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Synthesis, part of a Special Feature on Effects of Roads and Traffic on Wildlife Populations and Landscape Function

Effects of Roads on Animal Abundance: an Empirical Review and Synthesis

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ABSTRACT. We attempted a complete review of the empirical literature on effects of roads and traffic on animal abundance and distribution. We found 79 studies, with results for 131 species and 30 species groups. Overall, the number of documented negative effects of roads on animal abundance outnumbered the number of positive effects by a factor of 5; 114 responses were negative, 22 were positive, and 56 showed no effect. Amphibians and reptiles tended to show negative effects. Birds showed mainly negative or no effects, with a few positive effects for some small birds and for 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, along with information on species attributes, to develop a set of predictions of the conditions that lead to negative or positive effects or no effect of roads on animal abundance. Four species types are predicted to respond negatively to roads: (i) species that are attracted to roads and are unable to avoid individual cars; (ii) species with large movement ranges, low reproductive rates, and low natural densities; and (iii and iv) small animals whose populations are not limited by road-affected predators and either (a) avoid habitat near roads due to traffic disturbance or (b) show no avoidance of roads or traffic disturbance and are unable to avoid oncoming cars. Two species types are predicted to respond positively to roads: (i) species that are attracted to roads for an important resource (e.g., food) and are able to avoid oncoming cars, and (ii) species that do not avoid traffic disturbance but do avoid roads, and whose main predators show negative population-level responses to roads. Other conditions lead to weak or non-existent effects of roads and traffic on animal abundance. We identify areas where further research is needed, but we also argue that the evidence for population-level effects of roads and traffic is already strong enough to merit routine consideration of mitigation of these effects in all road construction and maintenance projects.

Key Words: *environmental impact; landscape connectivity; mortality; population density; road network; road density; road effect zone; road mitigation; species distribution; species richness; traffic density; traffic volume*

INTRODUCTION

In their research agenda for road ecology, Roedenbeck et al. (2007) identify the most pressing research question as: “Under what circumstances do roads affect population persistence?” They argue that this question remains unanswered because “very few studies evaluate the effects of roads at the population level.” In support of this claim, Roedenbeck et al. (2007) cite review papers published in 2000 and earlier. In one of these review papers, Underhill and Angold (2000) state that “[h]ard information is still lacking for the effect of roads and traffic at the population level,” and in support of this statement they cite a review paper published in 1991. So, the claim that there are only a few road ecology studies at the population level (Roedenbeck et al. 2007) is based on reviews and assertions that are now 8–17 years old.

Meanwhile, over the past 10 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

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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). This interest in the ecological effects of roads has increased along with the ever-expanding transportation network. The main concern among conservationists and environmental planners is that roads and traffic may be reducing or even eliminating wildlife populations (Trombulak and Frissell 2000, Forman et al. 2003). Is this concern backed up by empirical evidence? A current review of the state of population-level research into road effects is clearly needed. Therefore, the first objective of this paper is to conduct a complete review of the empirical literature on effects of roads on animal population abundance and distribution, to provide an up-to-date summary of the state of knowledge in this area.

Our second objective is to develop a set of working hypotheses and predictions in answer to Roedenbeck et al.'s (2007) question above: under what circumstances do roads affect population persistence? Our approach was to compare the findings of our literature review with hypotheses that have been proposed as explanations for road effects. These hypotheses fall into two main sets: hypotheses based on species behavioral responses to roads and traffic and hypotheses based on species attributes that are correlated with body size.

In the first set, Jaeger et al. (2005) proposed that there are three behavioral responses to roads and traffic: (i) avoidance of the road surface, (ii) avoidance of traffic emissions and disturbance (noise, lights, chemical emissions), and (iii) the ability of the animal to move out of the path of an oncoming vehicle (labeled "car avoidance" by Jaeger et al. (2005)). Avoidance of the road surface reduces animal mortality on roads but also reduces accessibility of habitats and other resources. Note that road-surface avoidance also includes situations where the animal may not behaviorally avoid the road, but the road design represents a physical barrier to animal movement (e.g., a fenced road). Jaeger and Fahrig (2004) referred to complete road avoidance as the "fence effect," emphasizing its functional equivalency to a physical barrier. Avoidance of traffic disturbance and emissions reduces habitat quality within the vicinity of roads; the higher the amount of traffic on the road, the more habitat is effectively lost to the species. Car avoidance, on the other hand, allows the animal to cross the road without being killed on it. An additional behavioral response to roads is attraction to the road, which increases the frequency with which animals enter the road and, therefore, increases the mortality risk (Forman et al. 2003).

Hypotheses in the second set argue that larger animals are more vulnerable to roads because they are more mobile, have lower reproductive rates, and occur naturally at lower densities than do small animals (Gibbs and Shriver 2002). Individuals of highly mobile species, i.e., species that move frequently and/or over large distances, are more likely to interact with a given road network, thus increasing the chance of road mortality (Carr and Fahrig 2001). Because of their lower reproductive rates and lower natural densities (larger home ranges), populations of large animals are less able than populations of small animals to rebound from low numbers resulting from road mortality, or to persist at low numbers due to the animal's avoidance of areas with high road density (Gibbs and Shriver 2002). In addition, roads could indirectly cause increases in populations of smaller animals, if these animals are prey for larger animals whose populations are reduced by roads, i.e., the road effect could cause release from predation (Rytwinski and Fahrig 2007).

