (1983)	<i>Microtus pennsylvanicus</i>	0.060	100	5
Adam and Geis (1983)	<i>Sorex vagrans</i>	0.080	70	5
Adam and Geis (1983)	<i>Sorex vagrans</i>	0.030	70	5
Barnes et al (1991)	<i>Loxodonta africana</i>	-0.642	24	4
Dickson and Beier (2002)	<i>Puma concolor</i>	0.000	11	2
Dyer et al (2001)	<i>Rangifer tarandus caribou</i>	-0.806	36	4
Huigser and Bergers (2000)	<i>Erinaceus europaeus</i>	-0.167	30	5
Jędrzejewski et al (2004)	<i>Canis lupus</i>	-0.243	73	2
Jędrzejewski et al (2004)	<i>Canis lupus</i>	-0.031	73	2
Johnson and Collinge (2004)	<i>Cynomys ludovicianus</i>	0.670	22	1
Kunkel and Pletscher (2000)	<i>Alces alces</i>	-0.060	30	3
Kunkel and Pletscher (2000)	<i>Alces alces</i>	-0.159	30	3

Table H1. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Lovallo and Anderson (1996)	<i>Lynx rufus</i>	-0.159	15	2
Lovallo and Anderson (1996)	<i>Lynx rufus</i>	0.083	11	2
Lovallo and Anderson (1996)	<i>Lynx rufus</i>	0.027	18	2
Mace et al (1996)	<i>Ursus arctos horribilis</i>	-0.230	15	3
McApline et al (2006)	<i>Phascolarctos cinereus</i>	-0.153	142	3
McGregor et al (2008)	<i>Tamias striatus</i>	-0.013	26	5
McGregor et al (2008)	<i>Peromyscus leucopus</i>	0.149	26	5
Mladenoff et al (1995)	<i>Canis lupus lycaon</i>	-0.742	15	2
Niedziałkowska et al (2006)	<i>Lynx lynx</i>	-0.236	57	2
Niedziałkowska et al (2006)	<i>Lynx lynx</i>	-0.106	57	2
Palma et al (1999)	<i>Lynx pardinus</i>	-0.361	30	2
Roedenbeck and Köhler (2006)	<i>Meles meles</i>	-0.700	23	1
Roedenbeck and Köhler (2006)	<i>Vulpes vulpes</i>	-0.700	24	1
Roedenbeck and Köhler (2006)	<i>Capreolus capreolus</i>	-0.810	24	1
Roedenbeck and Köhler (2006)	<i>Sus scrofa</i>	-0.550	24	1
Roedenbeck and Voser (2008)	<i>Lepus europaeus</i>	-0.599	31	1
Bissonette and Rosa (2009)	<i>Dipodomys microps</i>	0.786	10	4
Bissonette and Rosa (2009)	<i>Peromyscus maniculatus</i>	0.756	10	4
Bissonette and Rosa (2009)	<i>Perognathus parvus</i>	0.866	10	4
Bissonette and Rosa (2009)	<i>Tamias minimus</i>	0.982	10	4
Rost and Bailey (1979)	<i>Cervus canadensis</i>	-0.925	6	4
Rost and Bailey (1979)	<i>Cervus canadensis</i>	-0.742	6	4
Rost and Bailey (1979)	<i>Odocoileus hemionus</i>	-0.910	6	4
Rost and Bailey (1979)	<i>Odocoileus hemionus</i>	-0.524	6	4
Rytwinski and Fahrig (2007)	<i>Peromyscus leucopus</i>	0.860	19	1
van Dyke et al (1986)	<i>Puma concolor</i>	-0.174	10	2
van Dyke et al (1986)	<i>Puma concolor</i>	-0.020	8	2
King et al (1996)	<i>Mus musculus</i>	0.230	36	4
King et al (1996)	<i>Rattus rattus</i>	0.230	36	4
Kelly and Holub (2008)	<i>Lynx rufus</i>	0.051	4	3
Dodd et al (2007)	<i>Cervus elaphus nelsoni</i>	-0.985	33	4
Fortin et al (2008)	<i>Rangifer tarandus caribou</i>	-0.247	423	2
Ratnayeke et al (2007)	<i>Melursus ursinus</i>	-0.524	829	3
Bowman et al (2010)	<i>Rangifer tarandus caribou</i>	-0.294	114	2
Bowman et al (2010)	<i>Gulo gulo</i>	-0.170	139	2
Bowman et al (2010)	<i>Canis lupus</i>	0.210	185	2
Bowman et al (2010)	<i>Alces alces</i>	0.297	431	2
Bowman et al (2010)	<i>Odocoileus virginianus</i>	0.298	47	2
Rytwinski and Fahrig (2011)	<i>Zapus hudsonius</i>	0.187	38	1
Rytwinski and Fahrig (2011)	<i>Napaeozapus insignis</i>	0.000	38	1
Rytwinski and Fahrig (2011)	<i>Blarina brevicauda</i>	0.160	38	1

Table H1. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Rytwinski and Fahrig (2011)	<i>Clethrionomys gapperi</i>	-0.060	24	1
Rytwinski and Fahrig (2011)	<i>Mustela erminea</i>	0.060	53	1
Rytwinski and Fahrig (2011)	<i>Tamias striatus</i>	0.000	38	1
Rytwinski and Fahrig (2011)	<i>Tamiasciurus hudsonicus</i>	-0.122	53	1
Rytwinski and Fahrig (2011)	<i>Sylvilagus floridanus</i>	0.187	29	1
Rytwinski and Fahrig (2011)	<i>Sciurus carolinensis</i>	-0.138	24	1
Rytwinski and Fahrig (2011)	<i>Lepus americanus</i>	0.032	29	1
Rytwinski and Fahrig (2011)	<i>Mephitis mephitis</i>	-0.105	29	1
Rytwinski and Fahrig (2011)	<i>Marmota monax</i>	0.000	29	1
Rytwinski and Fahrig (2011)	<i>Martes pennanti</i>	-0.210	29	1
Rytwinski and Fahrig (2011)	<i>Vulpes vulpes</i>	0.000	29	1
Rytwinski and Fahrig (2011)	<i>Procyon lotor</i>	-0.195	53	1
Rytwinski and Fahrig (2011)	<i>Ursus americanus</i>	-0.207	29	1
Laurance et al (2008)	<i>Galago demidoff</i>	0.260	36	4
Laurance et al (2008)	<i>Galago alleni</i>	0.300	12	4
Laurance et al (2008)	<i>Euoticus elegantulus</i>	0.900	12	4
Laurance et al (2008)	<i>Perodicticus potto</i>	-1.000	12	4
Laurance et al (2008)	<i>Cephalophus monticola defriesi</i>	0.900	36	4
Laurance et al (2008)	<i>Cephalophus ogilbyi crusalbaum</i>	0.450	12	4
Laurance et al (2008)	<i>Cephalophus silvicultor</i>	0.880	12	4
Laurance et al (2008)	<i>Cephalophus dorsalis castaneus</i>	0.850	12	4
Laurance et al (2008)	<i>Cephalophus callipygus callipygus</i>	0.620	12	4
Laurance et al (2008)	<i>Hyemoschus aquaticus</i>	0.690	12	4
Laurance et al (2008)	<i>Zenkerella insignis</i>	0.950	36	4
Laurance et al (2008)	<i>Anomalurus beecrofti</i>	-0.520	12	4
Laurance et al (2008)	<i>Anomalurus derbianus</i>	-0.970	36	4
Laurance et al (2008)	<i>Anomalurus pusillus</i>	-0.480	36	4
Laurance et al (2008)	<i>Nandinia binotata</i>	-0.450	12	4
Laurance et al (2008)	<i>Civettictis civetta</i>	0.000	9	4
Laurance et al (2008)	<i>Poiana richardsonii</i>	-0.870	12	4
Laurance et al (2008)	<i>Atilax paludinosus</i>	0.000	12	4
Laurance et al (2008)	<i>Genetta servalina</i>	0.000	11	4
Laurance et al (2008)	<i>Panthera pardus</i>	-1.000	5	4
Laurance et al (2008)	<i>Atherurus africanus centralis</i>	0.950	12	4
Laurance et al (2008)	<i>Cricetomys gambianus</i>	0.830	12	4
Laurance et al (2008)	<i>Dendrohyrax dorsalis</i>	-0.060	12	4
Laurance et al (2008)	<i>Phataginus tricuspis</i>	-0.870	12	4
Laurance et al (2008)	<i>Loxondonta africana cyclotis</i>	0.830	5	4
Laurance et al (2008)	<i>Potamochoerus porcus</i>	0.000	11	4
Stewart et al (2010)	<i>Odocoileus hemionus</i>	-0.162	70	3
Stewart et al (2010)	<i>Cervus elaphus</i>	0.119	20	3

Table H1. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Schindler et al (2006)	<i>Rangifer tarandus caribou</i>	-0.475	5	4
Rhim and Lee (2007)	<i>Mustela sibirica</i>	0.269	8	5
Rhim and Lee (2007)	<i>Martes flavigula</i>	-0.395	8	5
Rhim and Lee (2007)	<i>Felis bengalensis</i>	-0.091	8	5
Rhim and Lee (2007)	<i>Sus scrofa</i>	-0.260	8	5
Rhim and Lee (2007)	<i>Hydropotes inermis</i>	0.629	8	5
Rhim and Lee (2007)	<i>Capreolus capreolus</i>	0.653	8	5
Rhim and Lee (2007)	<i>Lepus coreanus</i>	0.130	8	5
Rhim and Lee (2007)	<i>Sciurus vulgaris</i>	0.015	8	5
Munro (2009)	<i>Odocoileus virginianus</i>	0.432	21	1
Disney (2005)	<i>Procyon lotor</i>	0.401	91	3
Disney (2005)	<i>Procyon lotor</i>	-0.074	91	3
Disney (2005)	<i>Procyon lotor</i>	-0.181	91	3
Disney (2005)	<i>Didelphis virginiana</i>	-0.314	119	3
Disney (2005)	<i>Didelphis virginiana</i>	0.219	119	3
Disney (2005)	<i>Didelphis virginiana</i>	0.168	119	3

Table H2. Bird species used in meta-analysis with calculated effect sizes and adjusted sample sizes used for effect size weighting (N). Note: study design number refers to the six effects of roads and traffic on animal abundance categories in Table 2.1. Reprinted with permission from © 2012 Elsevier.

Study Reference	Species Name	ESr	Adjusted N	Study Design
Forman et al (2002)	<i>Dolichonyx oryzivorus</i>	0.124	25	3
Forman et al (2002)	<i>Dolichonyx oryzivorus</i>	0.020	25	3
Forman et al (2002)	<i>Dolichonyx oryzivorus</i>	-0.260	25	3
Forman et al (2002)	<i>Dolichonyx oryzivorus</i>	-0.214	25	3
Forman et al (2002)	<i>Sturnella magna</i>	0.025	15	3
Forman et al (2002)	<i>Sturnella magna</i>	0.025	15	3
Forman et al (2002)	<i>Sturnella magna</i>	-0.127	15	3
Forman et al (2002)	<i>Sturnella magna</i>	-0.175	15	3
Kuitunen et al (2003)	<i>Ficedula hypoleuca</i>	-0.240	30	4
Peris and Pescador (2004)	<i>Carduelis cannabina</i>	-0.651	4	3
Peris and Pescador (2004)	<i>Carduelis carduelis</i>	0.488	4	3
Peris and Pescador (2004)	<i>Carduelis chloris</i>	-0.084	4	3
Peris and Pescador (2004)	<i>Certhia brachydactyla</i>	-0.433	4	3
Peris and Pescador (2004)	<i>Fringilla coelebs</i>	-0.448	4	3
Peris and Pescador (2004)	<i>Galerida cristata</i>	0.501	4	3
Peris and Pescador (2004)	<i>Lanius senator</i>	-0.705	4	3
Peris and Pescador (2004)	<i>Lullula arborea</i>	-0.757	4	3
Peris and Pescador (2004)	<i>Miliaria calandra</i>	0.859	4	3
Peris and Pescador (2004)	<i>Oenanthe oenanthe</i>	-0.884	4	3
Peris and Pescador (2004)	<i>Parus caeruleus</i>	-0.204	4	3
Peris and Pescador (2004)	<i>Parus major</i>	-0.479	4	3
Peris and Pescador (2004)	<i>Passer domesticus</i>	0.982	4	3
Peris and Pescador (2004)	<i>Petronia petronia</i>	0.888	4	3
Peris and Pescador (2004)	<i>Phoenicurus ochruros</i>	-0.394	4	3
Peris and Pescador (2004)	<i>Phylloscopus ibericus</i> (<i>brehmii</i>)	-0.876	4	3
Peris and Pescador (2004)	<i>Serinus serinus</i>	-0.259	4	3
Peris and Pescador (2004)	<i>Sitta europaea</i>	-0.463	4	3
Peris and Pescador (2004)	<i>Sturnus unicolor</i>	-0.232	4	3
Peris and Pescador (2004)	<i>Turdus merula</i>	-0.828	4	3
Pocock and Lawrence (2005)	<i>Manorina melanocephala</i>	0.378	6	4
Pocock and Lawrence (2005)	<i>Anthochaera carunculata</i>	0.420	6	4
Pocock and Lawrence (2005)	<i>Acanthiza nana</i>	0.614	6	4
Pocock and Lawrence (2005)	<i>Malurus cyaneus</i>	0.428	6	4

Table H2. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Pocock and Lawrence (2005)	<i>Eolophus roseicapilla</i>	-0.366	6	4
Pocock and Lawrence (2005)	<i>Smicrornis brevirostris</i>	0.055	6	4
Pocock and Lawrence (2005)	<i>Psephotus haematonotus</i>	0.396	6	4
Pocock and Lawrence (2005)	<i>Corcorax melanorhamphos</i>	0.000	6	4
Pocock and Lawrence (2005)	<i>Lichenostomus leucotis</i>	0.176	6	4
Pocock and Lawrence (2005)	<i>Melithreptus brevirostris</i>	-0.251	6	4
Pocock and Lawrence (2005)	<i>Rhipidura albiscapa</i>	-0.245	6	4
Pocock and Lawrence (2005)	<i>Pardalotus punctatus</i>	-0.156	6	4
Pocock and Lawrence (2005)	<i>Lichenostomus melanops</i>	-0.589	6	4
Pocock and Lawrence (2005)	<i>Pachycephala pectoralis</i>	-0.047	6	4
Pocock and Lawrence (2005)	<i>Cacomantis flabelliformis</i>	0.231	6	4
Pocock and Lawrence (2005)	<i>Colluricincla harmonica</i>	-0.090	6	4
Pocock and Lawrence (2005)	<i>Glossopsitta concinna</i>	0.000	6	4
Pocock and Lawrence (2005)	<i>Zosterops lateralis</i>	0.171	6	4
Pocock and Lawrence (2005)	<i>Lichenostomus fuscus</i>	-0.207	6	4
Pocock and Lawrence (2005)	<i>Lichenostomus penicillatus</i>	-0.356	6	4
Pocock and Lawrence (2005)	<i>Melithreptus lunatus</i>	0.000	6	4
Pocock and Lawrence (2005)	<i>Microeca fascians</i>	-0.077	6	4
Pocock and Lawrence (2005)	<i>Pardalotus striatus</i>	-0.430	6	4
Pocock and Lawrence (2005)	<i>Pomatostomus superciliosus</i>	-0.266	6	4
Pocock and Lawrence (2005)	<i>Cormobates leucophaea</i>	-0.212	6	4
Pocock and Lawrence (2005)	<i>Daphoenositta chrysoptera</i>	-0.207	6	4
Pocock and Lawrence (2005)	<i>Eopsaltria australis</i>	-0.020	6	4
Pocock and Lawrence (2005)	<i>Oreoica gutturalis</i>	-0.415	6	4
Pocock and Lawrence (2005)	<i>Climacteris picumnus</i>	-0.411	6	4
Pocock and Lawrence (2005)	<i>Coracina novaehollandiae</i>	-0.179	6	4
Pocock and Lawrence (2005)	<i>Artamus cyanopterus</i>	-0.356	6	4
Pocock and Lawrence (2005)	<i>Oriolus sagittatus</i>	-0.434	6	4
Pocock and Lawrence (2005)	<i>Melithreptus gularis</i>	-0.298	6	4
Pocock and Lawrence (2005)	<i>Lichenostomus chrysops</i>	-0.485	6	4
van der Zande et al (1980)	<i>Haematopus ostralegus</i>	-0.636	10	4
van der Zande et al (1980)	<i>Limosa limosa</i>	-0.964	10	4
van der Zande et al (1980)	<i>Vanellus vanellus</i>	-0.973	10	4
van der Zande et al (1980)	<i>Tringa totanus</i>	-0.940	10	4
Kuhn-Hines (2008)	<i>Gavia immer</i>	-0.213	221	2
Bassett-Touchell (2008)	<i>Corvus brachyrhynchos</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Corvus brachyrhynchos</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Carduelis tristis</i>	0.000	56	5
Bassett-Touchell (2008)	<i>Carduelis tristis</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Setophaga ruticilla</i>	0.043	56	5
Bassett-Touchell (2008)	<i>Setophaga ruticilla</i>	-0.109	56	5

Table H2. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Bassett-Touchell (2008)	<i>Turdus migratorius</i>	0.373	56	5
Bassett-Touchell (2008)	<i>Turdus migratorius</i>	0.049	56	5
Bassett-Touchell (2008)	<i>Strix varia</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Mniotilta varia</i>	-0.059	56	5
Bassett-Touchell (2008)	<i>Mniotilta varia</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Coccyzus erythrophthalmus</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Dendroica fusca</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Dendroica fusca</i>	0.093	56	5
Bassett-Touchell (2008)	<i>Poecile atricapillus</i>	-0.049	56	5
Bassett-Touchell (2008)	<i>Poecile atricapillus</i>	0.000	56	5
Bassett-Touchell (2008)	<i>Dendroica caerulescens</i>	0.083	56	5
Bassett-Touchell (2008)	<i>Dendroica caerulescens</i>	-0.059	56	5
Bassett-Touchell (2008)	<i>Dendroica virens</i>	-0.169	56	5
Bassett-Touchell (2008)	<i>Dendroica virens</i>	-0.016	56	5
Bassett-Touchell (2008)	<i>Cyanocitta cristata</i>	-0.194	56	5
Bassett-Touchell (2008)	<i>Cyanocitta cristata</i>	0.059	56	5
Bassett-Touchell (2008)	<i>Vireo solitarius</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Certhia americana</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Molothrus ater</i>	0.000	56	5
Bassett-Touchell (2008)	<i>Molothrus ater</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Bombycilla cedrorum</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Spizella passerina</i>	0.000	56	5
Bassett-Touchell (2008)	<i>Spizella passerina</i>	0.090	56	5
Bassett-Touchell (2008)	<i>Geothlypis trichas</i>	0.000	56	5
Bassett-Touchell (2008)	<i>Geothlypis trichas</i>	0.000	56	5
Bassett-Touchell (2008)	<i>Picoides pubescens</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Picoides pubescens</i>	0.059	56	5
Bassett-Touchell (2008)	<i>Sayornis phoebe</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Pipilo erythrophthalmus</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Contopus virens</i>	0.017	56	5
Bassett-Touchell (2008)	<i>Contopus virens</i>	0.098	56	5
Bassett-Touchell (2008)	<i>Myiarchus crinitus</i>	-0.037	56	5
Bassett-Touchell (2008)	<i>Myiarchus crinitus</i>	0.095	56	5
Bassett-Touchell (2008)	<i>Picoides villosus</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Empidonax minimus</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Seiurus aurocapilla</i>	-0.059	56	5
Bassett-Touchell (2008)	<i>Seiurus aurocapilla</i>	-0.023	56	5
Bassett-Touchell (2008)	<i>Dendroica discolor</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Vireo olivaceus</i>	0.101	56	5
Bassett-Touchell (2008)	<i>Vireo olivaceus</i>	-0.033	56	5
Bassett-Touchell (2008)	<i>Agelaius phoeniceus</i>	-0.131	56	5

