Published by Associazione Teriologica Italiana
Hystrix, the Italian Journal of Mammalogy
Online first – 2019
OPEN ACCESS
Available online at:
`http://www.italian-journal-of-mammalogy.it`
doi:10.4404/hystrix-00185-2018

Commentary

Can we use body size and road characteristics to anticipate barrier effects of roads in mammals? A meta-analysis

Hsiang L. Chen[1,*], John L. Koprowski[2]

[1] *Department of Forestry, National Chung Hsing University*
[2] *School of Natural Resources & the Environment, University of Arizona*

Keywords:
systematic review
allometry
habitat fragmentation
anthropogenic disturbance
road ecology
animal movements

Article history:
Received: 08 March 2019
Accepted: 05 June 2019

Abstract

Habitat fragmentation and loss caused by road development are recognized as major threats to biodiversity and challenges to reconcile the pursuit of economic growth with the protection of wildlife habitats. Assessment of potential environmental impacts is essential in planning and design of road projects. Behavioral responses such as road avoidance that causes barrier effects are critical in assessment of effects of roads on species persistence. In this study, we synthesized literature of barrier effects on mammals to identify road characteristics and species traits that might serve as management indicators to anticipate barrier effects. We conducted a meta-analysis with 118 statistics of road crossings by 45 species from 36 studies. We used logit-transformed proportion of individuals not crossing roads as the effect size of barrier effect. Overall, all types of roads, from major highways to narrow forest roads, can impede movements for certain species of mammals. For data collected by observational methods, body mass, road width, road surface and data collection methods explained 53% of variation among data. Barrier effect decreased as body mass increased, and was increased by greater road width. Paved roads posed stronger barriers compared to gravel dirt roads. Capture-recapture methods tended to detect a weaker barrier effect compared to methods that tracked individual movements. For data collected by experimental translocation, the probability of crossing following translocation was not affected by road width and body mass. We showed that interspecific variation of mammals in barrier effects can be explained by road characteristics and body size under natural condition, and can be useful to anticipate the species-specific magnitude of barrier effects of roads and aid in planning and design of road projects, as well as reassessment of existing roads.

Introduction

Habitat fragmentation and loss caused by development of infrastructure such as roads, railways, and utility easements are recognized as major threats to biodiversity and challenges to reconcile the pursuit of economic growth with the protection of ecological integrity of wildlife habitats (Czech and Krausman, 1997; Fahrig, 2003; Forman and Alexander, 1998; Goosem, 2007). Road construction not only causes destruction and loss of habitat but also facilitates deforestation and landscape fragmentation (Trombulak and Frissell, 2000). Roads and traffic influence wildlife populations directly through mortality due to wildlife-vehicle collisions and indirectly by altering animal behavior via visual and auditory disturbance as well as through changing roadside environment (Barber et al., 2010; Fahrig and Rytwinski, 2009). To mitigate negative effects of road development, assessment of potential environmental impacts is essential in planning and design of road projects. Behavioral responses such as road avoidance that causes barrier effects are critical in assessment of effects of roads on species persistence (Barthelmess and Brooks, 2010; Chen and Koprowski, 2016a; Ford and Fahrig, 2007; Jaeger et al., 2005; Rytwinski and Fahrig, 2012, 2011). Animals may avoid roads because of the road surface, vehicle or human presence, traffic disturbance and changes in species composition or environment at roadside areas (Barber et al., 2010; Chen and Koprowski, 2015; Forman et al., 2003; Jaeger et al., 2005; Laurance et al., 2004). Thus, roads and traffic can serve as barriers that impede animal movements, decrease accessibility of resources such as food, shelter or mates, lead to reduction in reproductive success and gene flow, and ultimately threaten population persistence (Bennett, 1991; Holderegger and DiGiulio, 2010; Strasburg, 2006; Trombulak and Frissell, 2000). However, unlike road mortality, barrier effects are difficult to detect without data of animal movements and space use, which often require long term effort that is hard to incorporate in the assessment phase of projects due to time limitations. Our objective is to synthesize literature of barrier effects of roads to identify factors and trends that can serve as management tools to anticipate barrier effects with basic information that is easily collected or measured.

To what extent a road acts as a barrier depends on species-specific ability to cross roads as well as road characteristics such as road width, road surface, and traffic intensity (Bissonette and Adair, 2008; Francis and Barber, 2013; Gagnon et al., 2007; Goosem, 2007; Oxley et al., 1974). Allometry, the study of relationships between body size and other traits of an organism, is a fundamental topic in biology, and has been increasingly recognized as of great importance in ecology (Brown and West, 2002; Schmidt-Nielsen, 1986). Many life history traits of species such as metabolic rate (White and Seymour, 2003) and home range size (Harestad and Bunnell, 1979) have strong allometric relationship with body size. For instance, home range size scales with body mass typically in linear fashion (Lindstedt et al., 1986; Reiss, 1988). Such considerable predictive power of body size might usefully integrate information on space, and can be a tool in anticipating animal responses to anthropogenic disturbance like roads (Bissonette and Adair, 2008). Therefore, the species-specific magnitude of barrier

---

[*] Corresponding author
Email address: `hsiangling@dragon.nchu.edu.tw` (Hsiang L. Chen)

doi:10.4404/hystrix-00185-2018
4th July 2019

effects posed by roads may be a function of road characteristics and body size.

Herein, we searched peer-reviewed publications that investigate road crossing behavior of mammals and conducted a meta-analysis (Glass, 1976) to assess influences of body size and road characteristics on probability of road crossing. We aim to assess if interspecific variation in barrier effects of roads can be anticipate by basic information of roads and species, and the utility of body size as an indicator of road impacts. We focused on mammals because even though barrier effects of roads have been documented in a diversity of terrestrial fauna, including insects, reptiles, amphibians, birds and mammals (Bhattacharya et al., 2003; Burnett, 1992; Laurance et al., 2004; Marsh et al., 2005; Sheppard et al., 2008), mammals are the most common study taxon (58.3% of 96 studies) and are more likely to have sufficient publications for meta-analysis. The barrier effects of roads obtained by different methods can vary considerably. Previously, barrier effects of roads have been assessed primarily by observation or experimental translocation (e.g. Goosem, 2001; McDonald and St.Clair, 2004; McGregor et al., 2008), and collect animal movement with capture-recapture or tracking. Therefore, we also assessed effects of research type (experimental or observational) and data collection methods (capture-recapture or animal tracking methods) in the meta-analysis.