In this paper, we review the empirical literature on effects of roads and traffic on animal abundance and distribution. In addition, we synthesize this information, in the context of the ideas above, to develop what we believe to be the state-of-the-science on the circumstances under which roads affect population abundance and distribution.

METHODS

The purpose of the literature review was to collect and synthesize all published empirical information on the effects of roads and traffic on animal abundance. We used "animal abundance" as a rather general term to include population size (or relative size), population density (or relative density), species presence or absence, or species richness (i.e., species presence or absence summed across species). The studies in our review fall into three general categories. The first category includes studies that document animal abundances at different distances from a road. Some of these studies considered only two distances: adjacent to the road vs. farther from the road. The second general category includes studies comparing animal abundances in different landscapes or regions with different road densities. Studies that compare road densities within individual animals' territories (presence) with road densities in areas outside animal territories (absence) are a subset within this category. The third general category includes studies that document the effects of roads and traffic on animal reproduction or mortality, along with calculations of the consequences of these effects for animal abundance.

We attempted a complete literature review, with the following restrictions. First, the papers had to present a quantitative analysis relating animal abundance to roads and traffic. We did not include studies of road or traffic effects on animal mortality, reproduction, movement, or genetic differentiation, unless the authors quantitatively demonstrated the impact of the effect(s) on animal abundance. For example, Hels and Buchwald (2001) estimated that 5%–25% of some frog populations are killed by traffic mortality. However, as they did not determine the effect of this mortality on population abundance, we did not include the study in our review. We included all studies showing negative or positive effects of roads and traffic on animal abundance except when the road effect and habitat were completely confounded. For example, studies of species that preferentially live in or on road verges and studies comparing population sizes in grassy roadside verges vs. neighboring forest patches completely confound a habitat effect with the road effect, so were not included. Note, however, that many of the studies included in our review did contain correlations or likely correlations between roads and traffic and other variables that could have been fully or partly responsible for the patterns attributed to roads, or could have masked real effects of roads. We discuss the implications of these correlations in the Discussion. We included studies showing no effect of roads or traffic on animal abundance, except when statistical power was very low, i.e., very low sample sizes or very high variance around abundance estimates.

RESULTS

Altogether we found 79 studies, with results for 131 species and 30 species groups, documenting effects of roads and traffic on animal abundance (Table 1). The studies included animals from a wide range of taxa (invertebrates, herptiles, birds, and mammals), trophic levels (herbivores, carnivores, omnivores, and scavengers) and habitats (forests, grasslands, and wetlands). Studies were located predominantly in Europe and North America, but there were also studies in Australia, Africa, and India.

Some general patterns are evident from Table 1. First, the number of documented negative effects of roads on animal abundance outnumbered the number of positive effects by a factor of 5; overall, 114 responses were negative, 22 were positive, and 56 showed no effect. Note, in some cases, there was more than one result for a particular species because some species were included in more than one study (Table 1). Second, there were some clear differences among the groups in Table 1. Amphibians and reptiles tended to show negative effects. Birds showed mainly negative or no effects, with a few positive effects for some small birds and for 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. General patterns for invertebrates were not apparent, because of the small number of studies for this group.

In the following three sections, we synthesize the information in Table 1 into a set of hypotheses predicting species responses to roads and traffic. This is based on the patterns in Table 1 and information on: (i) species behavioral responses to roads and traffic, (ii) species reproductive rates, movement ranges, and natural densities, and (iii) trophic interactions.

REASONS FOR NEGATIVE ROAD EFFECTS

There are two general categories of species or species groups showing negative effects of roads on animal abundance: species that are vulnerable to traffic disturbances (noise, lights, pollution, traffic motion) and species that are vulnerable to road mortality. Vulnerability to traffic disturbance likely explains many of the bird responses and some of the mid- and large-sized mammal responses in Table 1. Traffic noise seems to be a problem for communication among songbirds (Reijnen et al. 1996, Forman et al. 2002, Rheindt 2003), possibly leading to low abundances near roads, and direct

Table 1. Documented effects of roads and traffic on animal abundance.

Species or Species Group	Direction of Road or Traffic Effect	Reference(s)
Invertebrates		
invertebrate order diversity	neutral	Luce and Crowe (2001)
butterfly species richness	negative neutral	White and Kerr (2007) Munguira and Thomas (1992)
butterfly total abundance	neutral	Munguira and Thomas (1992)
carabid species richness	negative	Koivula and Vermeulen (2005)
carabid total abundance	negative	Koivula and Vermeulen (2005)
Calathus micropterus	negative	Koivula and Vermeulen (2005)
Carabus nemoralis	neutral	Koivula and Vermeulen (2005)
Pterostichus melanarius	neutral	Koivula and Vermeulen (2005)
Herptiles		
herptile species richness	negative	Findlay and Bourdages (2000)
Amphibians		
amphibian species richness	negative neutral	Findlay and Houlahan (1997) Parris (2006) Houlahan and Findlay (2003) Loehle et al. (2005)
amphibian total abundance	negative	Houlahan and Findlay (2003)
anuran species richness	negative	Eigenbrod et al. (2008a)
anuran total abundance	negative neutral	Fahrig et al. (1995) Fahrig et al. (1995)
salamander relative species richness	negative	Porej et al. (2004)
salamander total abundance	negative	Semlitsch et al. (2007) deMaynadier and Hunter (2000)
American toad (*Bufo americanus*)	negative	Eigenbrod et al. (2008a) Trenham et al. (2003)
treefrog (*Hyla arborea*)	negative	Pellet et al. (2004a, b)
Cope's gray tree frog (*Hyla chrysoscelis*)	neutral	Trenham et al. (2003)
gray treefrog (*Hyla versicolor*)	negative neutral	Houlahan and Findlay (2003) Eigenbrod et al. (2008a) Trenham et al. (2003)