Table H2. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Bassett-Touchell (2008)	<i>Pheucticus ludovicianus</i>	-0.074	56	5
Bassett-Touchell (2008)	<i>Pheucticus ludovicianus</i>	0.083	56	5
Bassett-Touchell (2008)	<i>Piranga olivacea</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Piranga olivacea</i>	-0.083	56	5
Bassett-Touchell (2008)	<i>Cistothorus platensis</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Catharus ustulatus</i>	-0.183	56	5
Bassett-Touchell (2008)	<i>Catharus ustulatus</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Catharus fuscescens</i>	0.349	56	5
Bassett-Touchell (2008)	<i>Catharus fuscescens</i>	-0.059	56	5
Bassett-Touchell (2008)	<i>Vireo gilvus</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Sitta carolinensis</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Sitta carolinensis</i>	0.109	56	5
Bassett-Touchell (2008)	<i>Troglodytes troglodytes</i>	-0.131	56	5
Bassett-Touchell (2008)	<i>Hylocichla mustelina</i>	-0.083	56	5
Bassett-Touchell (2008)	<i>Dendroica petechia</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Sphyrapicus varius</i>	0.131	56	5
Bassett-Touchell (2008)	<i>Coccyzus americanus</i>	0.059	56	5
Bassett-Touchell (2008)	<i>Dendroica coronata</i>	0.000	56	5
Carrascal et al (2008)	<i>Chlamydotis undulata</i> <i>fuertaventurae</i>	-0.039	27	3
Dallimer and King (2008)	<i>Treron calva virescens</i>	-0.157	6	3
Dallimer and King (2008)	<i>Columba malherbii</i>	-0.178	51	3
Dallimer and King (2008)	<i>Columba larvata principalis</i>	0.013	5	3
Dallimer and King (2008)	<i>Psittacus erithacus</i>	-0.263	34	3
Dallimer and King (2008)	<i>Halcyon malimbica dryas</i>	0.142	32	3
Dallimer and King (2008)	<i>Turdus olivaceofuscus</i> <i>xanthorhynchus</i>	-0.287	13	3
Dallimer and King (2008)	<i>Horizorhinus dohrni</i>	0.235	58	3
Dallimer and King (2008)	<i>Anabathmis hartlaubii</i>	-0.122	14	3
Dallimer and King (2008)	<i>Speirops leucophaeus</i>	0.032	8	3
Dallimer and King (2008)	<i>Dicrurus modestus</i>	-0.198	7	3
Dallimer and King (2008)	<i>Lamprotornis ornatus</i>	-0.056	31	3
Dallimer and King (2008)	<i>Ploceus princeps</i>	0.007	9	3
Dallimer and King (2008)	<i>Serinus rufobrunneus</i> <i>rufobrunneus</i>	-0.177	36	3
Palomino and Carrascale (2007)	<i>Aegithalos caudatus</i>	0.015	23	3
Palomino and Carrascale (2007)	<i>Alauda arvensis</i>	-0.033	4	3
Palomino and Carrascale (2007)	<i>Alectoris rufa</i>	0.023	9	3
Palomino and Carrascale (2007)	<i>Anthus trivialis</i>	0.040	6	3
Palomino and Carrascale (2007)	<i>Apus apus</i>	0.056	24	3
Palomino and Carrascale (2007)	<i>Buteo buteo</i>	-0.029	20	3
Palomino and Carrascale (2007)	<i>Carduelis cannabina</i>	0.002	19	3

Table H2. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Palomino and Carrascale (2007)	<i>Carduelis carduelis</i>	0.090	18	3
Palomino and Carrascale (2007)	<i>Carduelis chloris</i>	0.033	31	3
Palomino and Carrascale (2007)	<i>Certhia brachydactyla</i>	-0.147	165	3
Palomino and Carrascale (2007)	<i>Cettia cetti</i>	0.131	14	3
Palomino and Carrascale (2007)	<i>Ciconia ciconia</i>	0.029	13	3
Palomino and Carrascale (2007)	<i>Columba livia</i>	0.077	13	3
Palomino and Carrascale (2007)	<i>Columba oenas</i>	-0.018	4	3
Palomino and Carrascale (2007)	<i>Columba palumbus</i>	0.164	88	3
Palomino and Carrascale (2007)	<i>Corvus corax</i>	-0.042	22	3
Palomino and Carrascale (2007)	<i>Corvus corone</i>	-0.018	55	3
Palomino and Carrascale (2007)	<i>Corvus monedula</i>	0.076	28	3
Palomino and Carrascale (2007)	<i>Coturnix coturnix</i>	0.001	7	3
Palomino and Carrascale (2007)	<i>Cuculus canorus</i>	0.048	76	3
Palomino and Carrascale (2007)	<i>Cyanopica (cyanus) cooki</i>	0.096	51	3
Palomino and Carrascale (2007)	<i>Delichon urbicum</i>	0.050	15	3
Palomino and Carrascale (2007)	<i>Dendrocopos major</i>	-0.143	35	3
Palomino and Carrascale (2007)	<i>Emberiza cia</i>	0.038	11	3
Palomino and Carrascale (2007)	<i>Emberiza cirius</i>	0.016	13	3
Palomino and Carrascale (2007)	<i>Erithacus rubecula</i>	-0.182	186	3
Palomino and Carrascale (2007)	<i>Ficedula hypoleuca</i>	-0.221	17	3
Palomino and Carrascale (2007)	<i>Fringilla coelebs</i>	-0.133	281	3
Palomino and Carrascale (2007)	<i>Garrulus glandarius</i>	-0.229	53	3
Palomino and Carrascale (2007)	<i>Hieraaetus pennatus</i>	0.056	14	3
Palomino and Carrascale (2007)	<i>Hippolais polyglotta</i>	0.093	30	3
Palomino and Carrascale (2007)	<i>Hirundo rustica</i>	0.106	25	3
Palomino and Carrascale (2007)	<i>Lanius excubitor</i>	0.061	10	3
Palomino and Carrascale (2007)	<i>Lanius senator</i>	0.024	7	3
Palomino and Carrascale (2007)	<i>Loxia curvirostra</i>	-0.090	22	3
Palomino and Carrascale (2007)	<i>Lullula arborea</i>	-0.001	50	3
Palomino and Carrascale (2007)	<i>Luscinia megarhynchos</i>	0.187	92	3
Palomino and Carrascale (2007)	<i>Merops apiaster</i>	0.112	20	3
Palomino and Carrascale (2007)	<i>Miliaria calandra</i>	0.122	56	3
Palomino and Carrascale (2007)	<i>Milvus migrans</i>	0.073	15	3
Palomino and Carrascale (2007)	<i>Milvus milvus</i>	0.059	17	3
Palomino and Carrascale (2007)	<i>Monticola saxatilis</i>	-0.022	4	3
Palomino and Carrascale (2007)	<i>Motacilla alba</i>	-0.049	9	3
Palomino and Carrascale (2007)	<i>Motacilla cinerea</i>	-0.098	4	3
Palomino and Carrascale (2007)	<i>Oenanthe oenanthe</i>	-0.030	14	3
Palomino and Carrascale (2007)	<i>Oriolus oriolus</i>	0.206	61	3
Palomino and Carrascale (2007)	<i>Parus ater</i>	-0.308	115	3
Palomino and Carrascale (2007)	<i>Parus caeruleus</i>	0.200	93	3

Table H2. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Palomino and Carrascale (2007)	<i>Parus cristatus</i>	-0.379	79	3
Palomino and Carrascale (2007)	<i>Parus major</i>	0.091	128	3
Palomino and Carrascale (2007)	<i>Passer domesticus</i>	0.140	40	3
Palomino and Carrascale (2007)	<i>Passer montanus</i>	0.016	18	3
Palomino and Carrascale (2007)	<i>Petronia petronia</i>	0.029	8	3
Palomino and Carrascale (2007)	<i>Phoenicurus ochruros</i>	-0.037	5	3
Palomino and Carrascale (2007)	<i>Phylloscopus bonelli</i>	0.124	91	3
Palomino and Carrascale (2007)	<i>Phylloscopus collybita</i>	-0.058	10	3
Palomino and Carrascale (2007)	<i>Pica pica</i>	0.234	112	3
Palomino and Carrascale (2007)	<i>Picus viridis</i>	0.061	72	3
Palomino and Carrascale (2007)	<i>Prunella modularis</i>	-0.011	15	3
Palomino and Carrascale (2007)	<i>Regulus ignicapillus</i>	-0.216	70	3
Palomino and Carrascale (2007)	<i>Regulus regulus</i>	-0.020	28	3
Palomino and Carrascale (2007)	<i>Saxicola torquata</i>	0.042	12	3
Palomino and Carrascale (2007)	<i>Serinus citrinella</i>	0.069	16	3
Palomino and Carrascale (2007)	<i>Serinus serinus</i>	0.066	148	3
Palomino and Carrascale (2007)	<i>Sitta europaea</i>	-0.088	32	3
Palomino and Carrascale (2007)	<i>Streptopelia decaocto</i>	0.042	7	3
Palomino and Carrascale (2007)	<i>Streptopelia turtur</i>	0.064	31	3
Palomino and Carrascale (2007)	<i>Sturnus unicolor</i>	0.226	126	3
Palomino and Carrascale (2007)	<i>Sylvia atricapilla</i>	-0.098	125	3
Palomino and Carrascale (2007)	<i>Sylvia borin</i>	0.076	12	3
Palomino and Carrascale (2007)	<i>Sylvia cantillans</i>	0.054	33	3
Palomino and Carrascale (2007)	<i>Sylvia communis</i>	-0.013	9	3
Palomino and Carrascale (2007)	<i>Sylvia melanocephala</i>	0.017	6	3
Palomino and Carrascale (2007)	<i>Sylvia undata</i>	-0.007	8	3
Palomino and Carrascale (2007)	<i>Troglodytes troglodytes</i>	-0.242	94	3
Palomino and Carrascale (2007)	<i>Turdus merula</i>	0.013	209	3
Palomino and Carrascale (2007)	<i>Turdus viscivorus</i>	0.053	34	3
Palomino and Carrascale (2007)	<i>Upupa epops</i>	0.065	36	3
Zabala et al (2006)	<i>Athene noctua</i>	-0.284	59	2
Morgado et al (2010)	<i>Melanocorypha calandra</i>	-0.124	20	3
Strickler (2008)	<i>Cinclus mexicanus</i>	-0.842	90	2
Dietz (2006)	<i>Zonotrichia leucophrys oriantha</i>	0.860	14	4
Ortega and Capen (1999)	<i>Seiurus aurocapilla</i>	-0.210	42	4
Summers (2009)	<i>Empidonax alnorum</i>	-0.306	20	5
Summers (2009)	<i>Carduelis tristis</i>	0.388	10	5
Summers (2009)	<i>Setophaga ruticilla</i>	0.404	20	5
Summers (2009)	<i>Turdus migratorius</i>	0.209	20	5
Summers (2009)	<i>Icterus galbula</i>	0.179	20	5

Table H2. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Summers (2009)	<i>Poecile atricapillus</i>	0.061	20	5
Summers (2009)	<i>Molothrus ater</i>	-0.306	20	5
Summers (2009)	<i>Vireo solitarius</i>	0.000	20	5
Summers (2009)	<i>Cyanocitta cristata</i>	-0.209	10	5
Summers (2009)	<i>Certhia americana</i>	-0.209	20	5
Summers (2009)	<i>Mniotilta varia</i>	0.000	20	5
Summers (2009)	<i>Bombycilla cedrorum</i>	0.209	10	5
Summers (2009)	<i>Spizella passerina</i>	0.000	20	5
Summers (2009)	<i>Quiscalus quiscula</i>	0.209	10	5
Summers (2009)	<i>Geothlypis trichas</i>	-0.137	20	5
Summers (2009)	<i>Picoides pubescens</i>	0.000	20	5
Summers (2009)	<i>Contopus virens</i>	-0.228	10	5
Summers (2009)	<i>Sturnus vulgaris</i>	0.306	10	5
Summers (2009)	<i>Spizella pusilla</i>	0.210	20	5
Summers (2009)	<i>Myiarchus crinitus</i>	-0.127	20	5
Summers (2009)	<i>Dendroica magnolia</i>	-0.210	20	5
Summers (2009)	<i>Vermivora ruficapilla</i>	0.210	20	5
Summers (2009)	<i>Cardinalis cardinalis</i>	-0.306	20	5
Summers (2009)	<i>Colaptes auratus</i>	-0.210	10	5
Summers (2009)	<i>Parula americana</i>	-0.210	20	5
Summers (2009)	<i>Seiurus aurocapilla</i>	-0.061	20	5
Summers (2009)	<i>Pheucticus ludovicianus</i>	-0.318	20	5
Summers (2009)	<i>Sitta canadensis</i>	-0.210	20	5
Summers (2009)	<i>Vireo olivaceus</i>	-0.256	20	5
Summers (2009)	<i>Bonasa umbellus</i>	-0.210	20	5
Summers (2009)	<i>Agelaius phoeniceus</i>	0.249	20	5
Summers (2009)	<i>Piranga olivacea</i>	-0.210	20	5
Summers (2009)	<i>Melospiza melodia</i>	0.105	20	5
Summers (2009)	<i>Melospiza georgiana</i>	0.095	20	5
Summers (2009)	<i>Catharus fuscescens</i>	0.000	20	5
Summers (2009)	<i>Vireo gilvus</i>	0.210	20	5
Summers (2009)	<i>Hylocichla mustelina</i>	-0.127	20	5
Summers (2009)	<i>Zonotrichia albicollis</i>	-0.288	20	5
Summers (2009)	<i>Dendroica coronata</i>	-0.210	20	5
Summers (2009)	<i>Dendroica petechia</i>	0.085	20	5

Table H3. Reptile species used in meta-analysis with calculated effect sizes and adjusted sample sizes used for effect size weighting (N). Note: study design number refers to the six effects of roads and traffic on animal abundance categories in Table 2.1. Reprinted with permission from © 2012 Elsevier.

Study Reference	Species Name	ESr	Adjusted N	Study Design
Boarman and Sazaki (2006)	<i>Gopherus agassizii</i>	-0.770	12	4
Fowle (1996)	<i>Chrysemys picta bellii</i>	-0.760	8	4
Steen et al (2007)	<i>Crotalus adamanteus</i>	0.157	90	3
Steen et al (2007)	<i>Crotalus horridus</i>	-0.175	87	3
Tanner and Perry (2007)	<i>Microlophus albemarlensis</i>	-0.970	64	4
Attum et al 2008	<i>Chrysemys picta marginata</i>	0.122	4	3
Crowley 2006	<i>Clemmys guttata</i>	-0.131	26	2
Crowley 2006	<i>Sistrurus catenatus catenatus</i>	-0.076	39	2
Crowley 2006	<i>Glyptemys insculpta</i>	-0.379	11	2
Crowley 2006	<i>Heterodon platirhinos</i>	-0.032	149	2
Griffin 2007	<i>Chrysemys picta bellii</i>	0.138	4	4
Schantz 2009	<i>Crotalus horridus</i>	-0.777	13	3
Schantz 2009	<i>Crotalus horridus</i>	-0.049	16	3
DeCatanzaro and Chow-Fraser 2010	<i>Chrysemys picta</i>	0.298	77	1
DeCatanzaro and Chow-Fraser 2010	<i>Sternotherus odoratus</i>	0.035	54	1
DeCatanzaro and Chow-Fraser 2010	<i>Chelydra serpentina</i>	0.011	77	1

Table H4. Amphibian species used in meta-analysis with calculated effect sizes and adjusted sample sizes used for effect size weighting (N). Note: study design number refers to the six effects of roads and traffic on animal abundance categories in Table 2.1. Reprinted with permission from © 2012 Elsevier.