Materials and Methods

Search and selection of studies for meta-analysis

We used the Web of Science literature search tool that includes publications from 1945 to December 2015 (accessed on 31 May 2016) to identify publications related to barrier effects of roads. We selected the "Title" search option and used search terms 'road' and 'highway' combined with 'permeability', 'movement', 'barrier', 'wildlife', 'animal', 'crossing', 'avoidance', 'gap', 'connectivity', 'corridor' and 'passage'. We browsed titles and abstracts in the search results and included publications related to terrestrial mammals in our analysis. We only included studies that quantified species-specific statistics of road crossings on individual roads and provide basic information about road width. Studies that combined rate of road crossing by multiple species as a collective group (e.g. road crossings by carnivores and ungulates, Alexander et al., 2005) or on different roads (e.g. Baker et al., 2007) were excluded.

Data extraction

For each study, we recorded year of publication, country of study sites, study species (including age class, sex), measurements of road crossing (e.g. number of road crossings, number of individual crossing roads, number of individual home ranges that intersect with roads), road width, road surface (paved or gravel dirt), average daily traffic volume, presence of wildlife road-crossing structures, presence of animal mortality due to wildlife-vehicle collisions, research type (observational or experimental translocation), and methods of data collection (e.g. capture-recapture, radio-telemetry). When a single study reported results on more than 1 road or for more than 1 species, we entered data for each species on each road as an independent statistic. We averaged measurements across years for data collected in multiple years with the same method. For studies that reported road width as number of lanes of traffic (e.g. 2-lane highway), we estimated road width in meters according to Federal Highway Administration, U.S. Department of Transportation (1 lane=3.6 m, shoulder width=1.2 m Federal Highway Administration, 2014). For each species, we obtained body mass (g) and head-body length (cm) from published literature and on-line sources to include: Animal Diversity Web hosted by University of Michigan (http://animaldiversity.org/), Smithsonian Institution's National Museum of Natural History-North America mammals (http://www.mnh.si.edu/mna/main.cfm), Queensland Museum (http://www.qm.qld.gov.au/), Wildscreen Arkive (http://www.arkive.org/), and World Association of Zoos and Aquariums (http://www.waza.org/en/site/home). Information from websites was used only when references were provided. We used the midpoint of adult body masses and body length and average of the sexes in sexually dimorphic species. We recorded the number of publications for each vertebrate order to assess taxonomic bias.

Effect size

To quantify magnitude of barrier effects across studies, we calculated a standardized effect size. The most common measurement for barrier effects was rate of road crossing that was estimated as proportion of individuals (e.g. Appendix S1: Brehme et al., 2013), or movements across roads (e.g. Appendix S1: Goosem, 2002). Ideally, a control comparator such as rate of road crossing by simulated movement models or rate of crossing reference lines at nearby roadless areas should be included. However, only 7 of 36 studies selected (Appendix S1) also provided control comparators to road crossings. Thus, we could only consider estimators for effect size of barrier effects based on studies that provided data for a single group with respect to a dichotomous dependent variable (i.e. cross or not cross, Viechtbauer, 2010a). As a result, we used logit-transformed proportion as an estimator for effect size that quantified magnitude of barrier effects. We calculated effect size as log (number of individuals or movements not crossing roads/ number of individuals or movements crossing roads). Greater effect sizes represented lower probability of road crossing, which indicates stronger barrier effects. The original effect size before weighting by sample size would be 0 if number of individuals that did not cross roads was equal to number of individuals that crossed roads, which indicates no barrier effect. Few studies were excluded due to inability to calculate the effect size on the basis of the information provided such as number of road crossings per km of roads (e.g. Schwab and Zandbergen, 2011). We calculated weighted effect size according to the sample size (i.e. total number of individuals [n=97] or movements [n=21]) and the corresponding sampling variances with the '`escalc`' function in the '`metafor`' (Viechtbauer, 2010b) package in R (version 3.1.0 -"Spring Dance", R Development Core Team 2014). Because cell entries with a zero count (i.e. all individuals crossed roads) can be problematic, we added 0.05 to records with zero cell entries (Viechtbauer, 2010a).

Influences of body size, road characteristics, and assessment methods

We used meta-regressions to assess the influence of body size and road characteristics or study-level moderators in determining the sign and magnitude of the barrier effects. Because the sample sizes of taxa for which the complete data set are available are quite limited and so we cannot truly assess effects of taxa. Measurements of body size that we examined included body mass (g) and head-body length (cm). We could not exclude data of juvenile in our analysis, as age class of the study species was not provided in most of the literature. For road characteristics, we only considered road width (m) and road surface (paved or not paved). We were not able to assess the effects of traffic volume, and presence of wildlife road crossing structures, due to a lack of information in the literature. Data collected by experimental translocation (n=26) were only available for species with body mass <150 g, most on paved roads (85%), and were collected mainly by capture-recapture method (96%). The data of translocation were so different form which of observational study that we did not feel comfortable to combine two dataset, with "type of experiment" as an independent variable, and run one model. With this approach, we would get estimates of effects that we did not have data to support, e.g. effect size of barrier effects for species with body mass >150 g, after translocation, collecting with tracking method. Thus, we did meta-regressions separately for data collected by different research type (observational or experimental translocation). For observational studies, we included body size, road width, road surface and data collection methods (capture-recapture or animal tracking methods including radio telemetry, track, spool and powder tracking) as independent variables. For experimental translocation studies, we only included body size and road width in the model, due to low variation in road type and data collecting method.

Due to high correlation between body mass (g) and head to body length (r=0.88, $p<0.001$), we chose to use body mass based on higher heterogeneity explained by the model (R^2). We applied a natural-log transformation to body mass and road width. We ran mixed-effects models with the '`rma`' function in the '`metafor`' package with restricted maximum-likelihood estimation. When both continuous and categorical variables were included in the models, we applied the Knapp and Hartung (2003) adjustment to the standard errors of the estimated coefficients (Viechtbauer, 2010a). Heterogeneity was assessed by formal tests of heterogeneity Q (Viechtbauer, 2010a). We used Cook's distances to identify potential outliers and removed records with the Cook's distances >1. We run permutation tests with 10000 iterations to assess significance of variables based on the p value obtained by the permutation tests. We used the best linear unbiased predictions to predict effect size based on the fitted models.