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spadefoot toad (*Pelobates fuscus*)	negative neutral	Nyström et al. (2007) Nyström et al. (2002)
spring peeper (*Pseudacris crucifer*)	negative neutral	Houlahan and Findlay (2003) Eigenbrod et al. (2008a) Trenham et al. (2003)
western chorus frog (*Pseudacris triseriata*)	neutral	Trenham et al. (2003)
moor frog (*Rana arvalis*)	negative	Vos and Chardon (1998)
green frog (*Rana clamitans*)	negative neutral	Houlahan and Findlay (2003) Eigenbrod et al. (2008a) Trenham et al. (2003) Carr and Fahrig (2001)
leopard frog (*Rana pipiens*)	negative neutral	Eigenbrod et al. (2008a) Carr and Fahrig (2001) Trenham et al. (2003)
mink frog (*Rana septentrionalis*)	negative	Houlahan and Findlay (2003)
wood frog (*Rana sylvatica*)	negative neutral positive	Houlahan and Findlay (2003) Eigenbrod et al. (2008a) Porej et al. (2004) Skidds et al. (2007) Trenham et al. (2003)
spotted salamander (*Ambystoma maculatum*)	neutral	Porej et al. (2004) Skidds et al. (2007)
smallmouth salamander (*Ambystoma texanum*)	neutral	Porej et al. (2004)
Jefferson's salamander (*Ambystoma jeffersonianum*)	neutral	Porej et al. (2004)
tiger salamander (*Ambystoma tigrinum tigrinum*)	negative	Porej et al. (2004)
blue-spotted salamander (*Ambystoma laterale*)	negative	Houlahan and Findlay (2003)
Appalachian seal salamander (*Desmognathus monticola*)	negative	Ward et al. (2008)
mountain dusky salamander (*Desmognathus ochrophaeus*)	negative	Ward et al. (2008)
northern two-lined salamander (*Eurycea bislineata*)	positive	Ward et al. (2008)
southern gray-cheeked salamander (*Plethodon metcalfi*)	negative	Semlitsch et al. (2007)
red-spotted newt (*Notophthalmus viridescens viridescens*)	negative	Porej et al. (2004)

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Reptiles		
reptile species richness	neutral	Loehle et al. (2005)
snake total abundance	negative neutral	Rudolph et al. (1999) Sullivan (2000)
turtle total abundance	negative	Gibbs and Shriver (2002)
large-bodied turtle total abundance	negative	Gibbs and Shriver (2002)
small-bodied turtle total abundance	neutral	Gibbs and Shriver (2002)
eastern diamondback rattlesnake (*Crotalus adamanteus*)	positive	Steen et al. (2007)
timber rattlesnake (*Crotalus horridus*)	negative	Steen et al. (2007)
black ratsnake (*Elaphe obsoleta*)	negative	Row et al. (2007)
Galápagos lava lizard (*Microlophus albemarlensis*)	negative	Tanner and Perry (2007)
painted turtle (*Chrysemys picta bellii*)	negative	Fowle (1990)
desert tortoise (*Gopherus agassizii*)	negative	Boarman and Sazaki (2006)
Birds		
bird species richness	negative	Findlay and Bourdages (2000) Findlay and Houlahan (1997)
Small birds		
small bird summed density	negative	Reijnen et al. (1996)
grassland bird presence	negative	Forman et al. (2002)
grassland passerines total abundance	neutral	Warner (1992)
Yellow Thornbill (*Acanthiza nana*)	positive*	Pocock and Lawrence (2005)
Skylark (*Alauda arvensis*)	negative	Reijnen et al. (1996)
Meadow Pipit (*Anthus pratensis*)	negative	Reijnen et al. (1996)
Florida Scrub Jay (*Aphelocoma coerulescens*)	negative	Mumme et al. (2000)
Linnet (*Carduelis cannabina*)	negative	Peris and Pescador (2004)
Goldfinch (*Carduelis carduelis*)	neutral	Peris and Pescador (2004)
Greenfinch (*Carduelis chloris*)	neutral	Peris and Pescador (2004)
Short-toed Treecreeper (*Certhia brachydactyla*)	neutral	Peris and Pescador (2004)
Bobolink (*Delichonyx oryzivorus*)	negative	Forman et al. (2002)