Study Reference	Species Name	ESr	Adjusted N	Study Design
Carr and Fahrig (2001)	<i>Rana clamitans</i>	0.132	30	1
Carr and Fahrig (2001)	<i>Rana pipiens</i>	-0.223	30	1
Houlahan and Findlay (2003)	<i>Rana pipiens</i>	-0.155	70	3
Houlahan and Findlay (2003)	<i>Rana clamitans</i>	-0.227	63	3
Houlahan and Findlay (2003)	<i>Rana catesbeiana</i>	0.263	18	3
Houlahan and Findlay (2003)	<i>Rana septentrionalis</i>	-0.266	18	3
Houlahan and Findlay (2003)	<i>Rana sylvatica</i>	-0.362	55	3
Houlahan and Findlay (2003)	<i>Bufo americanus</i>	0.067	41	3
Houlahan and Findlay (2003)	<i>Hyla versicolor</i>	-0.288	56	3
Houlahan and Findlay (2003)	<i>Pseudacris crucifer</i>	-0.558	71	3
Houlahan and Findlay (2003)	<i>Pseudacris triseriata</i>	-0.124	19	3
Houlahan and Findlay (2003)	<i>Notophthalmus viridescens</i>	-0.112	4	3
Houlahan and Findlay (2003)	<i>Ambystoma maculatum</i>	-0.144	9	3
Houlahan and Findlay (2003)	<i>Ambystoma laterale</i>	-0.234	14	3
Houlahan and Findlay (2003)	<i>Plethodon cinereus</i>	-0.118	4	3
Nyström et al (2007)	<i>Pelobates fuscus</i>	-0.151	85	2
Pellet et al (2004a)	<i>Hyla arborea</i>	-0.097	29	3
Pellet et al (2004a)	<i>Hyla arborea</i>	-0.246	29	3
Pellet et al (2004b)	<i>Hyla arborea</i>	-0.227	30	2
Porej et al (2004)	<i>Ambystoma tigrinum tigrinum</i>	-0.967	26	2
Semlitsch et al (2007)	<i>Plethodon metcalfi</i>	-0.890	55	4
Skidds et al (2007)	<i>Ambystoma maculatum</i>	-0.210	65	1
Skidds et al (2007)	<i>Rana sylvatica</i>	-0.320	65	1
Vos and Chardon (1998)	<i>Rana arvalis</i>	-0.241	74	2
Ward et al (2008)	<i>Desmognathus monticola</i>	-0.383	16	6
Ward et al (2008)	<i>Desmognathus ochrophaeus</i>	-0.155	16	6
Ward et al (2008)	<i>Eurycea bislineata</i>	0.172	16	6
Marsh (2007)	<i>Plethodon cinereus</i>	-0.900	18	4
Karraker et al (2008)	<i>Ambystoma maculatum</i>	-0.255	82	4
Karraker et al (2008)	<i>Rana sylvatica</i>	-0.326	82	4
Jacobs (2008)	<i>Rana catesbeiana</i>	-0.358	24	3
Jacobs (2008)	<i>Rana septentrionalis</i>	-0.389	11	3
Hoskin and Goosem (2010)	<i>Austrochaperina pluvialis</i>	-0.212	10	4
Hoskin and Goosem (2010)	<i>Litoria serrata</i>	-0.283	10	4

Table H4. Continued

Study Reference	Species Name	ESr	Adjusted N	Study Design
Rinehart et al (2009)	<i>Notophthalmus viridescens</i>	-0.245	43	2
Rinehart et al (2009)	<i>Notophthalmus viridescens</i>	-0.217	43	2
Eigenbrod et al (2008a)	<i>Bufo americanus</i>	-0.361	36	1
Eigenbrod et al (2008a)	<i>Hyla versicolor</i>	0.038	36	1
Eigenbrod et al (2008a)	<i>Rana clamitans</i>	0.110	36	1
Eigenbrod et al (2008a)	<i>Rana pipiens</i>	-0.283	36	1
Eigenbrod et al (2008a)	<i>Pseudacris crucifer</i>	-0.087	36	1
Eigenbrod et al (2008a)	<i>Rana sylvatica</i>	-0.267	36	1

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Appendix I. Life history trait values and reference information for species used in meta-analysis.

Table I1. Life history traits collected for bird species used in meta-analysis. Traits were collected as follows: reproductive rate = mean number of eggs per clutch multiplied by the maximum number of clutches per year; species mobility= territory size; body mass = average body mass of the two sexes; body length= average total body length of the two sexes; age at sexual maturity =mean age at sexual maturity of the two sexes in months. Order: PAS= Passeriformes; PSI= Psittaciformes; CUC= Cuculiformes; CHA= Charadriiformes; GAV=Gaviiformes; STR=Strigiformes; PIC=Piciformes; GRU=Gruiformes; COL=Columbiformes; COR=Coraciiformes; APO=Apodiformes; CIC=Ciconiiformes; FAL=Falconiformes; GAL=Galliformes. Reprinted with permission from © 2012 Elsevier.

Study*	Species name	Order	Reproductive Rate	Source	Mobility (ha)	Source	Mass (g)	Source	Length (cm)	Source	Maturity (mm)	Source
1	<i>Dolichonyx oryzivorus</i>	PAS	10.20	Martin and Gavin 1995	0.49	Bollinger 1988	31.60	Martin and Gavin 1995	17.0	Bezener 2000	24	Martin and Gavin 1995
1	<i>Dolichonyx oryzivorus</i>	PAS	10.20	Martin and Gavin 1995	0.49	Bollinger 1988	31.60	Martin and Gavin 1995	17.0	Bezener 2000	24	Martin and Gavin 1995
1	<i>Dolichonyx oryzivorus</i>	PAS	10.20	Martin and Gavin 1995	0.49	Bollinger 1988	31.60	Martin and Gavin 1995	17.0	Bezener 2000	24	Martin and Gavin 1995
1	<i>Dolichonyx oryzivorus</i>	PAS	10.20	Martin and Gavin 1995	0.49	Bollinger 1988	31.60	Martin and Gavin 1995	17.0	Bezener 2000	24	Martin and Gavin 1995
1	<i>Sturnella magna</i>	PAS	9.14	Lanyon 1995	2.80	Lanyon 1995	111.70	Lanyon 1995	22.5	Dexheimer and Fraser 2006	12	Lanyon 1995
1	<i>Sturnella magna</i>	PAS	9.14	Lanyon 1995	2.80	Lanyon 1995	111.70	Lanyon 1995	22.5	Dexheimer and Fraser 2006	12	Lanyon 1995
1	<i>Sturnella magna</i>	PAS	9.14	Lanyon 1995	2.80	Lanyon 1995	111.70	Lanyon 1995	22.5	Dexheimer and Fraser 2006	12	Lanyon 1995
1	<i>Sturnella magna</i>	PAS	9.14	Lanyon 1995	2.80	Lanyon 1995	111.70	Lanyon 1995	22.5	Dexheimer and Fraser	12	Lanyon 1995

										2006		
2	<i>Ficedula hypoleuca</i>	PAS	7.45	Moller et al 2010	n/a		14.30	Moller et al 2010	13.0	Snow and Perrins 1998	12	Dakota 2009a
3	<i>Carduelis cannabina</i>	PAS	13.20	Moller et al 2010	n/a		18.90	Moller et al 2010	13.5	Snow and Perrins 1998	n/a	
3	<i>Carduelis carduelis</i>	PAS	14.31	Moller et al 2010	0.01	Conder 1948	15.60	Moller et al 2010	12.0	Snow and Perrins 1998	n/a	
3	<i>Carduelis chloris</i>	PAS	9.66	Moller et al 2010	n/a		27.60	Moller et al 2010	15.0	Snow and Perrins 1998	n/a	
3	<i>Certhia brachydactyla</i>	PAS	11.80	Moller et al 2010	n/a		9.10	Moller et al 2010	12.0	Snow and Perrins 1998	n/a	
3	<i>Fringilla coelebs</i>	PAS	8.60	Moller et al 2010	n/a		24.20	Moller et al 2010	14.5	Snow and Perrins 1998	n/a	
3	<i>Galerida cristata</i>	PAS	11.70	Moller et al 2010	n/a		44.70	Moller et al 2010	17.0	Snow and Perrins 1998	n/a	
3	<i>Lanius senator</i>	PAS	5.38	Moller et al 2010	n/a		36.00	Moller et al 2010	18.0	Snow and Perrins 1998	n/a	
3	<i>Lullula arborea</i>	PAS	7.94	Moller et al 2010	1.00	Brambilla and Rubolini 2009	30.10	Moller et al 2010	15.0	Snow and Perrins 1998	n/a	
3	<i>Miliaria calandra</i>	PAS	11.91	Moller et al 2010	0.19	Shepard et al 1996	47.70	Moller et al 2010	18.0	Snow and Perrins 1998	n/a	
3	<i>Oenanthe oenanthe</i>	PAS	11.00	Moller et al 2010	1.60	Kren and Zoerb 1997	24.00	Moller et al 2010	15.0	Snow and Perrins 1998	12	Kren and Zoerb 1997
3	<i>Parus caeruleus</i>	PAS	23.52	Moller et al 2010	0.20	Arriero et al 2006	11.80	Moller et al 2010	11.5	Snow and Perrins 1998	n/a	
3	<i>Parus major</i>	PAS	21.84	Moller et al 2010	0.31	Naef-Daenzer 1994	18.50	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
3	<i>Passer domesticus</i>	PAS	16.00	Moller et al 2010	0.10	Vangestel et al 2010	30.40	Moller et al 2010	14.5	Snow and Perrins 1998	n/a	
3	<i>Petronia petronia</i>	PAS	5.70	Moller et al 2010	n/a		32.90	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
3	<i>Phoenicurus ochruros</i>	PAS	14.70	Moller et al 2010	1.21	Schwarzova and Exnerova 2004	16.00	Moller et al 2010	14.5	Snow and Perrins 1998	n/a	
3	<i>Phylloscopus ibericus (brehmii)</i>	PAS	n/a		n/a		n/a		n/a		n/a	
3	<i>Serinus serinus</i>	PAS	8.00	Moller et al 2010	n/a		11.90	Moller et al 2010	11.5	Snow and Perrins 1998	n/a	
3	<i>Sitta europaea</i>	PAS	7.10	Moller et al 2010	2.10	Enoksson and Nilsson 1983	23.90	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	

3	<i>Sturnus unicolor</i>	PAS	8.20	Moller et al 2010	n/a		90.60	Moller et al 2010	22.0	Snow and Perrins 1998	n/a	
3	<i>Turdus merula</i>	PAS	15.48	Moller et al 2010	0.20	Snow 1956	95.80	Moller et al 2010	24.5	Snow and Perrins 1998	n/a	
4	<i>Manorina melanocephala</i>	PAS	10.00	Põldmaa et al 1995	n/a				26.0	Pizzey and Doyle 1980	12	Põldmaa et al 1995
4	<i>Anthochaera carunculata</i>	PAS	4.00	Tokue and Ford 2007/Ford and Trémont 2000	n/a		125.00	Allen and Saunders 2002	35.6	Serventy and Whittell 1976	n/a	
4	<i>Acanthiza nana</i>	PAS	n/a	Pizzey and Doyle 1980	n/a		5.90	Allen and Saunders 2002	10.0	Pizzey and Doyle 1980	n/a	
4	<i>Malurus cyaneus</i>	PAS	7.50	Colombelli-Négrel et al 2010	8.60	Chan and Augusteyn 2003	8.40	Chan and Augusteyn 2003	14.0	Pizzey and Doyle 1980	12	Cockburn et al 2008
4	<i>Eolophus roseicapilla</i>	PSI	n/a	Doneley 2003	n/a		302.00	Doneley 2003	n/a		30	Doneley 2003
4	<i>Smicromis brevirostris</i>	PAS	3.00	Serventy and Whittell 1976	n/a		5.10	Allen and Saunders 2002	11.4	Serventy and Whittell 1976	n/a	
4	<i>Psephotus haematonotus</i>	PAS	5.00	Mettke-Hofmann 2000	n/a		65.00	Allen and Saunders 2002	26.0	Serventy and Whittell 1976	n/a	
4	<i>Corcorax melanorhamphos</i>	PAS	4.00	Heinsohn and Cockburn 1994/Heinsohn 1995	20.00	Beck and Heinsohn 2006	364.00	Allen and Saunders 2002	64.0	Serventy and Whittell 1976	48	Heinsohn and Cockburn 1994
4	<i>Lichenostomus leucotis</i>	PAS	7.50	Pizzey and Doyle 1980	n/a		23.10	Allen and Saunders 2002	20.3	Pizzey and Doyle 1980	n/a	
4	<i>Melithreptus brevirostris</i>	PAS	5.00	Pizzey and Doyle 1980	n/a		14.60	Allen and Saunders 2002	11.8	Pizzey and Doyle 1980	n/a	
4	<i>Rhipidura albiscapa</i>	PAS	6.00	Hoffman et al 2010/Munro 2007	0.81	Munro 2007	8.50	Hoffman et al 2010	15.3	Pizzey and Doyle 1980	n/a	
4	<i>Pardalotus punctatus</i>	PAS	6.00	Serventy and Whittell 1976/Berry 2001	3.44	Woinarski and Bulman 1984	9.20	Allen and Saunders 2002	8.8	Pizzey and Doyle 1980	n/a	
4	<i>Lichenostomus melanops</i>	PAS	6.03	Franklin et al 1995	0.64				20.8	Pizzey and Doyle 1980	n/a	
4	<i>Pachycephala pectoralis</i>	PAS	2.50	Serventy and Whittell 1976/Berry 2001	2.50	van Dongen and Yocom 2005	32.70	Allen and Saunders 2002	16.4	Serventy and Whittell 1976	n/a	

4	<i>Cacomantis flabelliformis</i>	CUC	n/a	Serventy and Whittell 1976	n/a		47.80	Allen and Saunders 2002	26.7	Serventy and Whittell 1976	n/a	
4	<i>Colluricincla harmonica</i>	PAS	9.00	Stevens and Watson 2005	n/a		75.60	Allen and Saunders 2002	24.3	Pizzey and Doyle 1980	n/a	
4	<i>Glossopsitta concinna</i>	PSI	n/a	Pizzey and Doyle 1980	n/a		75.80	Allen and Saunders 2002	21.0	Pizzey and Doyle 1980	n/a	
4	<i>Zosterops lateralis</i>	PAS	4.00	Pizzey and Doyle 1980/Berry 2001	0.13	Barnett and Briskie 2010	12.50	Barnett and Briskie 2010	11.3	Pizzey and Doyle 1980	12	Kikkawa and Wilson 1983
4	<i>Lichenostomus fuscus</i>	PAS	n/a	Pizzey and Doyle 1980	n/a				15.5	Pizzey and Doyle 1980	n/a	
4	<i>Lichenostomus penicillatus</i>	PAS	7.50	Pizzey and Doyle 1980	n/a		19.80	Allen and Saunders 2002	16.0	Pizzey and Doyle 1980	n/a	
4	<i>Melithreptus lunatus</i>	PAS	5.00	Pizzey and Doyle 1980	n/a				13.5	Pizzey and Doyle 1980	n/a	
4	<i>Microeca fascians</i>	PAS	4.00	Pizzey and Doyle 1980/Keast 1994	n/a		15.70	Allen and Saunders 2002	13.5	Pizzey and Doyle 1980	n/a	
4	<i>Pardalotus striatus</i>	PAS	7.00	Pizzey and Doyle 1980	n/a		12.20	Allen and Saunders 2002	10.5	Pizzey and Doyle 1980	n/a	
4	<i>Pomatostomus superciliosus</i>	PAS	n/a		n/a		43.50	Cale 2003	20.0	Pizzey and Doyle 1980	n/a	
4	<i>Cormobates leucophaea</i>	PAS	2.50	Doerr and Doerr 2006	5.96	Doerr and Doerr 2006	22.80	Noske 1991	17.5	McCarthy et al 2000	17	Doerr and Doerr 2006
4	<i>Daphoenositta chrysoptera</i>	PAS	6.00	Noske 1998	2.50	Noske 1998	11.90	Allen and Saunders 2002	12.0	Pizzey and Doyle 1980	n/a	
4	<i>Eopsaltria australis</i>	PAS	6.96	Berry 2001/Zanette 2000	5.50	Debus 2006	20.00	Zanette 2000	16.0	Pizzey and Doyle 1980	n/a	
4	<i>Oreoica gutturalis</i>	PAS	n/a	Serventy and Whittell 1976	n/a		62.00	Allen and Saunders 2002	21.6	Serventy and Whittell 1976	n/a	
4	<i>Climacteris picumnus</i>	PAS	5.00	Doerr and Doerr 2007/Doerr and Doerr 2006	3.41	Doerr and Doerr 2006	37.00	Allen and Saunders 2002	17.0	Pizzey and Doyle 1980	22.5	Doerr and Doerr 2006

4	<i>Coracina novaehollandiae</i>	PAS	n/a	Serventy and Whittell 1976	n/a		93.30	Allen and Saunders 2002	33.0	Serventy and Whittell 1976	n/a	
4	<i>Artamus cyanopterus</i>	PAS	n/a	Serventy and Whittell 1976	n/a		35.00	Maddocks and Geiser 2007	17.5	Pizzey and Doyle 1980	n/a	
4	<i>Oriolus sagittatus</i>	PAS	n/a	Serventy and Whittell 1976	n/a		96.00	Serventy and Whittell 1976	27.0	Pizzey and Doyle 1980	n/a	
4	<i>Melithreptus gularis</i>	PAS	4.00	Pizzey and Doyle 1980	n/a				16.5	Pizzey and Doyle 1980	n/a	
4	<i>Lichenostomus chrysops</i>	PAS	7.20	Clarke et al 2003	0.19	Clarke et al 2003			16.5	Pizzey and Doyle 1980	n/a	
5	<i>Haematopus ostralegus</i>	CHA	2.78	Moller et al 2010	n/a		531.00	Moller et al 2010	42.5	Snow and Perrins 1998	54	Harris 1970
5	<i>Limosa limosa</i>	CHA	3.50	Snow and Perrins 1998	n/a		211.00	Snow and Perrins 1998	42.0	Snow and Perrins 1998	n/a	
5	<i>Vanellus vanellus</i>	CHA	4.00	Snow and Perrins 1998	0.51	Parish and Coulson 1998	230.00	Snow and Perrins 1998	29.5	Snow and Perrins 1998	n/a	
5	<i>Tringa totanus</i>	PAS	4.00	Snow and Perrins 1998	6.12	Burton and Armitage 2005	116.50	Snow and Perrins 1998	28.0	Snow and Perrins 1998	n/a	
6	<i>Gavia immer</i>	GAV	2.00	Evers et al 2010	124.00	Evers et al 2010	5307.00	Evers et al 2010	80.0	Kirschbaum and Rodriguez 2002	72	Evers et al 2010
7	<i>Corvus brachyrhynchos</i>	PAS	5.00	Verbeek and Caffrey 2002	37.70	Verbeek and Caffrey 2002	516.00	Verbeek and Caffrey 2002	45.0	Verbeek and Caffrey 2002	24	Verbeek and Caffrey 2002
7	<i>Corvus brachyrhynchos</i>	PAS	5.00	Verbeek and Caffrey 2002	37.70	Verbeek and Caffrey 2002	516.00	Verbeek and Caffrey 2002	45.0	Verbeek and Caffrey 2002	24	Verbeek and Caffrey 2002
7	<i>Carduelis tristis</i>	PAS	10.00	Middleton 1979	n/a		13.60	Dewey and Roof 2007	12.1	Dewey and Roof 2007	12	Middleton 1979
7	<i>Carduelis tristis</i>	PAS	10.00	Middleton 1979	n/a		13.60	Dewey and Roof 2007	12.1	Dewey and Roof 2007	12	Middleton 1979
7	<i>Setophaga ruticilla</i>	PAS	3.56	Sherry and Holmes 1997	0.52	Sherry and Holmes 1997	8.65	Sherry and Holmes 1997	11.9	Sherry and Holmes 1997	12	Sherry and Holmes 1997