To assess if animals were more likely to cross roads after translocation, we used 2-tailed t tests to compare the effect size between observational studies (n=64) and experimental translocations (n=26) for species with body mass <150 g. Species >1 kg in our data were either ungulates (all are herbivore) or carnivores; data were collected by tracking method with observation. Hence, we used 2-tailed t tests to compare effect size between 2 groups to explore effects of diet on barrier effects of roads.

Results

Review statistics

We found 56 studies related to road crossings by mammals. Most of the studies were conducted in North America (33, 59%) and Europe (15, 27%) with few studies in Australia (5), Asia (1), Central America (1), and Africa (1). Thirty-six studies (Appendix S1) met our criteria for the meta-analysis. A total of 118 statistics of road crossings by 45 species (Appendix S2) were extracted. Mammals with body mass $\leqslant$150 g represented 75% of species included in the meta-analysis, 88% of which are rodents. This is reasonable given that about 90% of all mammals weight <5 kg (Merritt, 2010). The smallest species were pipistrelle bats (*Pipistrellus pipistrellus* and *P. pygmaeus*, 5.5 g), and the largest species was moose (*Alces alces*, ~400 kg). Among 45 species, the most common taxon was Rodentia (24, 53%) followed by Carnivora (7, 16%), Chiroptera (5, 11%), and Artiodactyla (4, 9%) with few studies on Diprotodontia (1, 2%), Dasyuromorphia (1, 2%), Erinaceomorpha (1, 2%), Marsupialia (1, 2%) and Soricomorpha (1, 2%). Road width ranged from 2 m to 90 m with a mean of 19 m (SE 1.75). When we examined the proportion of total species recorded in the meta-analysis against the proportion of total species of mammals in the world for each order (Wilson and Reeder, 2005), we did not see evident taxonomic bias, as rodents also represent 50% of total mammalian species in the world.

Effect size of barrier effects

We excluded 2 statistics of bats from analysis due to the greater mobility compared to other species with small body mass (~15.5 g). Therefore, our sample size for the meta-analysis was 116 statistics. Overall, roads were barriers for mammals indicated by the grand weighted-mean effect size (logit transformed proportion of individuals or movements not crossing roads) of 1.80 (SE 0.17, n=116), which differed from zero that would indicate no effect ($t_{115}=10.91$, $p<0.001$). Mean proportion of individuals or movements crossing roads was 21% (SE 0.02, n=116). The overall heterogeneity of effect sizes was large (Q=1525.59, $p<0.001$, n=116), suggesting that the individual effect sizes in our data did not come from a common population.

Influences of body size, road characteristics, and assessment methods

For data collected by experimental translocation (n=26), body mass and road width explained only 3.33% of heterogeneity among reported barrier effect (logit transformed proportion of individuals or movements not crossing roads) and did not affect probability of road crossing by mammals after translocation (Tab. 1). For data collected by observation, body mass, road width, road surface, and data collecting methods (i.e. capture-recapture or tracking) explained 53.4% of heterogeneity among reported barrier effects. Barrier effect decreased as body mass increased, and was affected positively by increasing road width (Fig. 1). A doubling of body mass decreased barrier effect by 0.2 and a doubling of road width increased barrier effect by 0.7 (Tab. 1). Odds of not crossing were 1.2 times greater on paved roads compared to on gravel dirt roads (Tab. 1). Data collected by capture-recapture methods showed stronger barrier effect of roads compared to data collected by animal tracking methods (Tab. 1). We used a model based on observational data with animal tracking methods to create a graph that shows how probability of road crossing changes with increasing road width or body mass when body mass of mammals or road width is fixed (Fig. 2). The model predicted that probability of road crossing was <50% even on narrow roads <10 m wide for species up to 100 kg.

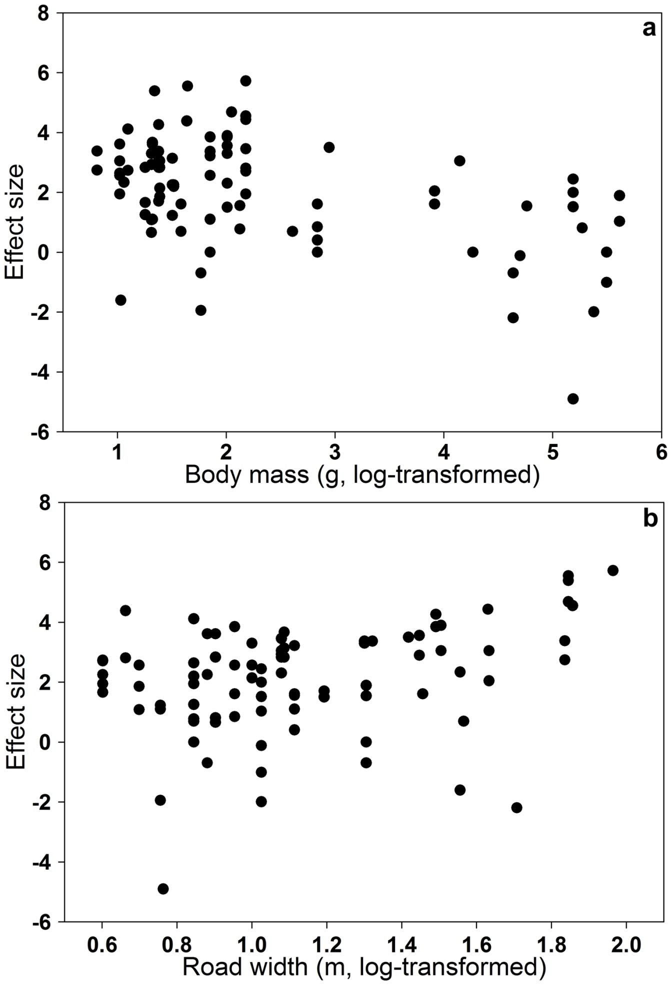

Figure 1 – Effect size of barrier effects of roads (logit-transformed proportion of individuals or movements not crossed roads) based on observational studies changes with (a) road width and (b) species body mass..

For species with body mass <150 g, animals were more likely to cross roads after translocation ($t_{88}=5.80$, $p<0.001$, Fig. 3). Barrier effect of roads estimated by observational studies was 2.5 times greater than barrier effect estimated by translocation, although mean road width where translocation was conducted (17.1 m [SE 3.75], n=26) was similar to road width of observational studies (18.3 m [SE 2.35], n=64, $t_{88}=0.15$, $p= 0.88$).