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Galah (*Eolophus roseicapillus*)	negative*	Pocock and Lawrence (2005)
Pied Flycatcher (*Ficedula hypoleuca*)	negative	Kuitunen et al. (2003)
Chafffinch (*Fringilla coelebs*)	neutral	Peris and Pescador (2004)
Crested Lark (*Galerida cristata*)	neutral	Peris and Pescador (2004)
Oystercatcher (*Haematopus ostralegus*)	negative neutral	Reijnen et al. (1996) van der Zande et al. (1980)
Woodchat Shrike (*Lanius senator*)	negative	Peris and Pescador (2004)
Yellow-Tufted Honeyeater (*Lichenostomus melanops*)	negative*	Pocock and Lawrence (2005)
Fuscous Honeyeater (*Lichenostomus fuscus*)	negative*	Pocock and Lawrence (2005)
Black-tailed Godwit (*Limosa limosa*)	negative	Reijnen et al. (1996) van der Zande et al. (1980)
Woodlark (*Lullula arborea*)	negative	Peris and Pescador (2004)
Superb Fairy-Wren (*Malurus cyaneus*)	positive*	Pocock and Lawrence (2005)
Corn Bunting (*Miliaria calandra*)	positive	Peris and Pescador (2004)
Yellow Wagtail (*Motacilla flava*)	neutral/negative	Reijnen et al. (1996)
Wheatear (*Oenanthe oenanthe*)	negative	Peris and Pescador (2004)
Striated Pardalote (*Pardalotus striatus*)	negative*	Pocock and Lawrence (2005)
Blue Tit (*Parus caeruleus*)	neutral	Peris and Pescador (2004)
Great Tit (*Parus major*)	neutral	Peris and Pescador (2004)
House Sparrow (*Passer domesticus*)	positive	Peris and Pescador (2004)
Rock Sparrow (*Passer petronia*)	positive	Peris and Pescador (2004)
Black Redstart (*Phoenicurus ochrurus*)	neutral	Peris and Pescador (2004)
Iberian Chiffchaff (*Phylloscopus brehmii*)	negative	Peris and Pescador (2004)
Serin (*Serinus serinus*)	neutral	Peris and Pescador (2004)
Nuthatch (*Sitta europaea*)	neutral	Peris and Pescador (2004)
Eastern Meadowlark (*Sturnella magna*)	negative	Forman et al. (2002)
Starling (*Sturnus unicolor*)	neutral	Peris and Pescador (2004)
Blackbird (*Turdus merula*)	negative	Peris and Pescador (2004)
Lapwing (*Vanellus vanellus*)	negative	Reijnen et al. (1996) van der Zande et al. (1980)

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Large birds		
Shoveler (*Anas clypeata*)	negative	Reijnen et al. (1996)
Mallard (*Anas platyrhynchos*)	neutral/negative	Reijnen et al. (1996)
Tufted Duck (*Aythya fuligula*)	neutral/negative	Reijnen et al. (1996)
Turkey Vulture (*Cathartes aura*)	positive	Coleman and Fraser (1989)
Black Vulture (*Coragyps atratus*)	positive	Coleman and Fraser (1989)
Mute Swan (*Cygnus olor*)	neutral/negative	Reijnen et al. (1996)
Coot (*Fulica atra*)	negative	Reijnen et al. (1996)
Sandhill Crane (*Grus canadensis*)	negative	Norling et al. (1992)
Bald Eagle (*Haliaeetus leucocephalus*)	negative	Anthongy and Isaacs (1989) Paruk (1987)
Redshank (*Tringa tetanus*)	neutral/negative	Reijnen et al. (1996)
Mammals		
mammal species richness	neutral/negative	Findlay and Houlahan (1997)
Small mammals		
small mammal species richness	neutral	Garland and Bradley (1984)
small mammal total abundance	neutral positive*	Garland and Bradley (1984) Rosa and Bissonette (2007) Adams and Geis (1983)
white-tailed antelope squirrel (*Ammospermophilus leucurus*)	neutral	Garland and Bradley (1984)
black-tailed prairie dog (*Cynomys ludovicianus*)	positive	Johnson and Collinge (2004)
Merriam's kangaroo rat (*Dipodomys merriami*)	neutral	Garland and Bradley (1984)
kangaroo rat (*Dipodomys microps*)	positive*	Rosa and Bissonette (2007)
prairie vole (*Microtus ochrogaster*)	neutral/positive	Adams and Geis (1983)
California vole (*Microtus californicus*)	neutral/positive	Adams and Geis (1983)
house mouse (*Mus musculus*)	positive	Garland and Bradley (1984)
woodrat (*Notoma lepida*)	neutral	Garland and Bradley (1984)
golden mouse (*Ochrotomys nuttalli*)	neutral/positive	Adams and Geis (1983)
long-tailed pocket mouse (*Perognathus formosus*)	neutral	Garland and Bradley (1984)
brush mouse (*Peromyscus boylii*)	neutral/negative*	Rosa and Bissonette (2007)

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white-footed mouse (*Peromyscus leucopus*)	neutral neutral/positive positive	McGregor et al. (2008) Adams and Geis (1983) Rytwinski and Fahrig (2007)
deer mouse (*Peromyscus maniculatus*)	neutral/positive	Adams and Geis (1983)
ship rat (*Rattus rattus*)	neutral	Garland and Bradley (1984)
eastern chipmunk (*Tamias striatus*)	positive	McGregor et al. (2008)
Medium-sized mammals		
chacoan peccary (*Catagonus wagneri*)	negative	Altrichter and Boaglio (2004)
hedgehog (*Erinaceus europaeus*)	negative	Huijser and Bergers (2000)
brown hare (*Lepus europaeus*)	negative	Roedenbeck and Voser (2008)
American marten (*Martes americana*)	neutral	Mowat (2006)
badger (*Meles meles*)	negative	van der Zee et al. (1992) Roedenbeck and Köhler (2006)
koala (*Phascolarctos cinereus*)	negative	McAlpine et al. (2006)
white-lipped peccary (*Tayassu pecari*)	neutral	Altrichter and Boaglio (2004)
collared peccary (*Tayassu tajacu*)	neutral	Altrichter and Boaglio (2004)
red fox (*Vulpes vulpes*)	negative	Roedenbeck and Köhler (2006)
Large mammals		
impala (*Aepyceros melampus*)	neutral	Newmark et al. (1996)
moose (*Alces alces*)	neutral	Kunkel and Pletscher (2000)
wolf (*Canis lupus*)	negative	Fuller (1989) Mech et al.)1988) Thiel (1985) Jedrzejewski et al. (2004) Karlsson et al. (2007)
eastern timber wolf (*Canis lupus lycaon*)	negative	Jensen et al. (1986) Mladenoff et al. (1995)
black-backed jackal (*Canis mesomelas*)	negative	Newmark et al. (1996)
roe deer (*Capreolus capreolus*)	negative	Roedenbeck and Köhler (2006)
elk (*Cervus canadensis*)	negative	Rost and Bailey (1979)
wildebeest (*Connochaetes taurinus*)	neutral/negative	Newmark et al. (1996)
zebra (*Equus quagga*)	neutral/negative	Newmark et al. (1996)
giraffe (*Giraffa camelopardalis*)	neutral	Newmark et al. (1996)
African elephant (*Loxondonta africana*)	negative	Newmark et al. (1996) Barnes et al. (1991)