7	<i>Setophaga ruticilla</i>	PAS	3.56	Sherry and Holmes 1997	0.52	Sherry and Holmes 1997	8.65	Sherry and Holmes 1997	11.9	Sherry and Holmes 1997	12	Sherry and Holmes 1997
7	<i>Turdus migratorius</i>	PAS	6.60	Sallabanks and James 1999	0.16	Sallabanks and James 1999	77.30	Sallabanks and James 1999	25.0	Dewey and Middlebrook 2001	12	Sallabanks and James 1999
7	<i>Turdus migratorius</i>	PAS	6.60	Sallabanks and James 1999	0.16	Sallabanks and James 1999	77.30	Sallabanks and James 1999	25.0	Dewey and Middlebrook 2001	12	Sallabanks and James 1999
7	<i>Strix varia</i>	STR	2.41	Mazur and James. 2000	282.00	Mazur and James. 2000	731.90	Mazur and James. 2000	47.2	Mazur and James. 2000	24	Mazur and James. 2000
7	<i>Mniotilta varia</i>	PAS	5.00	Kricher 1995	3.60	Kricher 1995	12.00	Kirschbaum and Foster 2001	11.5	Kricher 1995	n/a	
7	<i>Mniotilta varia</i>	PAS	5.00	Kricher 1995	3.60	Kricher 1995	12.00	Kirschbaum and Foster 2001	11.5	Kricher 1995	n/a	
7	<i>Coccyzus erythrophthalmus</i>	CUC	2.70	Hughes 2001	n/a		50.70	Hughes 2001	29.5	King and Francis 2009	12	Hughes 2001
7	<i>Dendroica fusca</i>	PAS	4.00	Morse 2004	0.50	Morse 2004	10.50	Clark 2011	13.0	Clark 2011	24	Clark 2011
7	<i>Dendroica fusca</i>	PAS	4.00	Morse 2005	0.50	Morse 2004	10.50	Clark 2011	13.0	Clark 2011	24	Clark 2011
7	<i>Poecile atricapillus</i>	PAS	7.00	Foote et al 2010	1.80	Foote et al 2010	10.40	Roof 2011	n/a		12	Foote et al 2010
7	<i>Poecile atricapillus</i>	PAS	7.00	Foote et al 2010	1.80	Foote et al 2010	10.40	Roof 2011	n/a		12	Foote et al 2010
7	<i>Dendroica caerulescens</i>	PAS	12.00	Holmes et al 2005	2.50	Holmes et al 2005	9.40	Holmes et al 2005	13.0	Dewey 2009a	12	Holmes et al 2005
7	<i>Dendroica caerulescens</i>	PAS	12.00	Holmes et al 2005	2.50	Holmes et al 2005	9.40	Holmes et al 2005	13.0	Dewey 2009a	12	Holmes et al 2005
7	<i>Dendroica virens</i>	PAS	4.00	Morse and Poole 2005	0.50	Morse and Poole 2005	8.50	Migliore and Fraser 2006	12.0	Migliore and Fraser 2006	12	Morse and Poole 2005
7	<i>Dendroica virens</i>	PAS	4.00	Morse and Poole 2005	0.50	Morse and Poole 2005	8.50	Migliore and Fraser 2006	12.0	Migliore and Fraser 2006	12	Morse and Poole 2005
7	<i>Cyanocitta cristata</i>	PAS	5.00	Tarvin and Woolfenden 2000	n/a		71.70	Tarvin and Woolfenden 1999	26.0	Tarvin and Woolfenden 1999	12	Tarvin and Woolfenden 2000
7	<i>Cyanocitta cristata</i>	PAS	5.00	Tarvin and Woolfenden 2001	n/a		71.70	Tarvin and Woolfenden 1999	26.0	Tarvin and Woolfenden 1999	12	Tarvin and Woolfenden 2001

7	<i>Vireo solitarius</i>	PAS	4.00	James 1998	3.00	James 1998	15.40	James 1998	13.8	James 1998	12	James 1998
7	<i>Certhia americana</i>	PAS	6.00	Hejl et al 2002	4.34	Hejl et al 2002	8.40	Hejl et al 2002	12.6	Hejl et al 2002	12	Hejl et al 2002
7	<i>Molothrus ater</i>	PAS	40.00	Lowther 1994	4.50	Lowther 1993	48.90	Lowther 1993	n/a		12	Lowther 1993
7	<i>Molothrus ater</i>	PAS	40.00	Lowther 1995	4.50	Lowther 1993	48.90	Lowther 1993	n/a		12	Lowther 1993
7	<i>Bombycilla cedrorum</i>	PAS	8.30	Witmer et al 1997	n/a		33.90	Witmer et al 1997	15.5	Klein 2003	12	Witmer et al 1997
7	<i>Spizella passerina</i>	PAS	7.40	Middleton 1998	0.60	Middleton 1998	12.50	Middleton 1998	13.7	Dewey 2009b	12	Middleton 1998
7	<i>Spizella passerina</i>	PAS	7.40	Middleton 1998	0.60	Middleton 1998	12.50	Middleton 1998	13.7	Dewey 2009b	12	Middleton 1998
7	<i>Geothlypis trichas</i>	PAS	8.00	Guzy and Ritchison 1999	1.20	Guzy and Ritchison 1999	10.00	Guzy and Ritchison 1999	12.5	Loiselle 2001	12	Guzy and Ritchison 1999
7	<i>Geothlypis trichas</i>	PAS	8.00	Guzy and Ritchison 1999	1.20	Guzy and Ritchison 1999	10.00	Guzy and Ritchison 1999	12.5	Loiselle 2001	12	Guzy and Ritchison 1999
7	<i>Picoides pubescens</i>	PIC	4.81	Jackson and Ouellet 2002	4.95	Jackson and Ouellet 2002	28.20	Jackson and Ouellet 2002	15.8	Dewey and Kirschbaum 2005	12	Jackson and Ouellet 2002
7	<i>Picoides pubescens</i>	PIC	4.81	Jackson and Ouellet 2003	4.95	Jackson and Ouellet 2003	28.20	Jackson and Ouellet 2002	15.8	Dewey and Kirschbaum 2005	12	Jackson and Ouellet 2002
7	<i>Sayornis phoebe</i>	PAS	9.12	Weeks 1994	3.00	Weeks 1994	21.60	Ivory 1999	15.5	Ivory 1999	12	Weeks 1994
7	<i>Pipilo erythrophthalmus</i>	PAS	3.60	Greenlaw 1996	0.26	Greenlaw 1996	40.50	Greenlaw 1996	n/a		12	Greenlaw 1996
7	<i>Contopus virens</i>	PAS	3.00	McCarty 1996	7.70	McCarty 1996	14.10	McCarty 1996	n/a		24	McCarty 1996
7	<i>Contopus virens</i>	PAS	3.00	McCarty 1996	7.70	McCarty 1996	14.10	McCarty 1996	n/a		24	McCarty 1996
7	<i>Myiarchus crinitus</i>	PAS	5.00	Lanyon 1997	2.40	Lanyon 1997	33.50	Lanyon 1997	n/a		12	Lanyon 1997
7	<i>Myiarchus crinitus</i>	PAS	5.00	Lanyon 1997	2.40	Lanyon 1997	33.50	Lanyon 1997	n/a		12	Lanyon 1997

7	<i>Picoides villosus</i>	PIC	3.93	Jackson et al 2002	1.05	Jackson et al 2002	70.40	Jackson et al 2002	21.6	Pappas 2002	12	Jackson et al 2002
7	<i>Empidonax minimus</i>	PAS	7.90	Tarof and Briskie 2008	0.07	Tarof and Briskie 2008	10.65	Tarof and Briskie 2008	n/a		12	Tarof and Briskie 2008
7	<i>Seiurus aurocapilla</i>	PAS	4.40	Van Horn and Donovan 1994	1.20	Van Horn and Donovan 1994	21.00	Foster 2000	14.5	Foster 2000	12	Van Horn and Donovan 1994
7	<i>Seiurus aurocapilla</i>	PAS	4.40	Van Horn and Donovan 1994	1.20	Van Horn and Donovan 1994	21.00	Foster 2000	14.5	Foster 2000	12	Van Horn and Donovan 1994
7	<i>Dendroica discolor</i>	PAS	7.78	Nolan et al 1999	1.62	Nolan et al 1999	7.50	Nolan et al 1999	n/a		12	Nolan et al 1999
7	<i>Vireo olivaceus</i>	PAS	3.10	Cimprich et al 2000	0.69	Cimprich et al 2000	20.30	Cimprich et al 2000	n/a		12	Cimprich et al 2000
7	<i>Vireo olivaceus</i>	PAS	3.10	Cimprich et al 2000	0.69	Cimprich et al 2000	20.30	Cimprich et al 2000	n/a		12	Cimprich et al 2000
7	<i>Agelaius phoeniceus</i>	PAS	6.58	Yasukawa and Searcy 1995	0.16	Yasukawa and Searcy 1995	57.20	Yasukawa and Searcy 1996	22.0	Rosenthal 2004	30	Yasukawa and Searcy 1995
7	<i>Pheucticus ludovicianus</i>	PAS	8.00	Wyatt and Francis 2002	0.77	Wyatt and Francis 2002	45.60	Wyatt and Francis 2002	19.8	Dewey 2009c	12	Wyatt and Francis 2002
7	<i>Pheucticus ludovicianus</i>	PAS	8.00	Wyatt and Francis 2002	0.77	Wyatt and Francis 2002	45.60	Wyatt and Francis 2002	19.8	Dewey 2009c	12	Wyatt and Francis 2002
7	<i>Piranga olivacea</i>	PAS	4.10	Mowbray 1999	2.50	Mowbray 1999	25.00	Mowbray 1999	16.5	Dewey and Street 1999	12	Mowbray 1999
7	<i>Piranga olivacea</i>	PAS	4.10	Mowbray 1999	2.50	Mowbray 1999	25.00	Mowbray 1999	16.5	Dewey and Street 1999	12	Mowbray 1999
7	<i>Cistothorus platensis</i>	PAS	14.00	Herkert et al 2001	0.18	Herkert et al 2001	7.99	Herkert et al 2001	11.0	Dewey 2009d	12	Herkert et al 2001
7	<i>Catharus ustulatus</i>	PAS	3.53	Mack and Yong 2000	1.00	Mack and Yong 2000	32.20	Mack and Yong 2000	17.0	Mack and Yong 2000	24	Mack and Yong 2000
7	<i>Catharus ustulatus</i>	PAS	3.53	Mack and Yong 2000	1.00	Mack and Yong 2000	32.20	Mack and Yong 2000	17.0	Mack and Yong 2000	24	Mack and Yong 2001
7	<i>Catharus fuscescens</i>	PAS	4.00	Bevier et al 2005	0.25	Bevier et al 2005	41.50	Bevier et al 2005	17.0	Bevier et al 2005	12	Bevier et al 2005
7	<i>Catharus fuscescens</i>	PAS	4.00	Bevier et al 2005	0.25	Bevier et al 2005	41.50	Bevier et al 2005	17.0	Bevier et al 2005	12	Bevier et al 2005

7	<i>Vireo gilvus</i>	PAS	3.50	Gardali and Ballard 2000	1.35	Gardali and Ballard 2000	13.50	Gardali and Ballard 2000	n/a		12	Gardali and Ballard 2000
7	<i>Sitta carolinensis</i>	PAS	6.40	Grubb and Pravosudov 2008	12.50	Grubb and Pravosudov 2008	21.10	Grubb and Pravosudov 2008	15.0	Dewey and Roof 1999	12	Grubb and Pravosudov 2008
7	<i>Sitta carolinensis</i>	PAS	6.40	Grubb and Pravosudov 2008	12.50	Grubb and Pravosudov 2008	21.10	Grubb and Pravosudov 2008	15.0	Dewey and Roof 1999	12	Grubb and Pravosudov 2008
7	<i>Troglodytes troglodytes</i>	PAS	10.60	Hejl et al 2002	1.38	Hejl et al 2002	8.90	Hejl et al 2002	9.0	Hejl et al 2002	12	Hejl et al 2002
7	<i>Hylocichla mustelina</i>	PAS	8.00	Evans et al 2011	2.40	Evans et al 2011	45.00	Lesperance and Kirschbaum 2002	20.0	Lesperance and Kirschbaum 2002	12	Evans et al 2011
7	<i>Dendroica petechia</i>	PAS	4.50	Lowther et al 1999	0.50	Lowther et al 1999	10.20	Lowther et al 1999	14.0	Bachynski and Kadlec 2003	12	Lowther et al 1999
7	<i>Sphyrapicus varius</i>	PIC	5.44	Walters 2002	0.65	Walters 2002	50.30	Walters 2002	n/a		12	Walters 2002
7	<i>Coccyzus americanus</i>	CUC	5.00	Hughes 1999	n/a		63.00	Hughes 1999	28.5	Hughes 1999	12	Hughes 1999
7	<i>Dendroica coronata</i>	PAS	8.00	Hunt and Flaspohler 1998	0.45	Hunt and Flaspohler 1998	12.60	Hunt and Flaspohler 1998	n/a		n/a	
8	<i>Chlamydotis undulata fuertaventurae</i>	GRU	2.50	Snow and Perrins 1998/Heredia 1995	60.00	Combreau et al 2000	1775.00	Snow and Perrins 1998	60.0	Snow and Perrins 1998	n/a	
9	<i>Treron calva virescens</i>	COL	n/a		n/a		n/a		n/a		n/a	
9	<i>Columba malherbii</i>	COL	n/a		n/a		n/a		n/a		n/a	
9	<i>Columba larvata principalis</i>	COL	n/a		n/a		n/a		n/a		n/a	
9	<i>Psittacus erithacus</i>	PSI	8.00	Holman and Lindsay 2008	n/a		407.00	Holman and Lindsay 2008	33.0	Holman and Lindsay 2008	48	Holman and Lindsay 2008
9	<i>Halcyon malimbica dryas</i>	COR	n/a		n/a		n/a		n/a		n/a	
9	<i>Turdus olivaceofuscus xanthorhynchus</i>	PAS	n/a		n/a		82.50	Melo et al 2010	n/a		n/a	

9	<i>Horizorhinus dohrni</i>	PAS	n/a		n/a		n/a		n/a		n/a	
9	<i>Anabathmis hartlaubii</i>	PAS	n/a		n/a		n/a		n/a		n/a	
9	<i>Speirops leucophaeus</i>	PAS	n/a		n/a		n/a		n/a		n/a	
9	<i>Dicrurus modestus</i>	PAS	n/a		n/a		n/a		n/a		n/a	
9	<i>Lamprotornis ornatus</i>	PAS	n/a		n/a		n/a		n/a		n/a	
9	<i>Ploceus princeps</i>	PAS	n/a		n/a		n/a		n/a		n/a	
9	<i>Serinus rufobrunneus rufobrunneus</i>	PAS	n/a		n/a		n/a		n/a		n/a	
10	<i>Aegithalos caudatus</i>	PAS	9.40	Moller et al 2010	17.00	Hatchwell et al 2001	8.80	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
10	<i>Alauda arvensis</i>	PAS	14.76	Moller et al 2010	3.11	Grynderup Poulsen et al 1998	36.40	Moller et al 2010	18.5	Snow and Perrins 1998	n/a	
10	<i>Alectoris rufa</i>	GAL	26.00	Snow and Perrins 1998	52.60	Buenestado et al 2008	487.50	Snow and Perrins 1998	33.0	Snow and Perrins 1998	n/a	
10	<i>Anthus trivialis</i>	PAS	13.59	Moller et al 2010	0.62	Kumstátová et al 2004	23.40	Moller et al 2010	15.0	Snow and Perrins 1998	n/a	
10	<i>Apus apus</i>	ADO	2.40	Moller et al 2010	n.a		39.60	Moller et al 2010	16.5	Snow and Perrins 1998	24	Thompson and Fraser 2006
10	<i>Buteo buteo</i>	FAL	3.50	Bologna 1981	n/a		850.00	Bologna 1981	54.5	Bologna 1981	n/a	
10	<i>Carduelis cannabina</i>	PAS	13.20	Moller et al 2010	n/a		18.90	Moller et al 2010	13.5	Snow and Perrins 1998	n/a	
10	<i>Carduelis carduelis</i>	PAS	14.31	Moller et al 2010	0.01	Conder 1948	15.60	Moller et al 2010	12.0	Snow and Perrins 1998	n/a	
10	<i>Carduelis chloris</i>	PAS	9.66	Moller et al 2010	n/a		27.60	Moller et al 2010	15.0	Snow and Perrins 1998	n/a	
10	<i>Certhia brachydactyla</i>	PAS	11.80	Moller et al 2010	n/a		9.10	Moller et al 2010	12.0	Snow and Perrins 1998	n/a	
10	<i>Cettia cetti</i>	PAS	9.10	Moller et al 2010	3.06	Bibby 1980	14.10	Moller et al 2010	13.5	Snow and Perrins 1998	12	Tasinazzo 1993

10	<i>Ciconia ciconia</i>	CIC	5.00	Snow and Perrins 1998/ Dewey 2006	706.50	Denac 2006	3296.30	Snow and Perrins 1998	107.5	Snow and Perrins 1998	48	Dewey 2006
10	<i>Columba livia</i>	COL	10.00	Snow and Perrins 1998/Johnston 1992	n/a		250.00	Snow and Perrins 1998	32.5	Snow and Perrins 1998	12	Roof 2001
10	<i>Columba oenas</i>	COL	8.00	Snow and Perrins 1998/Johnston 1992	n/a		302.50	Snow and Perrins 1998	33.0	Snow and Perrins 1998	n/a	
10	<i>Columba palumbus</i>	COL	3.00	Snow and Perrins 1998/Johnston 1992	n/a		570.00	Snow and Perrins 1998	41.0	Snow and Perrins 1998	n/a	
10	<i>Corvus corax</i>	PAS	4.50	Moller et al 2010	1310.00	Rosner and Selva 2005	1200.50	Moller et al 2010	64.0	Snow and Perrins 1998	36	Snow and Perrins 1998
10	<i>Corvus corone</i>	PAS	4.10	Moller et al 2010	13.00	Canestrari et al 2008	544.50	Moller et al 2010	46.0	Snow and Perrins 1998	36	Snow and Perrins 1998
10	<i>Corvus monedula</i>	PAS	4.40	Moller et al 2010	n/a		249.00	Moller et al 2010	33.5	Snow and Perrins 1998	24	Snow and Perrins 1998
10	<i>Coturnix coturnix</i>	GAL	20.40	Moller et al 2010	n/a		98.80	Moller et al 2010	17.0	Snow and Perrins 1998	n/a	
10	<i>Cuculus canorus</i>	CUC	9.20	Moller et al 2010	n/a		120.50	Moller et al 2010	33.0	Snow and Perrins 1998	n/a	
10	<i>Cyanopica (cyanus) cooki</i>	PAS	6.58	Moller et al 2010	n/a		71.00	Moller et al 2010	34.5	Snow and Perrins 1998	n/a	
10	<i>Delichon urbicum</i>	PAS	8.20	Moller et al 2010	n/a		19.50	Moller et al 2010	12.5	Snow and Perrins 1998	n/a	
10	<i>Dendrocopos major</i>	PIC	5.50	Moller et al 2010	20.00	Rolstad et al 1995	89.70	Moller et al 2010	22.5	Snow and Perrins 1998	n/a	
10	<i>Emberiza cia</i>	PAS	11.34	Moller et al 2010	0.79	Sánchez et al 2009	23.20	Moller et al 2010	16.0	Snow and Perrins 1998	n/a	
10	<i>Emberiza cirius</i>	PAS	10.59	Moller et al 2010	3.14	Stevens et al 2002	23.80	Moller et al 2010	15.5	Snow and Perrins 1998	n/a	
10	<i>Erithacus rubecula</i>	PAS	15.00	Moller et al 2010	0.23	Tobias and Seddon 2000	16.40	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
10	<i>Ficedula hypoleuca</i>	PAS	7.45	Moller et al 2010	n/a		14.30	Moller et al 2010	13.0	Snow and Perrins 1998	12	Dakota 2009a
10	<i>Fringilla coelebs</i>	PAS	8.60	Moller et al 2010	n/a		24.20	Moller et al 2010	14.5	Snow and Perrins 1998	n/a	
10	<i>Garrulus glandarius</i>	PAS	4.80	Moller et al 2010	12.30	Rolando et al 1995	161.70	Moller et al 2010	34.5	Snow and Perrins 1998	24	Dakota 2009b