For species with body mass >1 kg, effect size of barrier effects based on observation with tracking method were not different ($t_{16}=-0.08$, $p= 0.94$) between ungulates (0.35 [SE 0.73], n=8) and carnivores (0.42 [SE 0.65], n=10). Even though body mass of ungulates were greater than carnivores ($t_{16}=2.63$, $p=0.02$), and road width was narrower for records of ungulates ($t_{16}=3.04$, $p= 0.008$), suggest that carnivores were more likely to cross roads than ungulates.

Discussion

With the increase in wildlife-vehicle collisions, transportation and resource management agencies have elevated their concern about road impacts on wildlife and recognized the need to develop effective mitigation (Lesbarréres and Fahrig, 2012; Taylor and Goldingay, 2010). Understanding animal behavioral responses to roads and traffic provides insight into causes and mechanisms of effects of linear development on wildlife and aids effective mitigation and conservation (Haddad, 1999; Roedenbeck et al., 2007). Influences of species traits on risk of road mortality, animal abundance or population density have been assessed via systematic synthesis of literature and modeling (e.g. Benítez-López et al., 2010; Rytwinski and Fahrig, 2012). Yet, how body size affect the magnitude of barrier effects of roads across species have not been examined. On the basis of observational data, we showed that interspecific variation in barrier effects of roads can be explained by road characteristics and body mass for mammals. This relationship can be useful to anticipate the species-specific magnitude of barrier effects of roads and aid in planning and design of road projects and mitigation measures. All types of roads, from major highways to narrow forest roads, can impede movements for certain species of mammals. However, our knowledge of barrier effects of roads are mainly based on species with body mass <150 g in a few regions across the world. Despite the fact that mammals with of about body mass of 1 kg were more frequently encountered in surveys of road mortality (Ford and Fahrig, 2007), and medium size mammals such as porcupines (*Erithizon dorsatum*), raccoons (*Procyon lotor*), eastern cottontails (*Sylvilagus floridanus*) and striped skunks (*Mephitis mephitis*) were the most common species killed on roads (Barthelmess and Brooks, 2010). Little is known about barrier effects of roads on medium size (1–10 kg) mammals and only one species with body mass in this range was included in the meta-analysis (*Lynx rufus*, Appendix S2). To design effective mitigation for road mortality, research investigating road crossing behavior by mammals with medium body size is needed.

Barrier effects of roads depended on species body mass and road characteristics

We demonstrated that species-specific barrier effects of roads can be explained by body mass and basic information of roads under natural circumstance (i.e. without translocation). As predicted, barrier effects of roads decreased as species body mass increased, and increased as road width increased. Capture-recapture methods tended to detect a lower rate of road crossings compared to animal tracking methods such as radio-telemetry, likely because not all individuals that crossed roads were captured, and therefore barrier effects of roads may be overestimated (Clark et al., 2001). Whereas relatively narrow, low traffic roads inhibit movements of small mammals (Macpherson et al., 2011; Rondinini and Doncaster, 2002), mesocarnivores and large ungulates regularly cross minor roads but avoid high traffic roads such as major highways (Lovallo and Anderson, 1996; Riley, 2006; Underhill and Angold, 2000). Road clearance, the distance an animal has to move between forest margins to cross the roadways (Oxley et al., 1974), has been suggested as the main factor that causes inhibition of road crossing by small mammals. Many behavioral traits of species such as locomotor performance, scale with body size on the log scale, and therefore small species show a wider range of speeds when compared to larger species (Dial et al., 2008). The relationships between barrier effects of roads and body mass or road width also may be exponential. Consequently, probability of road crossing decrease the most when road width increase from 1 m to 10 m, and increase sharply when body mass increases from 1 g to 1 kg (Fig. 2).

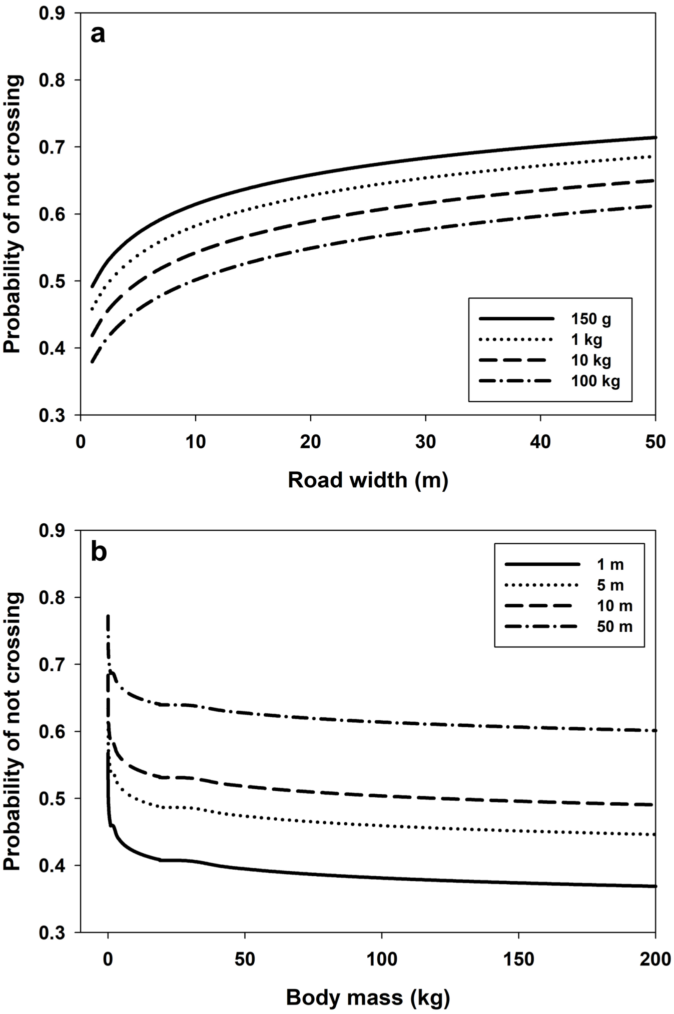

Figure 2 – Predicted probability of road crossing as (a) function of road width (m) for mammals with different body mass (kg), (b) function of body mass with different road width based on observational data with animal tracking methods. Model: Logit(not cross)=1.2694-1.16-0.1628×Log(body mass [g]+1)+0.6737×Log(road width [m]+1).