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bobcat (*Lynx rufus*)	negative	Lovallo and Anderson (1996)
Eurasian lynx (*Lynx lynx*)	negative	Niedzialkowska et al. (2006)
Iberian lynx (*Lynx pardinus*)	negative	Palma et al. (1999)
Mule Deer (*Odocoileus hemionus*)	negative	Rost and Bailey (1979)
Amur tiger (*Panthera tigris altaica*)	negative	Kerley et al. (2002)
warthog (*Phacochoerus africanus*)	neutral	Newmark et al. (1996)
cougar (*Puma concolor*)	negative	van Dyke et al. (1986) Dickson and Beier (2002)
woodland caribou (*Rangifer tarandus caribou*)	negative	Dyer et al. (2001)
bohor reedbuck (*Redunca redunca*)	negative	Newmark et al. (1996)
wild boar (*Sus scrofa*)	negative	Roedenbeck and Köhler (2006)
eland (*Taurotragus oryx*)	negative	Newmark et al. (1996)
brown bear (*Ursus arctos*)	negative	Suring et al. (2006)
grizzly bear (*Ursus arctos horribilis*)	negative	Ciarniello et al. (2007) Mace et al. (1996) McLellan and Shackleton (1988)

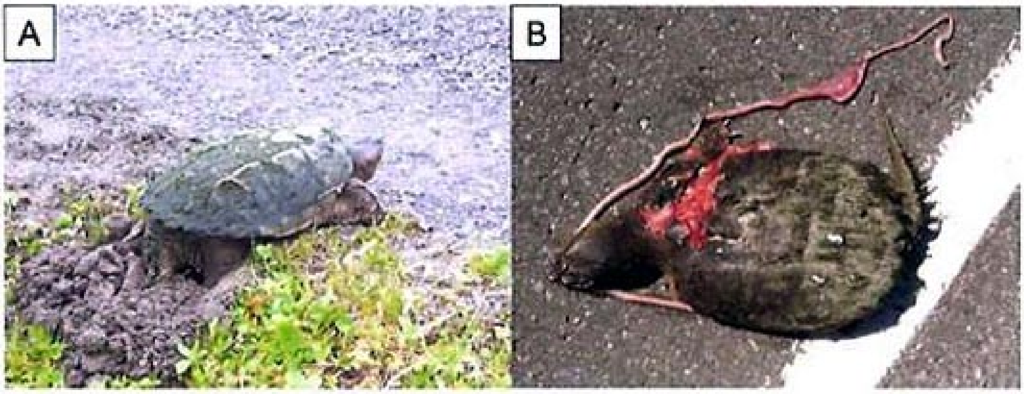
*based on our analyses of data presented in paper

observations and radiotelemetry studies of large mammals have documented behavioral avoidance of roads for some species (Brody and Pelton 1989, Lovallo and Anderson 1996, Dyer et al. 2002).

Vulnerability to road mortality likely explains most of the amphibian and reptile responses, as well as some of the mid-sized and large mammal responses. Several factors combine to make a species vulnerable to road mortality. Species that are either attracted to roads or do not avoid roads, and that show low car avoidance (e.g., slow-moving species) are particularly vulnerable (van Langevelde and Jaarsma 2005). This combination is most likely responsible for the frequent negative effects of roads and traffic on abundances of amphibians and reptiles. For example, some snakes use the road surface for thermoregulation (Sullivan 1981), some turtles lay their eggs in gravel roads or road shoulders (Aresco 2005, Steen et al. 2006; pers. obs., Fig. 1), and natterjack toads (*Bufo calamita*) apparently equate roads with open sandy habitats to which they are naturally attracted (Stevens et al. 2006). Other studies have found that some frogs and snakes, although not necessarily attracted to roads, do not behaviorally avoid them (Row et al. 2007; J. Bouchard, A. T. Ford, F. Eigenbrod, and L. Fahrig, unpublished manuscript). Therefore, these animals are likely to enter the road surface and, in combination with their need for seasonal migrations between breeding and overwintering sites, as well as their slow movement across the road, experience very high mortality rates (Hels and Buchwald 2001; J. Bouchard, A. T. Ford, F. Eigenbrod, and L. Fahrig, unpublished manuscript). Further exacerbating this low car avoidance is the fact that some species, including frogs (Mazerolle et al. 2005), actually respond to traffic on the road by stopping, thus increasing the time spent on the road and making them even more likely to be killed.