10	<i>Hieraaetus pennatus</i>	FAL	2.00	Snow and Perrins 1998	28.30	Martínez et al 2006	842.50	Snow and Perrins 1998	49.0	Snow and Perrins 1998	n/a	
10	<i>Hippolais polyglotta</i>	PAS	8.66	Moller et al 2010	n/a		11.40	Moller et al 2010	13.0	Snow and Perrins 1998	n/a	
10	<i>Hirundo rustica</i>	PAS	13.20	Moller et al 2010	0.08	Brown and Bomberger Brown 1999	19.10	Moller et al 2010	18.0	Snow and Perrins 1998	12	Dewey and Roth 2002
10	<i>Lanius excubitor</i>	PAS	6.20	Moller et al 2010	20.00	Cade and Atkinson 2002	66.90	Moller et al 2010	24.5	Snow and Perrins 1998	11	Cade and Atkinson 2002
10	<i>Lanius senator</i>	PAS	5.38	Moller et al 2010	n/a		36.00	Moller et al 2010	18.0	Snow and Perrins 1998	n/a	
10	<i>Loxia curvirostra</i>	PAS	11.10	Moller et al 2010	0.79	Adkisson 1996	40.60	Moller et al 2010	16.5	Snow and Perrins 1998	12	Adkisson 1996
10	<i>Lullula arborea</i>	PAS	7.94	Moller et al 2010	1.00	Brambilla and Rubolini 2009	30.10	Moller et al 2010	15.0	Snow and Perrins 1998	n/a	
10	<i>Luscinia megarhynchos</i>	PAS	9.50	Moller et al 2010	1.15	Naguib et al 2001	20.10	Moller et al 2010	16.5	Snow and Perrins 1998	12	Song and Omland 2008
10	<i>Merops apiaster</i>	COR	6.00	Moller et al 2010	0.02	Petroelje 2011	55.10	Moller et al 2010	28.0	Snow and Perrins 1998	12	Petroelje 2011
10	<i>Miliaria calandra</i>	PAS	11.91	Moller et al 2010	0.19	Shepard et al 1996	47.70	Moller et al 2010	18.0	Snow and Perrins 1998	n/a	
10	<i>Milvus migrans</i>	FAL	2.50	Snow and Perrins 1998	3.00	Forero et al 1999	812.30	Snow and Perrins 1998	57.5	Snow and Perrins 1998	n/a	
10	<i>Milvus milvus</i>	FAL	2.00	Snow and Perrins 1998	167.50	Nachtigall et al 2003	1075.00	Snow and Perrins 1998	63.0	Snow and Perrins 1998	36	Meyer and Franci 2008
10	<i>Monticola saxatilis</i>	PAS	9.00	Moller et al 2010	n/a		51.20	Moller et al 2010	18.5	Snow and Perrins 1998	n/a	
10	<i>Motacilla alba</i>	PAS	15.30	Moller et al 2010	0.39	Badyaev et al 1996	20.80	Moller et al 2010	18.0	Snow and Perrins 1998	12	Badyaev et al 1996
10	<i>Motacilla cinerea</i>	PAS	14.70	Moller et al 2010	n/a		17.40	Moller et al 2010	18.5	Snow and Perrins 1998	n/a	
10	<i>Oenanthe oenanthe</i>	PAS	11.00	Moller et al 2010	1.60	Kren and Zoerb 1997	24.00	Moller et al 2010	15.0	Snow and Perrins 1998	12	Kren and Zoerb 1997
10	<i>Oriolus oriolus</i>	PAS	3.80	Moller et al 2010	n/a		68.50	Moller et al 2010	24.0	Snow and Perrins 1998	n/a	
10	<i>Parus ater</i>	PAS	17.00	Moller et al 2010	1.20	Brottons 2000	9.20	Moller et al 2010	11.5	Snow and Perrins 1998	n/a	
10	<i>Parus caeruleus</i>	PAS	23.52	Moller et al 2010	0.20	Arriero et al 2006	11.80	Moller et al 2010	11.5	Snow and Perrins 1998	n/a	

10	<i>Parus cristatus</i>	PAS	13.00	Moller et al 2010	n/a		11.20	Moller et al 2010	11.5	Snow and Perrins 1998	n/a	
10	<i>Parus major</i>	PAS	21.84	Moller et al 2010	n/a		18.50	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
10	<i>Passer domesticus</i>	PAS	16.00	Moller et al 2010	0.10	Vangestel et al 2010	30.40	Moller et al 2010	14.5	Snow and Perrins 1998	n/a	
10	<i>Passer montanus</i>	PAS	14.67	Moller et al 2010	n/a		21.70	Moller et al 2010	14.0	Snow and Perrins 1998	10	Barlow and Sheridan 2000
10	<i>Petronia petronia</i>	PAS	5.70	Moller et al 2010	n/a		32.90	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
10	<i>Phoenicurus ochruros</i>	PAS	14.70	Moller et al 2010	1.21	Schwarzova and Exnerova 2004	16.00	Moller et al 2010	14.5	Snow and Perrins 1998	n/a	
10	<i>Phylloscopus bonelli</i>	PAS	10.60	Moller et al 2010	n/a		7.80	Moller et al 2010	11.5	Snow and Perrins 1998	n/a	
10	<i>Phylloscopus collybita</i>	PAS	11.00	Moller et al 2010	0.35	Rodrigues 1998	7.70	Moller et al 2010	10.5	Snow and Perrins 1998	n/a	
10	<i>Pica pica</i>	PAS	5.90	Moller et al 2010	n/a		228.00	Moller et al 2010	45.0	Snow and Perrins 1998	n/a	
10	<i>Picus viridis</i>	PIC	6.00	Snow and Perrins 1998	83.00	Alder and Marsden 2010	185.00	Snow and Perrins 1998	32.0	Snow and Perrins 1998	n/a	
10	<i>Prunella modularis</i>	PAS	15.30	Moller et al 2010	n/a		19.00	Moller et al 2010	14.5	Snow and Perrins 1998	n/a	
10	<i>Regulus ignicapillus</i>	PAS	17.60	Moller et al 2010	n/a		5.20	Moller et al 2010	9.0	Snow and Perrins 1998	n/a	
10	<i>Regulus regulus</i>	PAS	20.72	Moller et al 2010	n/a		5.80	Moller et al 2010	9.0	Snow and Perrins 1998	n/a	
10	<i>Saxicola torquata</i>	PAS	20.24	Moller et al 2010	n/a		14.90	Moller et al 2010	12.5	Snow and Perrins 1998	n/a	
10	<i>Serinus citrinella</i>	PAS	9.20	Moller et al 2010	n/a		12.80	Moller et al 2010	12.0	Snow and Perrins 1998	n/a	
10	<i>Serinus serinus</i>	PAS	8.00	Moller et al 2010	n/a		11.90	Moller et al 2010	11.5	Snow and Perrins 1998	n/a	
10	<i>Sitta europaea</i>	PAS	7.10	Moller et al 2010	2.10	Enoksson and Nilsson 1983	23.90	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
10	<i>Streptopelia decaocto</i>	COL	12.00	Romagosa 2002	0.14	Romagosa 2002	201.50	Romagosa 2002	32.0	Snow and Perrins 1998	12	Romagosa 2002
10	<i>Streptopelia turtur</i>	COL	4.50	Snow and Perrins 1998	2.50	Browne and Aebischer 2004	140.00	Snow and Perrins 1998	27.0	Snow and Perrins 1998	n/a	
10	<i>Sturnus unicolor</i>	PAS	8.20	Moller et al 2010	n/a		90.60	Moller et al 2010	22.0	Snow and Perrins 1998	n/a	

10	<i>Sylvia atricapilla</i>	PAS	9.30	Moller et al 2010	0.25	Remeš 2003	18.90	Moller et al 2010	13.0	Snow and Perrins 1998	n/a	
10	<i>Sylvia borin</i>	PAS	8.06	Moller et al 2010	n/a	Snow and Perrins 1998	19.00	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
10	<i>Sylvia cantillans</i>	PAS	8.40	Moller et al 2010	n/a		8.10	Moller et al 2010	12.0	Snow and Perrins 1998	n/a	
10	<i>Sylvia communis</i>	PAS	9.26	Moller et al 2010	n/a		14.50	Moller et al 2010	14.0	Snow and Perrins 1998	n/a	
10	<i>Sylvia melanocephala</i>	PAS	8.40	Moller et al 2010	1.00	Bas et al 2005	13.40	Moller et al 2010	13.5	Snow and Perrins 1998	n/a	
10	<i>Sylvia undata</i>	PAS	12.00	Moller et al 2010	0.49	Pons et al 2008	8.90	Moller et al 2010	12.5	Snow and Perrins 1998	n/a	
10	<i>Troglodytes troglodytes</i>	PAS	11.40	Moller et al 2010	0.32	Hejl et al 2002	8.90	Moller et al 2010	9.5	Snow and Perrins 1998	12	Hejl et al 2002
10	<i>Turdus merula</i>	PAS	15.48	Moller et al 2010	0.20	Snow 1956	95.80	Moller et al 2010	24.5	Snow and Perrins 1998	n/a	
10	<i>Turdus viscivorus</i>	PAS	11.76	Moller et al 2010	n/a		117.80	Moller et al 2010	27.0	Snow and Perrins 1998	n/a	
10	<i>Upupa epops</i>	COR	14.00	Moller et al 2010	n/a		67.00	Moller et al 2010	27.0	Snow and Perrins 1998	n/a	
11	<i>Athene noctua</i>	STR	3.80	Nieuwenhuys e et al 2008	12.30	Finck 1990	168.00	Moller et al 2010	22.0	Snow and Perrins 1998	n/a	
12	<i>Melanocorypha calandra</i>	PAS	8.40	Moller et al 2010	n/a		60.40	Moller et al 2010	18.5	Snow and Perrins 1998	n/a	
13	<i>Cinclus mexicanus</i>	PAS	8.20	Willson and Kingery 2011	10.00	Strickler 2008	57.80	Willson and Kingery 2011	17.0	Willson and Kingery 2011	12	Willson and Kingery 2011
14	<i>Zonotrichia leucophrys oriantha</i>	PAS	3.93	Chilton et al 1995	0.11	Chilton et al 1995	26.90	Chilton et al 1995	n/a		12	Chilton et al 1995
15	<i>Seiurus aurocapilla</i>	PAS	4.40	Van Horn and Donovan 1994	0.83	Van Horn and Donovan 1994	21.00	Foster 2000	14.5	Foster 2000	12	Van Horn and Donovan 1994
16	<i>Empidonax alnorum</i>	PAS	4.00	Lowther 1999	0.20	Lowther 1999	13.50	Lowther 1999	n/a		12	Lowther 1999
16	<i>Carduelis tristis</i>	PAS	10.00	Middleton 1979	n/a		13.60	Dewey and Roof 2007	12.1	Dewey and Roof 2007	12	Middleton 1979
16	<i>Setophaga ruticilla</i>	PAS	3.56	Sherry and Holmes 1997	0.52	Sherry and Holmes 1997	8.65	Sherry and Holmes 1997	11.9	Sherry and Holmes 1997	12	Sherry and Holmes 1997

16	<i>Turdus migratorius</i>	PAS	6.60	Sallabanks and James 1999	0.16	Sallabanks and James 1999	77.30	Sallabanks and James 1999	25.0	Dewey and Middlebrook 2001	12	Sallabanks and James 1999
16	<i>Icterus galbula</i>	PAS	5.00	Rising and Flood 1998	0.63	Rising and Flood 1998	35.50	Rising and Flood 1998	18.5	Backynski and Kennedy 2001	12	Rising and Flood 1998
16	<i>Poecile atricapillus</i>	PAS	7.00	Foote et al 2010	1.80	Foote et al 2010	10.40	Roof 2011	n/a		12	Foote et al 2010
16	<i>Molothrus ater</i>	PAS	40.00	Lowther 1993	4.50	Lowther 1993	48.90	Lowther 1993	n/a		12	Lowther 1993
16	<i>Vireo solitarius</i>	PAS	4.00	James 1998	3.00	James 1998	15.40	James 1998	13.8	James 1998	12	James 1998
16	<i>Cyanocitta cristata</i>	PAS	5.00	Tarvin and Woolfenden 1999	n/a		71.70	Tarvin and Woolfenden 1999	26.0	Tarvin and Woolfenden 1999	12	Tarvin and Woolfenden 1999
16	<i>Certhia americana</i>	PAS	6.00	Hejl et al 2002	4.34	Hejl et al 2002	8.40	Hejl et al 2002	12.6	Hejl et al 2002	12	Hejl et al 2002
16	<i>Mniotilta varia</i>	PAS	5.00	Kricher 1995	3.60	Kricher 1995	12.00	Kirschbaum and Foster 2001	11.5	Kricher 1995	n/a	
16	<i>Bombycilla cedrorum</i>	PAS	8.36	Witmer et al 1997	n/a		33.90	Witmer et al 1997	15.5	Klein 2003	12	Witmer et al 1997
16	<i>Spizella passerina</i>	PAS	7.40	Middleton 1998	0.60	Middleton 1998	12.50	Middleton 1998	13.7	Dewey 2009b	12	Middleton 1998
16	<i>Quiscalus quiscula</i>	PAS	4.80	Peer and Bollinger 1997	n/a		116.10	Peer and Bollinger 1997	31.0	Dewey and Ivory 1999	n/a	
16	<i>Geothlypis trichas</i>	PAS	8.00	Guzy and Ritchison 1999	1.20	Guzy and Ritchison 1999	10.00	Guzy and Ritchison 1999	12.5	Loiselle 2001	12	Guzy and Ritchison 1999
16	<i>Picoides pubescens</i>	PIC	4.81	Jackson and Ouellet 2004	4.95	Jackson and Ouellet 2004	27.87	Jackson and Ouellet 2002	15.8	Dewey and Kirschbaum 2005	12	Jackson and Ouellet 2002
16	<i>Contopus virens</i>	PAS	3.00	McCarty 1996	7.70	McCarty 1996	14.10	McCarty 1996	n/a		24	McCarty 1996
16	<i>Sturnus vulgaris</i>	PAS	10.20	Cabe 1993	n/a	Cabe 1993	86.00	Cabe 1993	21.5	Chow 2000	18	Cabe 1993
16	<i>Spizella pusilla</i>	PAS	6.74	Carey et al 2008	0.76	Carey et al 2008	13.10	Carey et al 2008	13.8	Dewey 2009e	12	Carey et al 2008
16	<i>Myiarchus crinitus</i>	PAS	5.00	Lanyon 1997	2.40	Lanyon 1997	33.50	Lanyon 1997	n/a		12	Lanyon 1997

16	<i>Dendroica magnolia</i>	PAS	4.00	Dunn and Hall 2010	0.57	Dunn and Hall 2010	8.60	Dunn and Hall 2010	12.5	Neuser 2003	12	Dunn and Hall 2010
16	<i>Vermivora ruficapilla</i>	PAS	4.50	Williams 1996	1.10	Williams 1996	8.75	Williams 1996	n/a		n/a	
16	<i>Cardinalis cardinalis</i>	PAS	6.00	Halkin and Linville 1999	1.34	Gottfried 1976	44.10	Halkin and Linville 1999	22.2	Dewey et al 2011	12	Halkin and Linville 1999
16	<i>Colaptes auratus</i>	PIC	7.81	Wiebe and Moore 2008	25.00	Wiebe and Moore 2008	132.00	Wiebe and Moore 2008	32.5	Wiebe and Moore 2008	12	Wiebe and Moore 2008
16	<i>Parula americana</i>	PAS	4.00	Moldenhauer and Regelski 1996	0.40	Moldenhauer and Regelski 1996	7.90	Moldenhauer and Regelski 1996	n/a		12	Moldenhauer and Regelski 1996
16	<i>Seiurus aurocapilla</i>	PAS	4.40	Van Horn and Donovan 1994	0.83	Van Horn and Donovan 1994	21.00	Foster 2000	14.5	Foster 2000	12	Van Horn and Donovan 1994
16	<i>Pheucticus ludovicianus</i>	PAS	8.00	Wyatt and Francis 2002	0.77	Wyatt and Francis 2002	45.60	Wyatt and Francis 2002	19.8	Dewey 2009c	12	Wyatt and Francis 2002
16	<i>Sitta canadensis</i>	PAS	6.00	Ghalambor and Martin 1999	0.20	Ghalambor and Martin 1999	10.00	Ghalambor and Martin 1999	11.5	Kirschbaum and Sands 2003	12	Ghalambor and Martin 1999
16	<i>Vireo olivaceus</i>	PAS	3.30	Cimprich et al 2000	0.69	Cimprich et al 2000	20.30	Cimprich et al 2000	n/a		12	Cimprich et al 2002
16	<i>Bonasa umbellus</i>	GAL	11.50	Rusch et al 2000	2.30	Rusch et al 2000	644.00	Haupt 2001	n/a		12	Rusch et al 2000
16	<i>Agelaius phoeniceus</i>	PAS	6.58	Yasukawa and Searcy 1995	0.58	Eckert and Weatherhead 1987	57.20	Yasukawa and Searcy 1995	22.0	Rosenthal 2004	30	Yasukawa and Searcy 1995
16	<i>Piranga olivacea</i>	PAS	3.40	Mowbray 1999	1.05	Mowbray 1999	25.00	Mowbray 1999	16.5	Dewey and Street 1999	12	Mowbray 1999
16	<i>Melospiza melodia</i>	PAS	12.00	Arcese et al 2002	0.29	Knapton and Krebs 1974	19.10	Arcese et al 2002	14.5	Gomez 2000	12	Arcese et al 2002
16	<i>Melospiza georgiana</i>	PAS	3.80	Mowbray 1997	0.17	Mowbray 1997	17.00	Mowbray 1997	n/a		12	Mowbray 1997
16	<i>Catharus fuscescens</i>	PAS	4.00	Bevier et al 2005	0.25	Bevier et al 2005	41.50	Bevier et al 2005	17.0	Bevier et al 2005	12	Bevier et al 2005
16	<i>Vireo gilvus</i>	PAS	3.50	Gardali and Ballard 2000	1.35	Gardali and Ballard 2000	13.50	Gardali and Ballard 2000	n/a		12	Gardali and Ballard 2000

16	<i>Hylocichla mustelina</i>	PAS	8.00	Evans et al 2011	2.40	Evans et al 2011	45.00	Lesperance and Kirschbaum 2002	20.0	Lesperance and Kirschbaum 2002	12	Evans et al 2011
16	<i>Zonotrichia albicollis</i>	PAS	4.00	Falls and Kopachena 2010	0.99	Falls and Kopachena 2010	25.90	Falls and Kopachena 2010	17.0	Galanti 2002	12	Falls and Kopachena 2010
16	<i>Dendroica coronata</i>	PAS	8.00	Hunt and Flaspohler 1998	0.45	Hunt and Flaspohler 1998	12.60	Hunt and Flaspohler 1998	n/a		n/a	
16	<i>Dendroica petechia</i>	PAS	4.50	Lowther et al 1999	0.50	Lowther et al 1999	10.20	Lowther et al 1999	14.0	Bachynski and Kadlec 2003	12	Lowther et al 1999

*Study: 1=Forman et al (2002); 2=Kuitunen et al (2003); 3=Peris and Pescador (2004); 4=Pocock and Lawrence (2005); 5=van der Zande et al (1980); 6=Kuhn-Hines (2008); 7=Bassett-Touchell (2008); 8=Carrascal et al (2008); 9=Dallimer and King (2008); 10=Palomino and Carrascale (2007); 11=Zabala et al (2006); 12=Morgado et al (2010); 13=Strickler (2008); 14=Dietz (2006); 15=Ortega and Capen (1999); 16=Summers (2009).