Table 1 – Estimated coefficients of meta-regressions for barrier effects of roads on mammals.

Variables	Logit	SE	*p* value[a]	95% CI	
Translocation study(n=26)					
Body mass (g)[b]	0.32	0.45	0.48	-0.62	1.26
Road width (m)[c]	0.17	0.32	0.60	-0.50	0.84
Intercept	-0.82	1.59	0.37	-3.32	2.68
Observational study (n=90)					
Body mass (g)[b]	-0.16	0.05	<0.001	-0.26	-0.07
Road width (m)[c]	0.67	0.20	<0.001	0.28	1.07
Road surface (paved)	0.77	0.36	0.04	0.06	1.50
Data collecting method (tracking)[d]	-1.16	0.37	0.003	-1.88	-0.43
Intercept	1.28	0.50	1.00	0.30	2.26

[a] *p* value was calculated by permutation test
[b] Body mass was natural-log transformed
[c] Road width was natural-log transformed
[d] Tracking methods included radio telemetry, track, spool and powder tracking

To what extent barrier effects of roads affect populations depends on accumulated barrier effects within movement range, mechanisms of road avoidance, and the impacts on reproductive activities. Large mammal species are less susceptible to barrier effects of individual roads, but are more vulnerable to negative road effects on animal abundance due to extended movements and ranges, and low reproductive rates and natural density (Fahrig and Rytwinski, 2009; Rytwinski and Fahrig, 2012, 2011). Small mammals are more susceptible to barrier effects of roads since even narrow roads can reduce probability of crossing significantly. Yet, the risk of mortality due to wildlife-vehicle collisions may be lower than for larger species. In addition to sampling error, faster removal rate by scavengers, and lower carcass persistence (Barthelmess and Brooks, 2010; Ford and Fahrig, 2007; Slater, 2002), we suggest that the infrequent detection of mammals with body size <1 kg in survey of road mortality (Barthelmess and Brooks, 2010) is also partly due to low probability of road crossing. Among species with similar body

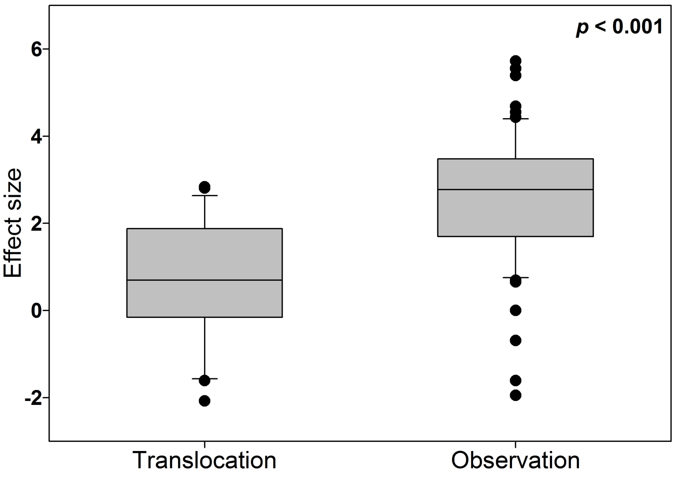

Figure 3 – Effect size of barrier effects of roads (logit-transformed proportion of individuals or movements not crossed roads) for mammals with body mass <150 g based on data collected by experimental translocation (n=26) and observational methods (n=64)..

sizes, barrier effects of roads may vary among taxa, because of differences in morphology and foraging ecology. Carnivores are more vagile with greater home ranges than herbivores (Sutherland et al., 2000), and were less likely to be found in road-kill surveys than omnivores or herbivores (Ford and Fahrig, 2007). Consistent with previous studies, we also found that for species >1 kg, carnivores were more likely to cross roads compared to herbivores.

Estimates of barrier effects differ between translocation and observation

We observed a marked difference between translocation and observational studies that likely reflects differential motivation of animal movements. Animals were more likely to cross roads after translocation compared to under natural circumstances. "Why do animals cross the road?" is not an easy question to answer. After translocation, animals often home or make long exploratory or unidirectional movements that may not be indicative of normal daily movements in their characteristics (Fischer and Lindenmayer, 2000; Massei et al., 2010). Although experimental manipulation such as translocation increases understanding of road crossing behavior by highly motivated individuals, the pattern of spontaneous movements is difficult to discern (Laurance et al., 2004). Hence, inference driven by data based on translocation should be made with caution. The effects of factors such as road width may be underappreciated as probability of road crossing was not affected by road width and body mass after translocation, whereas the results based on observational studies showed an opposite strong effect. We recognized the insignificance of body mass on barrier effects after translocation in the meta-regression is likely due to low variation in body mass of species among studies (all species <150 g) and therefore the result is not surprising. On the other hand, the insignificance of road width on barrier effects after translocation is of our concern as increased road width significantly increased barrier effects in observational studies even if we only included species with body mass <150 g in the meta-regression (p<0.001, n=64).

Other factors influence barrier effects of roads

Our meta-regression model for data collected by observational studies explained a considerable amount of variation (53%) in the data. However, about 46% of heterogeneity in reported barrier effects was not captured by our model. Barrier effects of roads are affected by several factors, including traffic intensity (Francis and Barber, 2013; Gagnon et al., 2007), presence of wildlife road crossing structures on the roads (Bissonette and Adair, 2008), variation in animal activity, such as during dispersal or mating (Chen and Koprowski, 2016a; Fahrig and Rytwinski, 2009), habitat preferences (Chen and Koprowski, 2016b) and habitat that surrounds the roads (Baigas et al., 2017; Medinas et al., 2019), individual heterogeneity in response to roads within a species (Ascensão et al., 2014; Blanco et al., 2005), and mechanism of road avoidance (e.g. avoidance of traffic disturbance or canopy gap created by roads, Forman et al., 2003; Greenberg, 1989; Robertson and Radford, 2009). For example, drivers of dispersal are likely to be different than those for routine daily movements. Foraging, marking or communication, and mate searching may be important daily influences on mammalian movement at a more proximate level (Hutchen and Hodges, 2019; Johansson et al., 2018); whereas natal and breeding dispersal are often related to larger evolutionary influences with ultimate consequences (Li and Kokko, 2019; Merrick and Koprowski, 2017).