As discussed above, a second group of species that is particularly vulnerable to road mortality are species that have large movement ranges and low reproductive rates, and do not avoid roads or traffic (Gibbs and Shriver 2002, Forman et al. 2003). These

Fig. 1. A. Snapping turtle (*Chelydra serpentina*) digging a nest on the shoulder of a paved road. B. Snapping turtle killed by traffic on the same road. (Photos courtesy of Ewen Eberhardt.)



attributes interact with the animal's behavioral responses to roads to affect animal abundances. If animals with very large movement ranges do not avoid roads, their high frequency of road crossing leads to a high overall probability of being killed at some point. Because animals with large movement ranges typically have low reproductive rates (e.g., large carnivores), they cannot quickly compensate for higher mortality through higher reproduction, so the mortality leads to population declines. For example, in California, Dickson and Beier (2002) showed that cougars readily cross roads within their territories, i.e., they do not avoid roads. However, cougar territories contain lower road densities than areas without cougars. In Florida, it was shown that road mortality killed over 20% of all cougars (Florida panthers (*Puma concolor*)) (Land and Lotz 1996). Therefore, it seems likely that cougars are absent from areas of high road density because of the high probability of mortality in those areas.

It is important to note that to determine whether a particular negative effect of roads on animal abundance is due to mortality or traffic disturbance, we need information on per capita traffic mortality rates and/or behavioral responses to roads and traffic (preferably both). If we only have information on the distribution of animals with respect to roads, we cannot distinguish between these two causes. Animal numbers may be low near roads and/or in landscapes with high road density either because the mortality rate is high in these areas, which depresses the populations, or because animals avoid these locations because of the traffic disturbance. Higher mortality rates in roaded areas would support the former (e.g., Fahrig et al. 1995), and analyses of movement paths showing deviations away from roads would support the latter (e.g., Whittington et al. 2004). Note that Roedenbeck et al. (2007) state that distinguishing between these is a priority for road-ecology research: their fourth research question is "What is the relative importance of the different mechanisms by which roads affect population persistence?"

REASONS FOR POSITIVE ROAD EFFECTS OR NO ROAD EFFECT

When animals are attracted to roads for a resource but have the cognitive ability and movement speed to allow them to avoid being killed by vehicles (i.e., car avoidance), there can be a net positive effect of roads on animal abundance. For example, some vultures have high densities near roads, presumably because of the availability of food (road-killed animals) (Table 1) and their ability to lift themselves off the road in time to avoid oncoming traffic (pers. obs.).

Species showing no effect of roads on abundance are those with the inverse of the factors above ("Reasons for negative effects"). Species that avoid going onto roads but are not disturbed by road traffic, and have small movement ranges, small territory sizes, and high reproductive rates are unlikely to be affected by roads because road mortality is low and viable populations can exist within areas bounded by roads. This combination of conditions likely explains the lack of effect or weak effects for several small birds and small mammals (Table 1).

Finally, if such a species is prey for other species that are negatively affected by roads, the abundance of the prey species may actually be positively related to roads, due to the release from predation in roaded areas. This combination of factors is most likely the cause of the predominantly positive effects of roads on small mammal abundances in Table 1. Several studies have shown that small mammals avoid going onto roads, presumably because of the lack of protective cover (Ford and Fahrig 2008, McGregor et al. 2008), and several predators of small mammals have been shown to be negatively affected by roads, including foxes, badgers, and snakes (Table 1).

SYNTHESIS

The results of the literature review (Table 1) and the information and ideas discussed above are summarized in Fig. 2. This figure represents a set of predictions of the conditions that lead to strong or weak negative or positive effects or no effect of roads and traffic on animal abundance.

Strong negative effects of roads are predicted in four situations. First, any species that is attracted to roads and is unable to avoid individual cars (e.g., species that are too slow moving) should be negatively affected by roads. Second, all species with large movement ranges, low reproductive rates, and low natural densities should be negatively affected by roads and traffic, irrespective of their behavioral response to roads. Those that do not avoid roads and traffic are susceptible to high mortality effects and those that do avoid roads or traffic disturbance or emissions are susceptible to habitat loss, i.e., otherwise suitable habitat becomes inaccessible or underused. Third, smaller animals whose populations are not limited by road-affected predators but who avoid habitat near roads are negatively affected by roads through habitat loss. Finally, small animals whose populations are not limited by road-affected predators, have no road or traffic avoidance, and are not able to avoid oncoming cars show negative responses to roads due to traffic mortality.