Table I2. Life history traits collected for mammal species used in meta-analysis. Traits were collected as follows: reproductive rate = mean number of offspring per litter multiplied by the maximum number of litters per year; species mobility= home range area; body mass = average body mass of the two sexes; body length= average total body length of the two sexes; age at sexual maturity =mean age at sexual maturity of the two sexes in months. Order: ROD= Rodentia; ART=Artiodactyla; CAR= Carnivora; DID= Didelphimorphia; DIP= Diprotodontia; ERI= Erinaceomorpha; LAG= Lagomorpha; PHO= Pholidota; PRI= Primates; PRO= Proboscidae; SOR= Soricomorpha; HYR=Hyracoidea. Reprinted with permission from © 2012 Elsevier.

Study*	Species name	Order	Reproductive Rate	Source	Mobility (ha)	Source	Mass (g)	Source	Length (cm)	Source	Maturity (mm)	Source
1	<i>Microtus californicus</i>	ROD	22.5	Peronne 2002	0.010	Peronne 2002	73.0	Peronne 2002	18.0	Peronne 2002	1	Peronne 2002
1	<i>Microtus californicus</i>	ROD	22.5	Peronne 2002	0.010	Peronne 2002	73.0	Peronne 2002	18.0	Peronne 2002	1	Peronne 2002
1	<i>Peromyscus maniculatus</i>	ROD	20.0	Bunker 2001	0.160	Bunker 2001	17.0	Bunker 2001	17.1	Bunker 2001	1	Bunker 2001
1	<i>Peromyscus maniculatus</i>	ROD	20.0	Bunker 2001	0.160	Bunker 2001	17.0	Bunker 2001	17.1	Bunker 2001	1	Bunker 2001
1	<i>Peromyscus maniculatus</i>	ROD	20.0	Bunker 2001	0.160	Bunker 2001	17.0	Bunker 2001	17.1	Bunker 2001	1	Bunker 2001
1	<i>Peromyscus maniculatus</i>	ROD	20.0	Bunker 2001	0.160	Bunker 2001	17.0	Bunker 2001	17.1	Bunker 2001	1	Bunker 2001
1	<i>Peromyscus maniculatus</i>	ROD	20.0	Bunker 2001	0.160	Bunker 2001	17.0	Bunker 2001	17.1	Bunker 2001	1	Bunker 2001
1	<i>Peromyscus maniculatus</i>	ROD	20.0	Bunker 2001	0.160	Bunker 2001	17.0	Bunker 2001	17.1	Bunker 2001	1	Bunker 2001
1	<i>Ochrotomys nuttalli</i>	ROD	31.8	Linzey and Packard 1977/ Riseman 1999	0.105	Linzey and Packard 1977/ Riseman 1999	22.5	Riseman 1999	15.4	Linzey and Packard 1977	1	Linzey and Packard 1977

1	<i>Ochrotomys nuttalli</i>	ROD	31.8	Linzey and Packard 1977/ Riseman 1999	0.105	Linzey and Packard 1977/ Riseman 1999	22.5	Riseman 1999	15.4	Linzey and Packard 1977	1	Linzey and Packard 1977
1	<i>Peromyscus leucopus</i>	ROD	14.8	Lackey et al 1985	0.100	Lackey et al 1985	23.0	Aguilar 2002	17.0	Lackey et al 1985	1	Aguilar 2002
1	<i>Peromyscus leucopus</i>	ROD	14.8	Lackey et al 1985	0.100	Lackey et al 1985	23.0	Aguilar 2002	17.0	Lackey et al 1985	1	Aguilar 2002
1	<i>Microtus ochrogaster</i>	ROD	17.5	Stalling 1990	0.010	Jike et al 1988	42.5	Stalling 1990	15.1	Stalling 1990	1	Stalling 1990
1	<i>Microtus ochrogaster</i>	ROD	17.5	Stalling 1990	0.010	Jike et al 1988	42.5	Stalling 1990	15.1	Stalling 1990	1	Stalling 1990
1	<i>Reithrodontomys humulis</i>	ROD	14.8	Stalling 1997	0.095	Stalling 1997	8.2	Stalling 1997	11.8	Stalling 1997	1	Stalling 1997
1	<i>Reithrodontomys humulis</i>	ROD	14.8	Stalling 1997	0.095	Stalling 1997	8.2	Stalling 1997	11.8	Stalling 1997	1	Stalling 1997
1	<i>Microtus pennsylvanicus</i>	ROD	60.0	Reich 1981/ Neuburger 1999	0.120	Blair 1940c	24.1	Reich 1981	16.8	Reich 1981	1	Neuburger 1999
1	<i>Microtus pennsylvanicus</i>	ROD	60.0	Reich 1981/ Neuburger 1999	0.120	Blair 1940c	24.1	Reich 1981	16.8	Reich 1981	1	Neuburger 1999
1	<i>Sorex vagrans</i>	SOR	19.5	Foresman and Long 1998/ Hawes 1977	0.220	Hawes 1977	6.0		10.0		5	Foresman and Long 1998
1	<i>Sorex vagrans</i>	SOR	19.5	Foresman and Long 1998/ Hawes 1977	0.220	Hawes 1977	6.0		10.0		5	Foresman and Long 1998
2	<i>Loxodonta africana</i>	PRO	0.3	Norwood 2002	7560.000	Blake et al 2008; (mean value for Loango)	2500000.0	Estes 1991	223.0	Norwood 2002	126	Laursen and Bekoff 1978
3	<i>Puma concolor</i>	CAR	2.4	Currier 1983	40950.000	Dickson and Beier 2002	50000.0	Currier 1983	215.0	Currier 1983	33	Currier 1983/ Dewey and Shivaraju 2003
4	<i>Rangifer tarandus caribou</i>	ART	1.0	in Dyer 1999	16536.000	Dyer 1999	186500.0	Shefferly and Joly 2000	265.0	Shefferly and Joly 2000	26.5	in Dyer 1999/ Shefferly and Joly 2000

5	<i>Erinaceus europaeus</i>	ERI	10.0	Lundrigan and Bidlingmeyer 2000	16.300	Doncaster et al 2001	880.0	Doncaster et al 2001	20.0	Lundrigan and Bidlingmeyer 2000	8	Lundrigan and Bidlingmeyer 2000
6	<i>Canis lupus</i>	CAR	6.3	Jędrzejewski et al (1996)	20 100	Jędrzejewski et al (2007)	51500.0	Dewey and Smith 2002	108.0	Dewey and Smith 2002	30	Dewey and Smith 2002
6	<i>Canis lupus</i>	CAR	6.3	Jędrzejewski et al (1996)	20 100	Jędrzejewski et al (2007)	51500.0	Dewey and Smith 2002	108.0	Dewey and Smith 2002	30	Dewey and Smith 2002
7	<i>Cynomys ludovicianus</i>	ROD	3.0	Hoogland 1996	0.330	Hoogland 1996	1070.0	Hoogland 1996	21.1	Hoogland 1996	21	Hoogland 1996
8	<i>Alces alces</i>	ART	1.0	Franzmann (1981)	26200.000	Demarchi (2003)	411075.0	Harestad and Bunnell (1979)	270.0	De Bord et al 2009	20	De Bord et al 2009
8	<i>Alces alces</i>	ART	1.0	Franzmann (1981)	26200.000	Demarchi (2003)	411075.0	Harestad and Bunnell (1979)	270.0	De Bord et al 2009	20	De Bord et al 2009
9	<i>Lynx rufus</i>	CAR	3.2	Larivière and Walton 1998	4445.000	Lovallo and Anderson 1996	8200.0	Larivière and Walton 1997	83.0	Larivière and Walton 1997	24	Larivière and Walton 1997/ Ciszek 2002
9	<i>Lynx rufus</i>	CAR	3.2	Larivière and Walton 1998	4445.000	Lovallo and Anderson 1997	8200.0	Larivière and Walton 1998	83.0	Larivière and Walton 1997	24	Larivière and Walton 1997/ Ciszek 2002
9	<i>Lynx rufus</i>	CAR	3.2	Larivière and Walton 1998	4445.000	Lovallo and Anderson 1998	8200.0	Larivière and Walton 1999	83.0	Larivière and Walton 1997	24	Larivière and Walton 1997/ Ciszek 2002
10	<i>Ursus arctos horribilis</i>	CAR	1.0	Pasitschniak-Arts 1993	31634.000	Mace et al 1996	164000.0	Pasitschniak-Arts 1993	157.7	Pasitschniak-Arts 1993	60	Pasitschniak-Arts 1993/ Dewey and Ballenger 2002
11	<i>Phascolarctos cinereus</i>	DIP	1.0	Dubuc and Eckroad 1999	24.700	White 1999	13800.0	Dubuc and Eckroad 1999	75.0	Dubuc and Eckroad 1999	24	Dubuc and Eckroad 1999
12	<i>Tamias striatus</i>	ROD	8.0	Smith and Smith 1972	0.100	Yerger 1953	102.5	Eder 2002	26.5	Eder 2002	12	Snyder 1982
12	<i>Peromyscus leucopus</i>	ROD	10.0	Eder 2002	0.600	Smith and Speller 1970	20.0	Eder 2002	17.5	Eder 2002	1	Aguilar 2002
13	<i>Canis lupus lycaon</i>	CAR	4.6	Mills et al 2008	15300.000	Mladenoff et al 1995	28450.0	Mech and Paul 2008	n/a		n/a	

14	<i>Lynx lynx</i>	CAR	2.5	Tumilson 1987	14690.000	Jędrzejewski et al 1996	18450.0	Jędrzejewski et al 1996	123.0	Foster and Croft 2010	22	Tumilson 1987
14	<i>Lynx lynx</i>	CAR	2.5	Tumilson 1987	14690.000	Jędrzejewski et al 1996	18450.0	Jędrzejewski et al 1996	123.0	Foster and Croft 2010	22	Tumilson 1987
15	<i>Lynx pardinus</i>	CAR	3.0	López-Bao et al 2010	1520.000	López-Bao et al 2010	11000.0	Johnson 2011	n/a		12	Johnson 2011
16	<i>Meles meles</i>	CAR	3.5	Ciszek 1999	100.000	Ciszek 1999	13000.0	Ciszek 1999	73.0	Ciszek 1999	14	Ciszek 1999
16	<i>Vulpes vulpes</i>	CAR	4.5	Larivière and Pasitschniak-Arts 1996	575.000	Larivière and Pasitschniak-Arts 1996	6050.0	Larivière and Pasitschniak-Arts 1996	104.3	Larivière and Pasitschniak-Arts 1996	10	Fox 2007/ Larivière and Pasitschniak-Arts 1996
16	<i>Capreolus capreolus</i>	ART	2.0	Sempéré et al 1996	26.300	Vanpé et al 2009	27000.0	Sempéré et al 1996	117.0	Sempéré et al 1996	13	Sempéré et al 1996
16	<i>Sus scrofa</i>	ART	5.8	Gethöffer and Sodeikat 2007/ Dewey and Hruby 2002	500.000	Keuling et al 2009	200000.0	Dewey and Hruby 2002	135.0	Dewey and Hruby 2002	9	Dewey and Hruby 2002
17	<i>Lepus europaeus</i>	LAG	13.0	Flux and Angermann 1990	330.000	Flux and Angermann 1990	3800.0	Flux and Angermann 1990	68.0	Vu 2001	8	Vu 2001
18	<i>Dipodomys microps</i>	ROD	4.8	Hayssen 1991	0.490	Hayssen 1991	53.2	Hayssen 1991	27.1	Hayssen 1991	7	Hayssen 1991
18	<i>Peromyscus maniculatus</i>	ROD	20.0	Bunker 2001	0.200	Wood et al 2010	17.0	Bunker 2001	17.1	Bunker 2001	1	Bunker 2001
18	<i>Perognathus parvus</i>	ROD	16.5	Verts and Kirkland 1988	1.720	Verts and Kirkland 1988	22.9	Verts and Kirkland 1988	17.3	Verts and Kirkland 1988	2	Luu 1999
18	<i>Tamias minimus</i>	ROD	5.9	Verts and Carraway 2001	0.640	Verts and Carraway 2001	41.0	Verts and Carraway 2001	18.8	Verts and Carraway 2001	10	Schlimme 2000
19	<i>Cervus canadensis</i>	ART	1.0	Senseman 2002	7968.000	Walsh 2007	211000.0	Cook et al 2003	215.0	Senseman 2002	16	Senseman 2002
19	<i>Cervus canadensis</i>	ART	1.0	Senseman 2002	7968.000	Walsh 2007	211000.0	Cook et al 2003	215.0	Senseman 2002	16	Senseman 2002

19	<i>Odocoileus hemionus</i>	ART	2.0	Anderson and Wallmo 1984	285.270	Harestad and Bunnell 1979	96500.0	Anderson and Wallmo 1984	143.0	Misuraca 1999	16	Misuraca 1999
19	<i>Odocoileus hemionus</i>	ART	2.0	Anderson and Wallmo 1985	286.270	Harestad and Bunnell 1980	96500.0	Anderson and Wallmo 1985	143.0	Misuraca 1999	16	Misuraca 1999
20	<i>Peromyscus leucopus</i>	ROD	10.0	Eder 2002	0.600	Smith and Speller 1970	20.0	Eder 2002	17.5	Eder 2002	1	Aguilar 2002
21	<i>Puma concolor</i>	CAR	2.4	Currier 1984	40950.000	Dickson and Beier 2002	50001.0	Currier 1984	216.0	Currier 1984	33	Currier 1983/ Dewey and Shivaraju 2003
21	<i>Puma concolor</i>	CAR	2.4	Currier 1985	40950.000	Dickson and Beier 2002	50002.0	Currier 1985	217.0	Currier 1985	33	Currier 1983/ Dewey and Shivaraju 2003
22	<i>Mus musculus</i>	ROD	49.0	King et al 1996/Ballenger 1999a	n/a		16.0	King et al 1996	21.3	Ballenger 1999a	1.5	Ballenger 1999a/ King et al 1996
22	<i>Rattus rattus</i>	ROD	40.0	Gillespie and Myers 2004	0.010	Gillespie and Myers 2004	200.0	Gillespie and Myers 2004	19.0	Gillespie and Myers 2004	4	Gillespie and Myers 2004
23	<i>Lynx rufus</i>	CAR	3.1	Larivière and Walton 1998	1560.000	Larivière and Walton 1998	8200.0	Larivière and Walton 2000	83.0	Larivière and Walton 1997	24	Larivière and Walton 1997/ Ciszek 2002
24	<i>Cervus elaphus nelsoni</i>	ART	1.0	Senseman 2002	24500.000	Witt 2008	238136.0	Witt 2008	246.0	Witt 2008	16	Senseman 2002
25	<i>Rangifer tarandus caribou</i>	ART	1.0	in Dyer 1999	80300.000	Faille et al 2010	186500.0	Shefferly and Joly 2000	265.0	Shefferly and Joly 2000	26.5	in Dyer 1999/ Shefferly and Joly 2002
26	<i>Melursus ursinus</i>	CAR	1.0	Garshelis et al 1999	300.000	Ratnayake et al 2007b	93750.0	Garshelis et al 1999	170.0	Bies 2002	48	Garshelis et al 1999
27	<i>Rangifer tarandus caribou</i>	ART	1.0	in Dyer 1999	402600.000	Brown 2005	186500.0	Shefferly and Joly 2000	265.0	Shefferly and Joly 2000	26.5	in Dyer 1999/ Shefferly and Joly 2000
27	<i>Gulo gulo</i>	CAR	2.5	Eder 2002	40500.000	Pasitschniak-Arts and Larivière 1995	12700.0	Pasitschniak-Arts and Larivière 1995	95.0	Pasitschniak-Arts and Larivière 1995	25	Pasitschniak-Arts and Larivière 1995

27	<i>Canis lupus</i>	CAR	5.0	Pimlott and Carbyn 1993	13900.000	Forshner et al 2003	31700.0	Forshner et al 2003	108.0	Dewey and Smith 2002	30	Dewey and Smith 2002
27	<i>Alces alces</i>	ART	1.0	Franzmann (1981)	4 770	Cobb 2004	411075.0	Harestad and Bunnell (1979)	270.0	De Bord et al 2009	20	De Bord et al 2009
27	<i>Odocoileus virginianus</i>	ART	2.0	Dewey et al 2003	190.000	Dechen Quinn 2010	112500.0	Smith 1991	172.0	Smith 1991	12.25	Smith 1991
28	<i>Zapus hudsonius</i>	ROD	11.0	Eder 2002	0.400	Blair 1940a	20.0	Eder 2002	20.5	Eder 2002	2	Smith 1999
28	<i>Napaeozapus insignis</i>	ROD	4.5	Eder 2002	1.100	Blair 1941	21.5	Eder 2002	14.0	Eder 2002	9.5	Harrington and Myers 2004
28	<i>Blarina brevicauda</i>	SOR	12.0	Blair 1940b	0.400	Blair (1941)	21.5	Eder 2002	9.0	Ballenger 2000	2	Ballenger 2000
28	<i>Clethrionomys gapperi</i>	ROD	10.0	Eder (2002)/ Ballenger 1999b	0.300	Blair (1941)	27.5	Eder 2002	14.0	Eder 2002	2.5	Eder 2002
28	<i>Mustela erminea</i>	CAR	8.0	King 1983	13.100	Simms 1979	75.0	Eder 2002	27.5	Eder 2002	6.75	Eder 2002
28	<i>Tamias striatus</i>	ROD	8.0	Smith and Smith 1972	0.100	Yerger 1953	102.5	Eder 2002	26.5	Eder 2002	12	Snyder 1982
28	<i>Tamiasciurus hudsonicus</i>	ROD	4.5	Eder 2002	2.200	Layne 1954	195.0	Eder 2002	31.5	Eder 2002	12	Eder 2002
28	<i>Sylvilagus floridanus</i>	LAG	22.5	Chapman et al. 1977	1.300	Trent and Rongstad 1974	1200.0	Eder 2002	42.5	Eder 2002	2.5	Mikita 1999
28	<i>Sciurus carolinensis</i>	ROD	4.5	Eder 2002	20.300	Bridges 2002	555.0	Eder 2002	46.5	Eder 2002	15	Lawniczak 2002
28	<i>Lepus americanus</i>	LAG	12.0	Eder 2002	5.900	O'Farrel 1965	1250.0	Eder 2002	45.5	Eder 2002	12	Shefferly 2007
28	<i>Mephitis mephitis</i>	CAR	6.0	Wade-Smith and Verts 1982	294.700	Storm 1972	3050.0	Eder 2002	67.5	Eder 2002	10	Wilke 2001
28	<i>Marmota monax</i>	ROD	4.5	Eder 2002	6.400	Ferron and Ouellett 1989	3600.0	Eder 2002	56.0	Eder 2002	12	Tobias and Myers 2011
28	<i>Martes pennanti</i>	CAR	2.5	Eder 2002	655.000	Koen et al 2007	3750.0	Eder 2002	100.0	Eder 2002	18	Eder 2002/ Rhines 2003