Yet, we were not able to consider these influences given that most information was not provided in the selected studies. We understand some information was not described due to irrelevance to the study objectives. Nonetheless, we advocate that clear basic information of study sites such as road width in meters, average daily traffic volume, and presence or absence of wildlife road crossing structures should be provided in future studies to maximize future value of studies.

Barrier effects of roads due to road avoidance should be distinguished clearly from effects due to road mortality, as both causes lead to reduced individuals crossing roads, but the mechanisms are fundamentally different and require different mitigation (Fahrig and Rytwinski, 2009). Nevertheless, road mortality was not addressed in most studies that investigated effects of roads on animal space use and movements. Potential confounding effects between road avoidance and road mortality are an important issue for records collected by capture-recapture methods, since for individuals not captured after crossing roads, the fate was unknown (Richardson et al., 1997). Thus, we could not completely exclude the likelihood of involving road mortality in the barrier effects for the present review.

Conservation implications

The global population has exceeded 7 billion in 2012 (World Population Clock, 2015) and over 65 million km of roads have been developed (Central Intelligence Agency, 2014). Predicting how wildlife will cope with anthropogenic disturbances and fragmented landscapes, and how the expanding transportation network may impact animal abundance, and persistence across species is therefore of importance in conservation biology (Bender and Fahrig, 2005; Laurance et al., 2004). Effects of roads on animal populations depend on species traits as well as behavioral responses to roads (Benítez-López et al., 2010; Jaeger et al., 2005; Rytwinski and Fahrig, 2012). For example, roads lead to greatly reduced habitat availability and can negatively affect animal populations (Goosem, 2007; Jaeger et al., 2005; Saunders et al., 2002) for species that exhibit not only avoidance of road surface but also avoid roadside environment (Huijser and Bergers, 2000). We found that roads have greater barrier effects on mammals than previously appreciated (Carvalho et al., 2018; Chen and Koprowski, 2015, 2016a; Fahrig and Rytwinski, 2009). Animal populations can become fragmented when roads act as barriers to movement and may further affect mating behavior, reducing gene flow, and population viability (Benítez-López et al., 2010; Coffin, 2007; Forman et al., 2003). The often chronic nature of indirect effects of roads can lead to an insidious impact on animal populations (Jackson and Fahrig, 2011; McCartney-Melstad et al., 2018).

We demonstrated that the species-specific magnitude of barrier effects of roads can be anticipated with basic information on species and road characteristics that are readily accessed through open sources or easily measured. The relationship between barrier effects, body mass and road characteristics that we estimated can be a management tool in the design and planning of road projects, as well as reassessment of existing roads. With information of road width and body mass of the mammalian species nearby, we can estimate the barrier effects of the road on daily movement of individual species. Road planning can be informed and studies of target species can be formulated. In addition, existing roads can be evaluated to identify regions that might be considered for road crossing enhancements or dissuasion technologies. Our approach provides a step forward in assessment of road impacts for multiple species. Given there will often be a paucity of funds and information to use for multiple species, the relationship between body size and road impacts may provide a cost-effective way to quickly scan the entire road system. Finally, from a more basic science perspective, this is yet another ecological metric that scales with body size. Such relationships promote the importance of large scale comparative studies to determine the key predictors of road impacts.

Supporting Information

Studies included in meta-analysis (Appendix S1), values of life history traits and reference information for species used in meta-analysis (Appendix S2), and table of summary data for meta-analysis (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

References

Alexander, S. M., Waters, N. M., Paquet, P. C., 2005. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. Can. Geogr. 49, 321–331. https://doi.org/10.1111/j.0008-3658.2005.00099.x

Ascensão, F., Grilo, C., LaPoint, S., Tracey, J., Clevenger, A. P., Santos-Reis, M., 2014. Inter-individual variability of stone marten behavioral responses to a highway. PLoS One 9, 1–9. doi:10.1371/journal.pone.0103544

Baigas, P. E., Squires, J. R., Olson, L. E., Ivan, J. S., Roberts, E. K., 2017. Using environmental features to model highway crossing behavior of Canada lynx in the Southern Rocky Mountains. Landsc. Urban Plan. 157, 200–213. doi:10.1016/j.landurbplan.2016.06.007

Baker, P. J., Dowding, C. V., Molony, S. E., White, P. C. L., Harris, S., 2007. Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. Behav. Ecol. 18, 716–724. doi:10.1093/beheco/arm035

Barber, J. R., Crooks, K. R., Fristrup, K. M., 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180–189. doi:10.1016/j.tree.2009.08.002

Barthelmess, E. L., Brooks, M. S., 2010. The influence of body-size and diet on road-kill trends in mammals. Biodivers. Conserv. 19, 1611–1629. doi:10.1007/s10531-010-9791-3

Bender, D. J., Fahrig, L., 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. Ecology 86, 1023–1033. doi:10.1890/03-0769

Benítez-López, A., Alkemade, R., Verweij, P. A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. Biol. Conserv. 143, 1307–1316. doi:10.1016/j.biocon.2010.02.009

Bennett, A. F., 1991. Roads, roadsides and wildlife conservation: a review, in: Hobbs, D. A., Saunders, R. J. (Eds.), Nature Conservation 2: The Role of Corridors. Surrey Beatty & Sons, Chipping Norton, Australia., pp. 99–118.

Bhattacharya, M., Primack, R. B., Gerwein, J., 2003. Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? Biol. Conserv. 109, 37–45. doi:10.1016/s0006-3207(02)00130-1

Bissonette, J. A., Adair, W., 2008. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. Biol. Conserv. 141, 482–488. doi:10.1016/j.biocon.2007.10.019

Blanco, J. C., Cortés, Y., Virgós, E., 2005. Wolf response to two kinds of barriers in an agricultural habitat in Spain. Can. J. Zool. 83, 312–323. doi:10.1139/z05-016

Brehme, C. S., Tracey, J. A., Mcclenaghan, L. R., Fisher, R. N., 2013. Permeability of roads to movement of scrubland lizards and small mammals. Conserv. Biol. 27, 710–720. doi:10.1111/cobi.12081

Brown, J. H., West, G. B., 2002. Scaling in biology. Oxford University Press, Oxford, UK.

Burnett, S. E., 1992. Effects of a rain-forest road on movements of small mammals-mechanisms and implications. Wildl. Res. 19, 95–104.