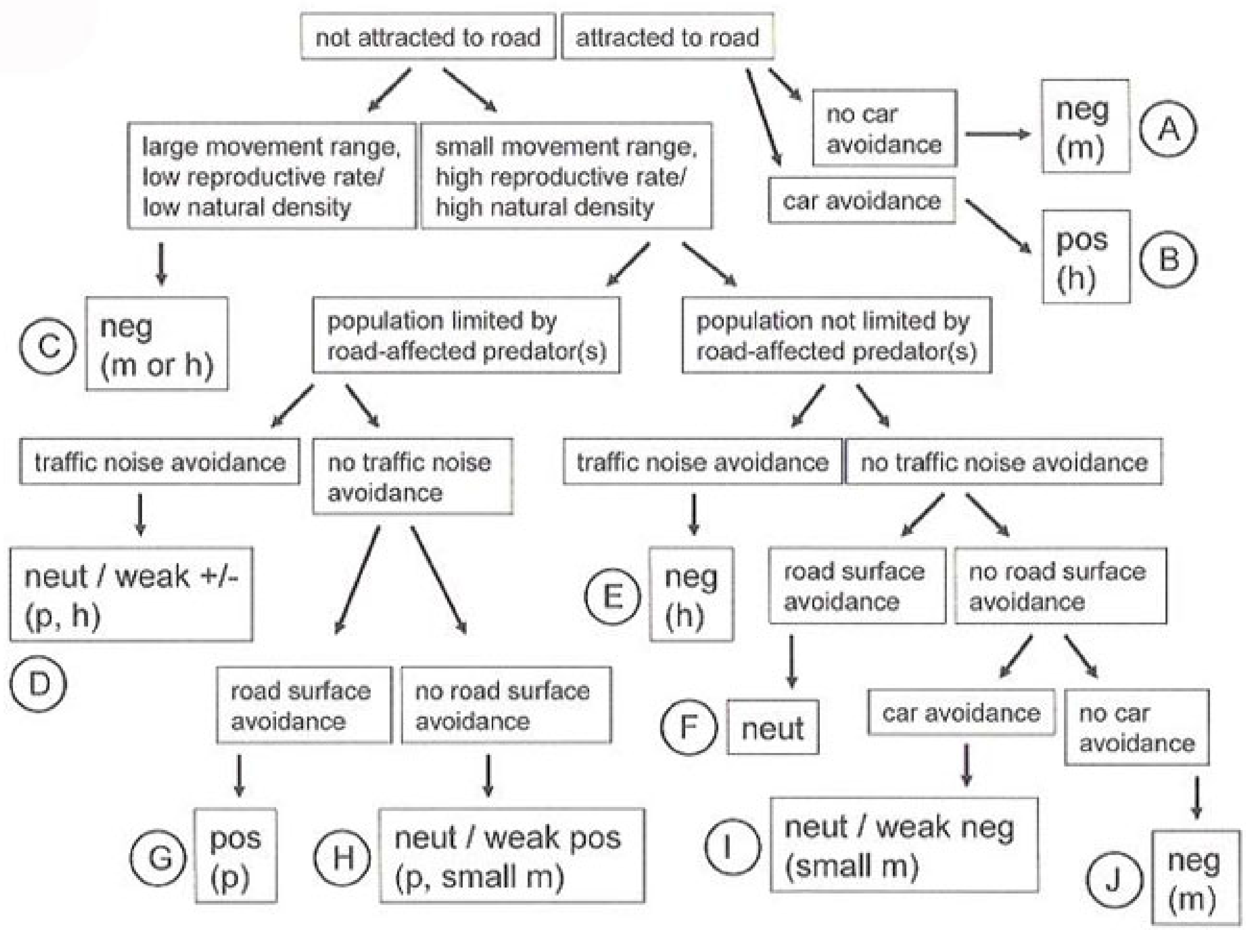
Strong positive effects of roads on animal abundance are predicted in two situations. First, roads should produce a net increase in abundance for species that are attracted to roads for an important resource (e.g., food) and are able to avoid oncoming cars. Second, roads should produce a net increase in abundance for species that do not avoid traffic disturbance or emissions (low habitat loss) but do avoid roads (low road mortality), and whose main predators show negative population-level responses to roads (predator release).

The four conditions leading to negative road effects are likely much more common than the two conditions leading to positive road effects, which most likely is the reason that there are five times as many recorded negative road effects as positive road effects (Table 1). Note, however, that this estimate may be biased if researchers purposefully select study species and situations in which they expect a negative effect of roads a priori. The remaining four (of 10) conditions in Fig. 2 lead to either no effect or only a weak positive or negative effect of roads. We hypothesize that this is the reason for the 35% of effects in Table 1 that are neutral or weak.

DISCUSSION

Probably the most surprising result of this study, at least to us, is the very large number of studies, 79 in all, that quantified the relationships between animal abundance and roads or traffic. Before completing this review, we had been under the apparently mistaken impression that very few such studies existed. There are several reasons for this discrepancy. First, 71% (56 of 79) of the studies were published within the last 8 years (since 2000; Table 1), so the impression that there are few population-level studies (see Introduction) is simply outdated. Second, many of the studies we found were not primarily "about" road effects. Roads were included in a set of possible predictor variables, but the author(s) did not focus on roads as the main "story" in the paper, so these papers are not widely known among road ecologists. We found these papers mainly by reading papers that cited well-known, older road-ecology papers. It is possible that there are still more papers in this category that we have missed in our review. The third reason for the discrepancy is that, although papers showing a lack of animals in roaded areas are in fact evidence for effects of roads on animal abundance, the authors sometimes do not present the work in this way. Rather, it is fairly common to interpret such studies

Fig. 2. Summary of the factors affecting the size and direction of road effects on animal abundance, with 10 possible cases. Each case is defined by all the conditions leading to it through the arrows above. “neg,” “pos,” and “neut” refer to negative, positive, and neutral effects of roads on abundance (respectively). “m,” “h,” and “p” refer to the mechanisms creating road effects on the populations: mortality, habitat loss or increase, and predation release (respectively). Mortality and habitat loss are negative effects, and habitat increase and predation release are positive effects of roads on animal abundance. Examples of species in each case are: some turtles and snakes (A), vultures (B), large mammals, some mid-sized mammals, and some large birds (C), some small birds (D and E), small mammals (F, G, H, I), and amphibians (J).



as evidence for a behavioral avoidance of roads by these animals. As discussed above, this inference is not valid; the mechanism (mortality or avoidance) for reduced abundance cannot be inferred without additional information. Finally, it may not be widely appreciated that studies of road density in animal territories are actually studies of road effects on animal abundance: if territories have lower road densities than control areas, the corollary is that areas with high road densities have lower abundances (or lower probability of occurrence) than areas with low road densities.