28	<i>Vulpes vulpes</i>	CAR	5.5	Eder 2002	900.000	Voigt and Macdonald 1984	5200.0	Eder 2002	100.0	Eder 2002	10	Fox 2007/ Larivière and Pasitschniak-Arts 1996
28	<i>Procyon lotor</i>	CAR	4.5	Eder 2002	391.000	Rosatte et al 2010	9500.0	Eder 2002	82.5	Eder 2002	17	Dewey and Fox 2001
28	<i>Ursus americanus</i>	CAR	1.5	Eder 2002	4020.000	Maxie 2009	155000.0	Eder 2002	160.0	Eder 2002	51	Dewey and Kronk 2007/ Larivière 2001
29	<i>Galago demidoff</i>	PRI	1.0	Sampson and Lundrigan 2004	1.300	Estes 1991	60.0	Estes 1991	12.0	Estes 1991	9	Sampson and Lundrigan 2004
29	<i>Galago alleni</i>	PRI	1.0	Dengel 2004	26.000	Estes 1991	250.0	Estes 1991	20.0	Dengel 2004	9	Dengel 2004
29	<i>Euoticus elegantulus</i>	PRI	2.0	Santilli 2002	n/a	Santilli 2002	315.0	Santilli 2002	52.5	Santilli 2002	n/a	Santilli 2002
29	<i>Perodicticus potto</i>	PRI	1.0	McCann and Rasmussen 2009/ Estes 1991	16.000	Estes 1991	1100.0	McCann and Rasmussen 2009	35.0	McCann and Rasmussen 2009	18	McCann and Rasmussen 2009
29	<i>Cephalophus monticola defriesi</i>	ART	1.0	Estes 1991	3.000	Estes 1991	4900.0	Estes 1991	64.0	Siciliano 2011	15	Estes 1991
29	<i>Cephalophus ogilbyi crusalbaum</i>	ART	n/a		n/a		19000.0	Fa et al 1995	112.4	Grubb 1978	20	Fa et al 1995
29	<i>Cephalophus silvicultor</i>	ART	2.0	DeWitt and Yahnke 2006	n/a		6800.0	Estes 1991	130.0	DeWitt and Yahnke 2006	15	DeWitt and Yahnke 2006
29	<i>Cephalophus dorsalis castaneus</i>	ART	n/a		48.000	in van Vliet et al 2010	21700.0	Estes 1991	n/a		11	in van Vliet et al 2010
29	<i>Cephalophus callipygus callipygus</i>	ART	n/a		12.000	Estes 1991	20100.0	Estes 1991	n/a		n/a	
29	<i>Hyemoschus aquaticus</i>	ART	1.0	Edwards 2000	19.300	Edwards 2000	10800.0	Estes 1991	65.0	Edwards 2000	13	Edwards 2000
29	<i>Zenkerella insignis</i>	ROD	1.5	Harvey and Lundrigan 2004	n/a	Harvey and Lundrigan 2004	200.0	Harvey and Lundrigan 2004	22.0	Harvey and Lundrigan 2004	n/a	Harvey and Lundrigan 2004

29	<i>Anomalurus beecrofti</i>	ROD	2.0	Merkel 2004	n/a		650.0	Merkel 2004	28.0	Merkel 2004	n/a	
29	<i>Anomalurus derbianus</i>	ROD	5.0	Normile 1999	3.300	Julliot et al 1998	720.0	Julliot et al 1998	35.0	Julliot et al 1998	n/a	
29	<i>Anomalurus pusillus</i>	ROD	n/a		n/a		170.0	Julliot et al 1998	20.0	Julliot et al 1998	n/a	
29	<i>Nandinia binotata</i>	CAR	4.0	Nocon 1999a	100.000	Estes 1991	2650.0	Estes 1991	49.0	Estes 1991	36.5	Nocon 1999a
29	<i>Civettictis civetta</i>	CAR	6.0	Estes 1991	1110.000	Admasu et al 2004	13500.0	Estes 1991	78.5	Estes 1991	7	Shalu 2000
29	<i>Poiana richardsonii</i>	CAR	5.0	Gillette and Arbogast 2005	n/a	Gillette and Arbogast 2005	600.0	Gillette and Arbogast 2005	73.0	Gillette and Arbogast 2005	n/a	
29	<i>Atilax paludinosus</i>	CAR	6.0	Estes 1991; Nocon 1999b	54.000	Ray 1997	3750.0	Estes 1991	63.0	Estes 1991	8.5	Nocon 1999b
29	<i>Genetta servalina</i>	CAR	5.0	Estes 1991	262.000	Estes 1991	n/a		n/a		n/a	
29	<i>Panthera pardus</i>	CAR	0.8	Estes 1991	5580.000	Jenny 1996	55000.0	Estes 1991	54.0	Estes 1991	36	Hunt and Myers 2011
29	<i>Atherurus africanus centralis</i>	ROD	2.0	Ellis 2000	13.400	Jori et al 1998	3000.0	Jori et al 1998	45.0	Jori et al 1998	n/a	
29	<i>Cricetomys gambianus</i>	ROD	3.0	Joo and Myers 2004	n/a	Joo and Myers 2004	1235.0	Joo and Myers 2004	77.8	Joo and Myers 2004	6	Joo and Myers 2004
29	<i>Dendrohyrax dorsalis</i>	HYR	1.0	In Jones 1978	n/a		3175.0	Jones 1978	52.5	Jones 1978	16	Lundrigan and Yurk 2000
29	<i>Phataginus tricuspis</i>	PHO	1.0	Andrews 2011	14.200	Andrews 2011	2300.0	Kingdon 1971	38.0	Kingdon 1971	n/a	
29	<i>Loxondonta africana cyclotis</i>	PRO	0.3	Connor and Franci 2009	7560.000	Blake et al 2008; (mean value for Loango)	2500000.0	Estes 1991	223.0	Connor and Franci 2009	126	Laursen and Bekoff 1978
29	<i>Potamochoerus porcus</i>	ART	3.0	Estes 1991	510.000	Estes 1991	70000.0	Estes 1991	67.5	Estes 1991	21	Estes 1991
30	<i>Odocoileus hemionus</i>	ART	2.0	Anderson and Wallmo 1986	287.270	Harestad and Bunnell 1981	96500.0	Anderson and Wallmo 1986	143.0	Misuraca 1999	16	Misuraca 1999

30	<i>Cervus elaphus</i>	ART	1.0	Senseman 2002	48000.000	Strohmeyer and Peck (1996)	154200.0	Senseman 2002	215.0	Senseman 2002	16	Senseman 2002
31	<i>Rangifer tarandus caribou</i>	ART	1.0	in Dyer 1999	50900.000	Metsaranta and Mallory 2007	186500.0	Shefferly and Joly 2000	265.0	Shefferly and Joly 2000	26.5	in Dyer 1999/ Shefferly and Joly 2000
32	<i>Mustela sibirica</i>	CAR	5.0	Kreutzer 2003	n/a		590.0	Kreutzer 2003	32.0	Kreutzer 2003	24	Kreutzer 2003
32	<i>Martes flavigula</i>	CAR	n/a		720.000	Grassman et al 2005	3000.0	Grassman et al 2005	n/a		n/a	
32	<i>Felis bengalensis</i>	CAR	2.0	Young 2002	1320.000	Grassman et al 2005	2605.0	Grassman et al 2005	56.0	Grassman et al 2005	8	Young 2002
32	<i>Sus scrofa</i>	ART	n/a		513.000	Choi et al 2006	200000.0	Dewey and Hruby 2002	135.0	Dewey and Hruby 2002	9	Dewey and Hruby 2002
32	<i>Hydropotes inermis</i>	ART	6.0	Katopodes 1999	n/a	n/a	12900.0	Katopodes 1999	89.0	Katopodes 1999	6.5	Katopodes 1999
32	<i>Capreolus capreolus</i>	ART	2.0	Sempéré et al 1996	n/a		27000.0	Sempéré et al 1996	117.0	Sempéré et al 1996	13	Sempéré et al 1996
32	<i>Lepus coreanus</i>	LAG	n/a		20.000	Flux and Angermann 1990	2350.0	Flux and Angermann 1990	n/a		n/a	
32	<i>Sciurus vulgaris</i>	ROD	10.0	Lurz et al 2005	47.000	in Lurz et al 2005	600.0	Seinfeld 1999	22.8	Lurz et al 2005	9.5	Lurz et al 2005
33	<i>Odocoileus virginianus</i>	ART	2.0	Dewey et al 2003	190.000	Dechen Quinn 2011	112500.0	Smith 1992	172.0	Smith 1991	12.25	Smith 1991
34	<i>Procyon lotor</i>	CAR	4.0	Dewey and Fox 2001	78.000	Beasley et al 2007	6350.0	Lotze and Anderson 1979	77.8	Dewey and Fox 2001	17	Dewey and Fox 2001
34	<i>Procyon lotor</i>	CAR	4.0	Dewey and Fox 2001	78.000	Beasley et al 2007	6350.0	Lotze and Anderson 1979	77.8	Dewey and Fox 2001	17	Dewey and Fox 2001
34	<i>Procyon lotor</i>	CAR	4.0	Dewey and Fox 2001	78.000	Beasley et al 2007	6350.0	Lotze and Anderson 1979	77.8	Dewey and Fox 2001	17	Dewey and Fox 2001
34	<i>Didelphis virginiana</i>	DID	20.4	Lay 1942/McManus 1974	4.650	Lay 1942	3350.0	Newell and Berg 2003	74.0	Newell and Berg 2003	9	Newell and Berg 2003/ McManus 1974

34	<i>Didelphis virginiana</i>	DID	20.4	Lay 1942/ McManus 1974	4.650	Lay 1942	3350.0	Newell and Berg 2003	74.0	Newell and Berg 2003	9	Newell and Berg 2003/ McManus 1974
34	<i>Didelphis virginiana</i>	DID	20.4	Lay 1942/ McManus 1974	4.650	Lay 1942	3350.0	Newell and Berg 2003	74.0	Newell and Berg 2003	9	Newell and Berg 2003/ McManus 1974

*Study: 1=Adam and Geis (1983); 2=Barnes et al (1991); 3=Dickson and Beier (2002); 4=Dyer et al (2001); 5=Huigser and Bergers (2000); 6=Jędrzejewski et al (2004); 7=Johnson and Collinge (2004); 8=Kunkel and Pletscher (2000); 9=Lovallo and Anderson (1996); 10=Mace et al (1996); 11=McApline et al (2006); 12=McGregor et al (2008); 13=Mladenoff et al (1995); 14=Niedziałkowska et al (2006); 15=Palma et al (1999); 16=Roedenbeck and Köhler (2006); 17=Roedenbeck and Voser (2008); 18=Bissonette and Rosa (2009); 19=Rost and Bailey (1979); 20=Rytwinski and Fahrig (2007); 21=van Dyke et al (1986); 22=King et al (1996); 23=Kelly and Holub (2008); 24=Dodd et al (2007); 25=Fortin et al (2008); 26=Ratnayake et al (2007); 27=Bowman et al (2010); 28=Rytwinski and Fahrig (2011); 29=Laurance et al (2008); 30=Stewart et al (2010); 31=Schindler et al (2007); 32=Rhim and Lee (2007); 33=Munro (2009); 34=Disney (2005).

Table I3. Life history traits collected for amphibian species used in meta-analysis. Traits were collected as follows: reproductive rate = mean number of eggs per clutch multiplied by the maximum number of clutches per year; species mobility= home range area/ seasonal migration distance; body mass = average body mass of the two sexes; body length= average total body length of the two sexes; age at sexual maturity =mean age at sexual maturity of the two sexes in months. Reprinted with permission from © 2012 Elsevier.

Study*	Species name	Order	Reproductive Rate	Source	Mobility (ha)	Source	Mass (g)	Source	Length (cm)	Source	Maturity (mm)	Source
1	<i>Rana clamitans</i>	Anura	3750	Hecnar and M'Closkey 1997	1.4700	Oldham 1967	n/a		8.50	Fisher et al 2007	48	Fisher et al 2007
1	<i>Rana pipiens</i>	Anura	4000	Hecnar and M'Closkey 1997	78.0000	COSEWIC 2009	29.00	Dewey 1999	7.50	COSEWIC 2009	24	Fisher et al 2007
2	<i>Rana pipiens</i>	Anura	4000	Hecnar and M'Closkey 1997	78.0000	COSEWIC 2009	29.00	Dewey 1999	7.50	COSEWIC 2009	24	Fisher et al 2007
2	<i>Rana clamitans</i>	Anura	3750	Hecnar and M'Closkey 1997	1.4700	Oldham 1967	n/a		8.50	Fisher et al 2007	48	Fisher et al 2007
2	<i>Rana catesbeiana</i>	Anura	8000	Fisher et al 2007	12.6000	Casper and Hendricks 2011	n/a		15.70	Lu and Sopory 2000	48	Bruening 2002
2	<i>Rana septentrionalis</i>	Anura	2000	Casper 2011b	n/a		n/a		6.50	Fisher et al 2007	54	Casper 2011b
2	<i>Rana sylvatica</i>	Anura	650	Berven 2009	2.2400	Baldwin et al 2006	7.88	Kiehl 2011	6.50	Fisher et al 2007	27	Fisher et al 2007/ Redmer and Trauth 2011
2	<i>Bufo americanus</i>	Anura	6000	Hecnar and M'Closkey 1997	0.3800	Oldham 1966	21.77	Grossman 2002	8.50	Fisher et al 2007	33	Green 2011
2	<i>Hyla versicolor</i>	Anura	1800	Fisher et al 2007/Cline 2011	9.6900	Johnson et al 2007	7.17	Mueller and Harding 2006	4.60	Cline 2011	24	Cline 2011

2	<i>Pseudacris crucifer</i>	Anura	900	Fisher et al 2007	1.2300	Werner et al 2009/Delzell 1958	4.00	Largett et al 1999	2.25	Butterfield et al 2011	22	Delzell 1958
2	<i>Pseudacris triseriata</i>	Anura	1000	Chantasirivisal 2005	0.7850	Kramer 1973	n/a		3.00	Chantasirivisal 2005	n/a	
2	<i>Notophthalmus viridescens</i>	Caudata	300	Fisher et al 2007	0.0450	Healy 1975	n/a		10.25	Hunsinger and Lannoo 2011	42	Hunsinger and Lannoo 2011
2	<i>Ambystoma maculatum</i>	Caudata	250	Fisher et al 2007	3.1400	Houlahan and Findlay 2003	12.84	Pajerski et al 2007	20.00	Fisher et al 2007	43.5	Fisher et al 2007
2	<i>Ambystoma laterale</i>	Caudata	200	Fisher et al 2007	7.1000	Houlahan and Findlay 2003	n/a		10.00	Fisher et al 2007	24	Donato 2000
2	<i>Plethodon cinereus</i>	Caudata	9	Searcy 2003	0.0001	Searcy 2003	n/a		7.60	Searcy 2003	24	Casper 2011a
3	<i>Pelobates fuscus</i>	Anura	1762	Hels 2002	4.9000	Hels 2002	n/a		8.00	Hels 2002	36	Hels and Nachman 2002
4	<i>Hyla arborea</i>	Anura	1100	Kuzmin 2011a	11.9000	Carlson and Edenhamn 2000	6.00	Pellet et al 2006	5.00	Pellet et al 2004a	24	Friedl and Klump 1997
4	<i>Hyla arborea</i>	Anura	1100	Kuzmin 2011a	11.9000	Pellet et al 2006	6.00	Pellet et al 2006	5.00	Pellet et al 2004a	24	Friedl and Klump 1997
5	<i>Hyla arborea</i>	Anura	1100	Kuzmin 2011a	11.9000	Pellet et al 2006	6.00	Pellet et al 2006	5.00	Pellet et al 2004a	24	Friedl and Klump 1997
6	<i>Ambystoma tigrinum tigrinum</i>	Caudata	421	Lannoo 2011	3.3500	Semlitsch 1998	9.40	Wentz 2001	20.00	Fisher et al 2007	48	Wentz 2001
7	<i>Plethodon metcalfi</i>	Caudata	n/a		0.0003	Beamer and Lannoo 2011	4.50	Ash et al 2003	6.50	Ash et al 2003	57	Ash et al 2003
8	<i>Ambystoma maculatum</i>	Caudata	250	Fisher et al 2007	4.3000	Semlitsch 1998	12.84	Pajerski et al 2007	20.00	Fisher et al 2007	43.5	Fisher et al 2007
8	<i>Rana sylvatica</i>	Anura	650	Berven 2009	2.2400	Baldwin et al 2006	7.88	Kiehl 2011	6.50	Fisher et al 2007	27	Fisher et al 2007/Redmer and Trauth 2011
9	<i>Rana arvalis</i>	Anura	900	Räsänen et al 2008	n/a		n/a		4.60	Babik and Rafiński 2000	30	Räsänen et al 2008

