Biological Conservation 147 (2012) 87–98

Contents lists available at SciVerse ScienceDirect

Biological Conservation

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

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

Trina Rytwinski *, Lenore Fahrig

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

ARTICLE INFO

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

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

ABSTRACT

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

1. Introduction

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

Several hypotheses have been suggested for the types of species whose populations should be most negatively affected by roads (summarized in Fig. 2 in Fahrig and Rytwinski, 2009). These hypotheses fall into two main sets: (i) hypotheses based on species life history traits and (ii) hypotheses based on species behavioral responses to roads and traffic. The first set of hypotheses argues that highly mobile species should be more negatively affected because they interact with roads more often than do less-mobile species (Carr and Fahrig, 2001; Gibbs and Shriver, 2002; Forman et al., 2003; Rytwinski and Fahrig, 2011). Similarly, species with larger territories or home ranges should be more susceptible to road effects than those with smaller territories or home ranges. Species with lower reproductive rates, later sexual maturity, and longer generation times, should also be more susceptible to road effects because they will be less able to rebound quickly from population declines (Gibbs and Shriver, 2002; Rytwinski and Fahrig, 2011). Since species with large home ranges and low reproductive rates naturally occur at low densities, we also expect that species that naturally occur at low densities should be more susceptible to road effects than those that occur at high densities. Taken together, these hypotheses also suggest that, in general, larger species should be more negatively affected by roads than smaller species because larger species generally occur naturally at lower densities, have lower reproductive rates, longer generation times, and are more mobile than smaller species (Gibbs and Shriver, 2002; Forman et al., 2003). Interestingly, since larger species are often predators on smaller species, it is also possible that negative effects of roads on populations of large animals could lead to reduced predation on small animals in areas of high road density. This could indirectly reduce the impact of roads on animals. In fact, release from predation has been suggested as a possible cause for the frequently observed positive effects of roads on small mammal populations (Johnson and Collinge, 2004; Rytwinski and Fahrig, 2007; Bissonette and Rosa, 2009; Fahrig and Rytwinski, 2009).

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

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

0006-3207/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2011.11.023

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

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

2. Materials and methods

2.1. Search and selection of studies for meta-analysis

We conducted a thorough literature search to find all relevant studies that quantify the relationship between roads and/or traffic and population abundance of at least one species. Here we use a broad definition of "population abundance" to include population size (or relative size), population density (or relative density), and species presence or absence (as an index of high vs. low abundance). Only studies based on quantitative data were included. We limited our analyses to include only animals that are terrestrial for at least part of their life cycle. Studies were excluded if they combined abundance or presence/absence data across species, such that values for individual species could not be extracted. To be included in the analysis, studies had to report (a) the test statistic for the effect of roads and/or traffic on animal abundance, and/or summary statistics (e.g. mean and variance) from which an effect size could be calculated and (b) the sample size (or the *P* value of the test if a test statistic was reported). In some cases where these values were not provided, we calculated them using raw data if they were provided in the paper, could be extracted from graphs using GetData Graph Digitizer 2.24 (Fedorov, S. (2008), *unpublished internet freeware*), or were provided to us by authors. To reduce publication bias, we attempted a thorough search, including data available in theses.

2.2. Database and data extraction

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

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