Although our literature review revealed many more studies than we anticipated, the evidence for population-level effects of roads in many of these studies is compromised because of weaknesses in study design. Studies where road effects were not the main interest of the author were typically not designed a priori with the intention of quantifying the effects of roads independent of other variables. Roads or areas of high road density are, therefore, frequently correlated with other variables. For example, if areas of high road density typically have lower habitat amounts, it is not possible to state conclusively that the negative effects of roads are real, i.e., they could be effects of habitat loss. This problem is recognized by some authors (e.g., Houlahan and Findlay 2003, Roedenbeck and Köhler 2006), and is bound to occur in any study in which the sample sites are selected randomly or systematically in space, without attention to the distribution of possible confounding variables. Such correlations are one of the main reasons that road-ecology research generally has low inferential strength (Roedenbeck et al. 2007).

There are three possible solutions to this problem. The first is to select sites while controlling for possible confounding variables. For example, in our study of effects of road density on small mammal abundance, we selected landscapes ranging in road density, but with the constraint that small mammal habitat variables had to be constant across sites and landscapes (Rytwinski and Fahrig 2007). A second approach is to select sites such that road density varies independently of possible confounding variables. For example, Eigenbrod et al. (2008a) purposefully selected landscapes varying widely in traffic density and forest cover such that there was no correlation across landscapes between these two variables. This was accomplished by searching for landscapes with unusual combinations such as both high traffic density and high forest cover. These first two approaches are termed “mensurative experiments.” The final and arguably best solution is to conduct a full “before–after–control–impact” (BACI) experiment in which animal abundance is studied for several years both before and after road construction, at both control and road construction sites (Roedenbeck et al. 2007). This sort of study is extremely rare; we are aware of a few before–after studies of animal use of road mitigation structures, but we are not aware of any road BACI studies on animal abundance. Therefore, despite the large number of studies in Table 1, there is still an urgent need for well-designed studies of road effects on animal abundance.

Although derived from the existing literature, the predictions in Fig. 2 still need to be tested with independent data. This requires obtaining not only information on road effects on population abundance, but also information on the species’ movement range and its behavioral responses to roads, traffic emissions, and oncoming vehicles, and in some cases, information on the population responses of its major predators to roads and traffic. Although some of this information is available for some species, usually the full set is not available for a particular species. In addition, we emphasize that information on behavioral responses to roads needs to be clearly distinguished from information on road mortality (Karlsson et al. 2007). For example, deMaynadier and Hunter (2000) showed reduced salamander movements and Noordijk et al. (2006) showed reduced ground beetle movements across roads, but their sampling methods did not allow them to determine whether this reduction was due to mortality or avoidance, so this information cannot be used in testing predictions in Fig. 2.

On first reading, it may seem that our synthesis and the predictions in Fig. 2 miss one of the main mechanisms proposed for negative population-level effects of roads, namely the movement barrier effect, or reduction in landscape connectivity. If roads are a barrier to animal movement, they should reduce animal abundance by fragmenting habitat, thus increasing local extinction rate and reducing colonization rate, and by reducing animal access to critical resources (Jaeger et al. 2005). These processes are actually subsumed within the main effects of mortality and traffic disturbance because both of these processes result in an underutilization of the available habitat. In fact, Eigenbrod et al. (2008b) showed that “accessible habitat,” defined as the habitat available to pond-dwelling amphibians without individuals needed to cross a major road, was a better predictor of amphibian species richness than simply the amount of habitat within some distance of the ponds. This reduction in species richness is likely caused by lack of immigration to ponds with low amounts of accessible habitat, where the low immigration may be due to either mortality of individuals attempting to cross the road, or avoidance of the road due to traffic noise or other emissions. Note again that when the road presents a physical barrier to movement, e.g., because of fencing along the road, the effect on the population is equivalent to the animal showing an extremely strong behavioral avoidance of the road itself.

In conclusion, our review of the empirical literature revealed many more population-level studies on road effects than we were initially expecting based on statements in the literature (Underhill and Angold 2000, Roedenbeck et al. 2007). Studies have been conducted on a wide range of taxa, and overall there is strong evidence for negative effects of roads at the population level. Although more research in this area is still needed because of the issues discussed above, it seems the evidence is certainly strong enough to merit routine consideration of mitigation of these effects in road construction and maintenance projects. The synthesis in Fig. 2 suggests that appropriate mitigation will depend on whether the species of concern in a particular instance are affected mainly through road mortality or through traffic disturbance. Fencing and wildlife crossings (ecopassages) can be used to mitigate road effects for species affected mainly through mortality (amphibians, reptiles, some mammals), whereas road and traffic effects on species affected mainly through traffic disturbance (birds, some large mammals) can likely only be mitigated by reducing road and traffic density in the landscape. Finally, we note that the large base of research on population-level effects is sufficient to justify increased research attention to the other questions raised in the Rauischholzhausen agenda (Roedenbeck et al. 2007) such as: what is the relative importance of road effects vs. other impacts on population persistence (e.g., Eigenbrod et al. 2008a) and under what circumstances can road effects be mitigated (van der Ree et al. 2007)?

Responses to this article can be read online at:
http://www.ecologyandsociety.org/vol14/iss1/art21/responses/

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