Carvalho, F., Lourenço, A., Carvalho, R., Alves, P. C., Mira, A., Beja, P., 2018. The effects of a motorway on movement behaviour and gene flow in a forest carnivore: Joint evidence from road mortality, radio tracking and genetics. Landsc. Urban Plan. 178, 217–227. doi:10.1016/j.landurbplan.2018.06.007

Central Intelligence Agency, 2014. The world factbook [WWW Document]. Cent. Intell. Agency. URL https://www.cia.gov/library/publications/the-world-factbook/ (accessed 12.20.14).

Chen, H. L., Koprowski, J. L., 2016a. Barrier effects of roads on an endangered forest obligate: Influences of traffic, road edges, and gaps. Biol. Conserv. 199. doi:10.1016/j.biocon.2016.03.017

Chen, H. L., Koprowski, J. L., 2016b. Differential effects of roads and traffic on space use and movements of native forest-dependent and introduced edge-tolerant Species. PLoS One 11, e0148121. doi:10.1371/journal.pone.0148121

Chen, H. L., Koprowski, J. L., 2015. Animal occurrence and space use change in the landscape of anthropogenic noise. Biol. Conserv. 192, 315–322. doi:10.1016/j.biocon.2015.10.003

Clark, B. K., Clark, B. S., Johnson, L. A., Haynie, M. T., 2001. Influence of roads on movements of small mammals. Southwest. Nat. 46, 338–344.

Coffin, A. W., 2007. From roadkill to road ecology: A review of the ecological effects of roads. J. Transp. Geogr. 15, 396–406. doi:10.1016/j.jtrangeo.2006.11.006

Czech, B., Krausman, P. R., 1997. Distribution and causation of species endangerment in the United States. Science (80-.). 277, 1116–1117. doi:10.1126/science.277.5329.1116

Dial, K. P., Greene, E., Irschick, D. J., 2008. Allometry of behavior. Trends Ecol. Evol. 23, 394–401. doi:10.1016/j.tree.2008.03.005

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L., Rytwinski, T., 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecol. Soc. 14, 21.

Federal Highway Administration., 2014. Mitigation strategies for design exceptions. Federal Highway Administration, U.S. Department of Transportation.

Fischer, J., Lindenmayer, D. B., 2000. An assessment of the published results of animal relocations. Biol. Conserv. doi:10.1016/S0006-3207(00)00048-3

Ford, A. T., Fahrig, L., 2007. Diet and body size of North American mammal road mortalities. Transp. Res. Part D Transp. Environ. 12, 498–505. doi:10.1016/j.trd.2007.07.002

Forman, R. T. T., Alexander, L. E., 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst. 29, 207–231.

Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C .D., Dale, V. H., Fahrig, L., France, R. L., Goldman, C. R., Heanue, K., Jones, J., Swanson, F., Turrentine, T., Winter, T. C., 2003. Road ecology: science and solutions, 2nd ed. Island Press, Washington, D.C., USA.

Francis, C. D., Barber, J. R., 2013. A framework for understanding noise impacts on wildlife: An urgent conservation priority. Front. Ecol. Environ. 11, 305–313. doi:10.1890/120183

Gagnon, J. W., Theimer, T. C., Dodd, N. L., Boe, S., Schweinsburg, R. E., 2007. Traffic volume alters elk distribution and highway crossings in Arizona. J. Wildl. Manage. 71, 2318. doi:10.2193/2006-224

Glass, G. V., 1976. Primary, secondary, and meta-analysis of research. Educ. Res. 5, 3–8.

Goosem, M., 2007. Fragmentation impacts caused by roads through rainforests. Curr. Sci. 93, 1587–1595.

Goosem, M., 2002. Effects of tropical rainforest roads on small mammals: Fragmentation, edge effects and traffic disturbance. Wildl. Res. 29, 277–289. doi:10.1071/WR01058

Goosem, M., 2001. Effects of tropical rainforest roads on small mammals: Inhibition of crossing movements. Wildl. Res. 28, 351–364. doi:10.1071/WR99093

Greenberg, R., 1989. Neophobia, aversion to open space, and ecological plasticity in Song and Swamp sparrows. Can. J. Zool. 67, 1194–1199. doi:10.1139/z89-172

Haddad, N. M., 1999. Corridor use predicted from behaviors at habitat boundaries. Am. Nat. 153, 215–227.

Harestad, A. S., Bunnell, F. L., 1979. Home range and body weight: a reevaluation. Ecology 60, 389–402. doi:10.2307/1937667

Holderegger, R., DiGiulio, M., 2010. The genetic effects of roads: A review of empirical evidence. Basic Appl. Ecol. 11, 522–531. doi:10.1016/j.baae.2010.06.006

Huijser, M. P., Bergers, P. J. M., 2000. The effect of roads and traffic on hedgehog (Erinaceus europaeus) populations. Biol. Conserv. 95, 111–116.

Hutchen, J., Hodges, K. E., 2019. Foraging behaviour of snowshoe hares (*Lepus americanus*) in conifer forests regenerating after fire. Can. J. Zool. 97, 446–452. doi:10.1139/cjz-2018-0222

Jackson, N. D., Fahrig, L., 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. Biol. Conserv. 144, 3143–3148. doi:10.1016/j.biocon.2011.09.010

Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., vonToschanowitz, K. T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol. Modell. 185, 329–348. doi:10.1016/j.ecolmodel.2004.12.015

Johansson, Ö., Koehler, G., Rauset, G. R., Samelius, G., Andrén, H., Mishra, C., Lhagvasuren, P., McCarthy, T., Low, M., 2018. Sex-specific seasonal variation in puma and snow leopard home range utilization. Ecosphere 9, e02371. doi:10.1002/ecs2.2371

Knapp, G., Hartung, J., 2003. Improved tests for a random effects meta-regression with a single covariate. Stat. Med. 22, 2693–710. doi:10.1002/sim.1482

Laurance, S. G. W., Stouffer, P. C., Laurance, W. E., 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conserv. Biol. 18, 1099–1109.

Lesbarrères, D., Fahrig, L., 2012. Measures to reduce population fragmentation by roads: What has worked and how do we know? Trends Ecol. Evol. 27, 374–380. doi:10.1016/j.tree.2012.01.015

Li, X. Y., Kokko, H., 2019. Sex-biased dispersal: a review of the theory. Biol. Rev. 94, 721–736. doi:10.1111/brv.12475

Lindstedt, S. L., Miller, B. J., Buskirk, S. W., 1986. Home range, time, and body size in mammals. Ecology 67, 413–418. doi:10.2307/1938584

Lovallo, M. J., Anderson, E. M., 1996. Bobcat movements and home ranges relative to roads in Wisconsin. Wildl. Soc. Bull. 24, 71–76.