10	<i>Desmognathus monticola</i>	Caudata	27	Camp and Tilley	0.1450	Kleeberger 1985	n/a		7.25	Camp and Tilley	66	Camp and Tilley
10	<i>Desmognathus ochrophaeus</i>	Caudata	19	Pauley and Watson 2011	0.000 015	Huheey and Brandon 1973	n/a		7.15	Pauley and Watson 2011	36	Pauley and Watson 2011
10	<i>Eurycea bislineata</i>	Caudata	30	Sever 2011	0.013 2	Ashton and Ashton 1978	n/a		9.00	Sever 2011	36	Sever 2011
11	<i>Plethodon cinereus</i>	Caudata	9	Searcy 2003	0.000 1	Searcy 2003	n/a		7.60	Searcy 2003	24	Casper 2011a
12	<i>Ambystoma maculatum</i>	Caudata	250	Fisher et al 2007	4.3000	Semlitsch 1998	12.84	Pajerski et al 2007	20.00	Fisher et al 2007	43.5	Fisher et al 2007
12	<i>Rana sylvatica</i>	Anura	650	Berven 2009	2.2400	Baldwin et al 2006	7.88	Kiehl 2011	6.50	Fisher et al 2007	27	Fisher et al 2007/ Redmer and Trauth 2011
13	<i>Rana catesbeiana</i>	Anura	8000	Fisher et al 2007	12.6000	Casper and Hendricks 2011	n/a		15.70	Lu and Sopory 2000	48	Bruening 2002
13	<i>Rana septentrionalis</i>	Anura	2000	Casper 2011b	n/a		n/a		6.50	Fisher et al 2007	54	Casper 2011b
14	<i>Austrochaperina pluvialis</i>	Anura	n/a		n/a		1.21	Williams 2007	2.35	Williams 2007	n/a	
14	<i>Litoria serrata</i>	Anura	n/a		n/a		n/a		4.55	Richards et al 2010	n/a	
15	<i>Notophthalmus viridescens</i>	Caudata	280	Hunsinger and Lannoo 2011	0.0450	Healy 1975	n/a		10.25	Hunsinger and Lannoo 2011	30	Hunsinger and Lannoo 2011
15	<i>Notophthalmus viridescens</i>	Caudata	280	Hunsinger and Lannoo 2011	0.0450	Healy 1975	n/a		10.25	Hunsinger and Lannoo 2011	30	Hunsinger and Lannoo 2011
16	<i>Bufo americanus</i>	Anura	6000	Hecnar and M'Closkey 1997	0.3800	Oldham 1966	21.77	Grossman 2002	8.50	Fisher et al 2007	33	Green 2011
16	<i>Hyla versicolor</i>	Anura	1800	Fisher et al 2007/Cline 2011	9.6900	Johnson et al 2007	7.17	Mueller and Harding 2006	4.60	Cline 2011	24	Cline 2011
16	<i>Rana clamitans</i>	Anura	3750	Hecnar and M'Closkey 1997	1.4700	Oldham 1967	n/a		8.50	Fisher et al 2007	48	Fisher et al 2007

16	<i>Rana pipiens</i>	Anura	4000	Hecnar and M'Closkey 1997	78.0000	COSEWIC 2009	29.00	Dewey 1999	7.50	COSEWIC 2009	24	Fisher et al 2007
16	<i>Pseudacris crucifer</i>	Anura	900	Fisher et al 2007	1.2300	Werner et al 2009/Delzell 1958	4.00	Largett et al 1999	2.25	Butterfield et al 2011	22	Delzell 1958
16	<i>Rana sylvatica</i>	Anura	650	Berven 2009	2.2400	Baldwin et al 2006	7.88	Kiehl 2011	6.50	Fisher et al 2007	27	Fisher et al 2007/ Redmer and Trauth 2011

*Study: 1=Carr and Fahrig (2001); 2=Houlahan and Findlay (2003); 3=Nyström et al (2007); 4=Pellet et al (2004a); 5=Pellet et al (2004b); 6=Porej et al (2004); 7=Semlitsch et al (2007); 8=Skidds et al (2007); 9=Vos and Chardon (1998); 10=Ward et al (2008); 11=Marsh (2007); 12=Karraker et al (2008); 13=Jacobs (2008); 14=Hoskin and Goosem (2010); 15=Rinehart et al (2009); 16=Eigenbrod et al (2008).

Table I4. Life history traits collected for reptile species used in meta-analysis. Traits were collected as follows: reproductive rate = mean number of eggs per clutch multiplied by the maximum number of clutches per year; species mobility= home range area/ seasonal migration distance; body mass = average body mass of the two sexes; body length= average total body length of the two sexes; age at sexual maturity =mean age at sexual maturity of the two sexes in months. Order: TES= Testudine; SQU= Squamata.

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Study*	Species name	Order	Reproductive Rate	Source	Mobility (ha)	Source	Mass (g)	Source	Length (cm)	Source	Maturity (mm)	Source
1	<i>Gopherus agassizii</i>	TES	12.5	Wallis et al 1999/ Turner et al 1986	31.85	Harless 2009	2597	Wallis et al 1999	23.5	Wallis et al 1999	224	Curtin et al 2009
2	<i>Chrysemys picta bellii</i>	TES	21.5	Rowe 1994	1.20	Rowe 2003	n/a		25.0	MacCulloch 2002	135	COSEWIC 2006
3	<i>Crotalus adamanteus</i>	SQU	4.7	Kain 1995	25.54	Hoss et al 2010	1295.2	Steen et al 2007	110.6	Steen et al 2007	n/a	
3	<i>Crotalus horridus</i>	SQU	2.7	Schantz 2009	39.60	Waldron et al 2006	1100.7	Steen et al 2007	110.2	Steen et al 2007	81	Schantz 2009/ Aldridge and Brown 1995
4	<i>Microlophus albemarlensis</i>	SQU	8.0	Chow 2004	0.02	Stone and Baird 2002	24.3	Jordan et al 2005	9.7	Jordan et al 2005	22.5	Chow 2004
5	<i>Chrysemys picta marginata</i>	TES	12.4	Rowe et al 2003/ Fisher et al 2007	1.20	Rowe 2003	500	Brooks et al 2003	15.0	MacCulloch 2002	129	Fisher et al 2007
6	<i>Clemmys guttata</i>	TES	5.0	COSEWIC 2004	2.72	COSEWIC 2004	n/a		12.0	MacCulloch 2002	156	COSEWIC 2004
6	<i>Sistrurus catenatus catenatus</i>	SQU	6.5	COSEWIC 2002a	25.00	Weatherhead and Prior 1992	265	Jellen et al 2007	76.0	COSEWIC 2002a	47	COSEWIC 2002a
6	<i>Glyptemys insculpta</i>	TES	9.0	COSEWIC 2007/ Smith 2002	31.78	Smith 2002	1301.2	Smith 2002	22.0	MacCulloch 2002	198	COSEWIC 2007
6	<i>Heterodon platirhinos</i>	SQU	20.0	Fisher et al 2007	50.20	Plummer and Mills 2000	455.2	Lagory et al 2009	69.1	Lagory et al 2009	24	Fisher et al 2007

7	<i>Chrysemys picta bellii</i>	TES	21.5	Rowe 1994	1.20	Rowe 2003	n/a		25.0	MacCulloch 2002	135	COSEWIC 2006
8	<i>Crotalus horridus</i>	SQU	2.7	Schantz 2009	124.50	Reinert and Zappalorti 1988	1100.7	Steen et al 2007	110.2	Steen et al 2007	81	Schantz 2009/ Aldridge and Brown 1995
8	<i>Crotalus horridus</i>	SQU	2.7	Schantz 2009	124.50	Reinert and Zappalorti 1988	1100.7	Steen et al 2007	110.2	Steen et al 2007	81	Schantz 2009/ Aldridge and Brown 1995
9	<i>Chrysemys picta</i>	TES	12.4	Rowe et al 2003/ Fisher et al 2007	1.20	Rowe 2003	500	Brooks et al 2003	15.0	MacCulloch 2002	129	Fisher et al 2007
9	<i>Sternotherus odoratus</i>	TES	4.7	COSEWIC 2002b	102.10	Edmonds 1998	173.5	Edmonds 1998	10.0	Edmonds 1998	84	COSEWIC 2002b
9	<i>Chelydra serpentina</i>	TES	37.5	Fisher et al 2007	5.68	Pettit et al 1995	7300	COSEWIC 2008	32.3	Fisher et al 2007	210	COSEWIC 2008

*Study: 1=Boarman and Sazaki (2006); 2=Fowle (1996); 3=Steen et al (2007); 4=Tanner and Perry (2007); 5=Attum et al (2008); 6=Crowley(2006); 7=Griffin (2007); 8=Schantz (2009); 9=Rinehart et al (2009).

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Appendix J. Univariate meta-analytical regression model testing the effects of life history traits on species responses to roads and/or traffic at the population-level within various subgroups of data.

Table J1. Mean Fisher's z-transformed effect sizes (ES_{Zr}) and back-transformed effect-sizes (ES_r) with statistical significance of moderators, for the subset of effect sizes using distance based study designs (see Table 2.1 categories 4 & 5) for bird species, to determine whether the effect of mobility on species responses to roads and/or traffic at the population-level remained significant after controlling for study-level moderators. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_{Zr}	ES_r	CI (lb)	CI (ub)	$p (ES_{Zr})$	Q_E^a	Q_M^b	$p(Q_M)$	n
Mobility	-0.012	-0.012	-0.035	0.010	0.2900	113.58	1.12	0.2900	106

^a Residual heterogeneity.

^b Between groups/model heterogeneity.

Table J2. Mean Fisher's z-transformed effect sizes (ES_{Zr}) and back-transformed effect-sizes (ES_r) with statistical significance of moderators, for the subset of effect sizes using area-based study designs (see Table 2.1 categories 1, 2, & 3) for amphibian+reptile species, to determine whether life history characteristics explained variation in effect sizes for amphibians+reptiles after controlling for study-level moderators. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_{Zr}	ES_r	CI (lb)	CI (ub)	p (ES_{Zr})	Q_E^a	Q_M^b	p(Q_M)	n
Reproductive rate	-0.005	-0.004	-0.050	0.041	0.8462	142.32	0.04	0.8462	40
Mobility	-0.001	-0.001	-0.057	0.055	0.9735	147.29	0.00	0.9735	40
Body Length	-0.010	-0.010	-0.130	0.110	0.8713	144.30	0.03	0.8713	40
Age at Sexual Maturity	0.076	0.075	-0.111	0.262	0.4276	137.68	0.63	0.4276	40
Taxon (Order)						116.56	7.00	0.0713	40
<i>Anura</i>	-0.190	-0.187	-0.331	-0.049	0.0084				21
<i>Caudata</i>	-0.515	-0.474	-0.795	-0.235	0.0003				8
<i>Squamata</i>	-0.286	-0.278	-0.506	0.089	0.1694				5
<i>Testudines</i>	0.019	0.019	-0.273	0.311	0.8998				6

^a Residual heterogeneity.

^b Between groups/model heterogeneity.

Table J3. Mean Fisher's z-transformed effect sizes (ES_z) and back-transformed effect-sizes (ES_r) with statistical significance of moderators for mammal species having removed effect size values from Rytwinski and Fahrig (2011). This analysis was conducted to determine whether the results for mammals (Table 2.3) depended on the inclusion of the empirical results from Rytwinski and Fahrig (2011). Excluding these results did not qualitatively change the conclusions. Reprinted with permission from © 2012 Elsevier.

Moderator variable	ES_z	ES_r	CI (lb)	CI (ub)	p (ES_z)	Q_E^a	Q_M^b	p(Q_M)	n
Reproductive rate	0.162	0.161	0.034	0.290	0.0129	1141.57	6.18	0.0129	92
Mobility	-0.047	-0.047	-0.079	-0.015	0.0042	1182.47	8.19	0.0042	92
Body Mass	-0.068	-0.068	-0.112	-0.024	0.0024	1159.82	9.23	0.0024	92
Taxon (Order)						1093.60	15.47	0.1157	92
<i>Artiodactyla</i>	-0.327	-0.315	-0.674	0.021	0.0653				21
<i>Carnivora</i>	-0.285	-0.277	-0.590	0.020	0.0674				27
<i>Didelphimorphia</i>	0.022	0.022	-0.835	0.880	0.9591				3
<i>Diprotodontia</i>	-0.154	-0.153	-1.637	1.329	0.8385				1
<i>Erinaceomorpha</i>	-0.169	-0.167	-1.690	1.353	0.8280				1
<i>Lagomorpha</i>	-0.692	-0.599	-2.211	0.828	0.3723				1
<i>Pholidota</i>	-1.333	-0.870	-2.945	-0.107	0.1050				1
<i>Primates</i>	-1.004	-0.763	-1.927	-0.176	0.0286				3
<i>Proboscidae</i>	-0.050	-0.049	-1.272	1.173	0.9367				2
<i>Rodentia</i>	0.240	0.235	-0.041	0.520	0.0936				30
<i>Soricomorpha</i>	0.055	0.055	-1.001	1.111	0.9185				2
Study Design						119.32	1.98	0.7400	92
<i>Landscape or region</i>	-0.208	-0.205	-0.770	0.355	0.4693				8
<i>Home range area</i>	-0.115	-0.115	-0.490	0.260	0.5468				18
<i>Plot size</i>	-0.073	-0.073	-0.499	0.352	0.7355				14
<i>Distance from road</i> <i>(multiple distances)</i>	-0.302	-0.293	-0.631	0.027	0.0716				27
<i>Distance from road</i> <i>(near vs. far)</i>	0.011	0.011	-0.303	0.326	0.9432				25
Road Category						1193.45	6.35	0.0956	92
<i>4-lane divided</i> <i>highways</i>	0.295	0.287	-0.091	0.681	0.1343				16
<i>2-lane paved roads</i>	-0.133	-0.132	-0.423	0.158	0.3702				28

Table J3. Continued

Moderator variable	ES _{Zr}	ES _r	CI (lb)	CI (ub)	p (ES _{Zr})	Q _E ^a	Q _M ^b	p(Q _M)	n
Road Category									
<i>1-lane paved or gravel/dirt roads</i>	-0.242	-0.238	-0.576	0.091	0.1544				24
<i>all or multiple road types</i>	-0.316	-0.306	-0.639	0.008	0.0557				24

^a Residual heterogeneity.^b Between groups/model heterogeneity.

Appendix K. Descriptive statistics of life history traits for the datasets belonging to passerine birds.

Table K1. Descriptive statistics for the three life history traits included in the bird meta-analysis of the datasets belonging to passerine birds only (n=147 datasets). Reprinted with permission from © 2012 Elsevier.

Life History Trait	Mean	Standard Error	Range
Reproductive rate	8.35	0.51	2.5-40
Species mobility	11.67	8.90	0.013-1310
Body mass	48.85	10.28	7.5-1200.5

Appendix L. Example probabilities of animal behavioural responses to roads and traffic, and traffic mortality as a function of traffic density.

(a)

Figure L1. a) Probability of an animal avoiding the road from a distance, as a function of traffic density V (held constant at 3 for the current runs). Probability of traffic disturbance avoidance was estimated by the avoidance parameter k (note: probability of vehicle avoidance was estimated by the same avoidance parameter k); b) Probability of being killed on a road for a given animal, as a function of traffic density. Probability of traffic mortality was estimated by varying the mortality parameter d . In the current runs, k was either 0 or 200, corresponding to 0% and 100% probabilities (respectively) and d was either 0 or 2.5, corresponding to 0% and 88% probabilities (respectively).

Appendix M. Raw mean abundance data for simulation experiments.

Table M1. Simulated predictions of the relative abundance of the small species types as a function of increasing road density, for different assumed behavioural responses to roads.

Relative abundance was measured as the mean abundance over the last 10 generations (zero if the population went extinct). Small species types had small territory sizes/high natural densities, small movement ranges, and high reproductive rates. Large species types had large territory sizes/low natural densities, large movement ranges, and low reproductive rates. Predictions are separated into tables for results from: (a) the single-species runs with no predators in the model (small single species), (b) predator-prey version, where the small species was prey for a road mortality-affected large predator, (c) the single-species runs with no predators in the model (large single species), and (d) predator-prey version, where the large species was prey for a road mortality-affected large predator. Assumed behavioural responses to roads: RA + VA = Road attraction + vehicle avoidance, RA + No VA = Road attraction + no vehicle avoidance, VA = vehicle avoidance, TDA = Traffic disturbance avoidance, RSA = Road surface avoidance, and No A = No avoidance.

(a)

No. of Roads	Mean Abundance					
	RA + VA	RA + No VA	VA	TDA	RSA	No A
0	282,001.0	282,001.0	282,001.0	282,001.0	282,001.0	282,001.0
2	282,001.0	280,883.1	281,166.6	281,250.0	281,250.0	281,163.0
4	282,001.0	279,818.6	280,241.6	280,501.0	280,501.0	280,326.6
6	282,001.0	278,771.9	279,320.1	279,752.0	279,752.0	279,548.9
8	282,001.0	277,706.0	278,651.0	279,005.0	279,005.0	278,639.5
10	282,000.0	276,479.6	277,701.6	278,258.0	278,258.0	277,794.9
12	282,001.0	275,463.2	276,634.7	277,513.0	277,513.0	277,023.3
14	282,000.0	274,363.8	275,728.6	276,768.0	276,768.0	276,194.3

(b)

No. of Roads	Mean Abundance					
	RA + VA	RA + No VA	VA	TDA	RSA	No A
0	0.0	0.0	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0	0.0	0.0
4	0.0	279,783.3	280,303.8	260,611.7	264,164.7	277,610.7
6	282,001.0	269,555.9	268,779.2	279,752.0	279,752.0	279,688.6
8	282,001.0	278,573.9	278,985.5	261,911.8	279,005.0	278,835.4
10	282,001.0	278,182.8	279,585.3	263,010.5	278,258.0	277,994.1
12	282,001.0	276,988.1	277,478.1	268,893.5	279,456.2	276,564.2
14	282,001.0	278,343.9	276,768.0	257,404.0	279,365.4	278,452.3

(c)

No. of Roads	Mean Abundance					
	RA + VA	RA + No VA	VA	TDA	RSA	No A
0	38.0	38.0	38.0	38.0	38.0	38.0
2	38.0	0.0	38.0	20.0	32.9	0.0
4	37.0	0.0	37.0	18.0	28.1	0.0
6	37.0	0.0	36.9	13.0	25.1	0.0
8	36.4	0.0	37.0	0.0	18.2	0.0
10	37.0	0.0	37.0	0.0	0.0	0.0
12	39.1	0.0	36.9	0.0	0.0	0.0
14	37.0	0.0	36.9	0.0	0.0	0.0

(d)

No. of Roads	Mean Abundance					
	RA + VA	RA + No VA	VA	TDA	RSA	No A
0	14.1	14.1	14.2	14.0	14.0	14.2
2	0.0	6.7	26.6	18.1	25.2	10.0
4	4.0	0.0	31.9	15.7	24.4	0.0
6	28.2	0.0	35.9	11.5	20.2	0.0
8	21.1	0.0	35.7	0.0	11.7	0.0
10	23.4	0.0	36.2	0.0	0.0	0.0
12	36.6	0.0	35.9	0.0	0.0	0.0
14	25.1	0.0	35.9	0.0	0.0	0.0