Macpherson, D., Macpherson, J. L., Morris, P., 2011. Rural roads as barriers to the movements of small mammals. Appl. Ecol. Environ. Res. 9, 167–180. doi:10.15666/aeer/0902_167180

Marsh, D. M., Milam, G. S., Gorham, N. R., Beckman, N. G., 2005. Forest roads as partial barriers to terrestrial salamander movement. Conserv. Biol. 19, 2004–2008. doi:10.1111/j.1523-1739.2005.00238.x

Massei, G., Quy, R. J., Gurney, J., Cowan, D. P., 2010. Can translocations be used to mitigate human - wildlife conflicts? Wildl. Res. 37, 428. doi:10.1071/wr08179

McCartney-Melstad, E., Vu, J. K., Shaffer, H. B., 2018. Genomic data recover previously undetectable fragmentation effects in an endangered amphibian. Mol. Ecol. 27, 4430–4443. doi:10.1111/mec.14892

McDonald, W. R., St.Clair, C. C., 2004. The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. Oikos 105, 397–407. doi:10.1111/j.0030-1299.2004.12640.x

McGregor, R. L., Bender, D. J., Fahrig, L., 2008. Do small mammals avoid roads because of the traffic? J. Appl. Ecol. 45, 117–123. doi:10.1111/j.1365-2664.2007.01403.x

Medinas, D., Ribeiro, V., Marques, J. T., Silva, B., Barbosa, A. M., Rebelo, H., Mira, A., 2019. Road effects on bat activity depend on surrounding habitat type. Sci. Total Environ. 660, 340–347. doi:10.1016/j.scitotenv.2019.01.032

Merrick, M. J., Koprowski, J. L., 2017. Altered natal dispersal at the range periphery: The role of behavior, resources, and maternal condition. Ecol. Evol. 7, 58–72. doi:10.1002/ece3.2612

Merritt, J. F., 2010. The biology of small mammals. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Oxley, D. J., Fenton, M. B., Carmody, G. R., 1974. Effects of roads on population of small mammals. J. Appl. Ecol. 11, 51–59.

Reiss, M., 1988. Scaling of home range size: Body size, metabolic needs and ecology. Trends Ecol. Evol. 3, 85–86. doi:10.1016/0169-5347(88)90025-0

Richardson, J. H., Shore, R. F., Treweek, J. R., Larkin, S. B. C., 1997. Are major roads a barrier to small mammals? J. Zool. 243, 840–846. doi:10.1111/j.1469-7998.1997.tb01982.x

Riley, S. P. D., 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. J. Wildl. Manage. 70, 1425–1435. doi:10.2193/0022-541x(2006)70[1425:seobag]2.0.co;2

Robertson, O. J., Radford, J. Q., 2009. Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecol. 34, 435–446. doi:10.1111/j.1442-9993.2009.01945.x

Roedenbeck, I. A., Fahrig, L., Findlay, C. S., Houlahan, J. E., Jaeger, J. A. G., Klar, N., Kramer-Schadt, S., van derGrift, E. A., 2007. The Rauischholzhausen agenda for road ecology. Ecol. Soc. 12, 11.

Rondinini, C., Doncaster, C. P., 2002. Roads as barriers to movement for hedgehogs. Funct. Ecol. 16, 504–509. doi:10.1046/j.1365-2435.2002.00651.x

Rytwinski, T., Fahrig, L., 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biol. Conserv. 147, 87–98. doi:10.1016/j.biocon.2011.11.023

Rytwinski, T., Fahrig, L., 2011. Reproductive rate and body size predict road impacts on mammal abundance. Ecol. Appl. 21, 589–600. doi:10.1890/10-0968.1

Saunders, S. C., Mislivets, M. R., Chen, J., Cleland, D. T., 2002. Effects of roads on landscape structure within nested ecological units of the Northern Great Lakes Region, USA.pdf 103, 209–225.

Schmidt-Nielsen, K., 1986. Why is animal size so important? Cambridge University Press, Cambridge, UK.

Schwab, A. C., Zandbergen, P. A., 2011. Vehicle-related mortality and road crossing behavior of the Florida panther. Appl. Geogr. 31, 859–870. doi:10.1016/j.apgeog.2010.10.015

Shepard, D. B., Kuhns, A. R., Dreslik, M. J., Phillips, C. A., 2008. Roads as barriers to animal movement in fragmented landscapes. Anim. Conserv. 11, 288–296. doi:10.1111/j.1469-1795.2008.00183.x

Slater, F. M., 2002. An assessment of wildlife road casualties - the potential discrepancy between numbers counted and numbers killed. Web Ecol. 3, 33–42.

Strasburg, J. L., 2006. Conservation biology - roads and genetic connectivity. Nature 440, 875–876. doi:10.1038/440875a

Sutherland, G., Harestad, A., Price, K., Lertzman, K., 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conserv. Ecol. 4.

Taylor, B. D., Goldingay, R. L., 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. Wildl. Res. 37, 320–331. doi:10.1071/wr09171

Trombulak, S. C., Frissell, C. A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18–30.

Underhill, J. E., Angold, P. G., 2000. Effects of roads on wildlife in an intensively modified landscape. Environ. Rev. 8, 21–39. doi:10.1139/er-8-1-21

Viechtbauer, W., 2010a. Conducting meta-analyses in R with the `metafor` package. J. Stat. Softw. 36, 1–48.

Viechtbauer, W., 2010b. metafor: meta-analysis package for R. R package.

White, C. R., Seymour, R. S., 2003. Mammalian basal metabolic rate is proportional to body mass2/3. Proc. Natl. Acad. Sci. 100, 4046–9. doi:10.1073/pnas.0436428100

Wilson, D. E., Reeder, D. M., 2005. Mammal species of the world, 3rd ed. The Johns Hopkins University Press, Baltimore, Maryland, USA.

World Population Clock – Worldometers [WWW Document], 2015. Worldometers.info. URL http://www.worldometers.info/world-population (accessed 1.31.15).

Associate Editor: Wauters L.A.

Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplemental Table S1 Studies included in meta-analysis.

Supplemental Table S2 Life history traits and reference information for species used in meta-analysis.

Supplemental Table S3 Table of summary data for meta-analysis