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REVIEW OF THE FACTORS UNDERLYING THE MECHANISMS AND EFFECTS OF ROADS ON VERTEBRATES

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ABSTRACT

Road ecology is an emerging discipline that attempts to understand the patterns and processes related with road-ecosystem interactions to establish effective mitigation measures of the negative effects of roads on wildlife. Although many advances have been made over the past 10 years, many questions are still unanswered or the information is incomplete. We discussed the factors (characteristics of roads) involved in mechanisms and effects of roads on vertebrates and the knowledge gaps. The factors evaluated were road density, road maintenance involving chemicals, presence of vehicles and traffic volume. We identified five mechanisms resulting from these factors: car avoidance, noise avoidance, road surface avoidance, road attraction and wildlife-vehicle-collisions (WVC). Density of roads causes road surface avoidance, road attraction and WVC; maintenance of roads with chemicals causes noise avoidance, road attraction and WVC; vehicle presence causes noise avoidance, car avoidance and WVC; and traffic volume causes noise avoidance and WVC. WVC was the only mechanism linked to all road factors and it occurs in combination with another mechanism (road attraction); therefore, we believe this to be the mechanism that affects most organisms. We identified many knowledge gaps related primarily to identifying the mechanisms triggered by various factors, especially for tropical organisms. We believe that studies involving tropical species could provide new results due to their greater ecological demands compared with temperate species.
Keywords: Roadkill; road surface avoidance; noise avoidance; car avoidance; road attraction.

RESUMO

REVISÃO DOS FATORES SUBJACENTES AOS MECANISMOS E EFEITOS DE RODOVIAS EM VERTEBRADOS. A ecologia de estradas é uma disciplina emergente que busca entender os padrões e processos envolvidos na interação rodovias-ecossistemas para estabelecer medidas efetivas de mitigação aos efeitos negativos da rodovia sobre a vida selvagem. Embora muitos avanços tenham sido feitos nos últimos 10 anos, muitas questões ainda estão sem resposta ou possuem informações incompletas. Nós apontamos os fatores (características da rodovia) envolvidos nos mecanismos e efeitos da rodovia sobre vertebrados e as lacunas de conhecimento. Os fatores avaliados foram densidade de rodovias, manutenção de rodovias com substâncias químicas, presença do veículo e tráfego de veículos. Nós identificamos cinco mecanismos resultantes desses fatores: repulsa do veículo, repulsa do ruído, repulsa da superfície da rodovia, atração pela rodovia e atropelamento (WVC). Densidade da rodovia causa repulsa da superfície da rodovia, atração pela rodovia e WVC; manutenção da rodovia com substâncias químicas causa repulsa do ruído, atração pela rodovia e WVC; presença do veículo causa repulsa do ruído, repulsa do veículo e WVC; e tráfego de veículos causa repulsa do ruído e WVC. WVC foi o único mecanismo relacionado a todos os fatores da rodovia e ocorrer associado a outro mecanismo (atração pela rodovia); portanto, nós acreditamos que esse seja o mecanismo que mais afeta os organismos. Nós identificamos muitas lacunas de conhecimento relacionadas principalmente a identificação dos mecanismos desencadeados pelos fatores, especialmente para organismos tropicais. Nós acreditamos que estudos envolvendo espécies tropicais possam fornecer novos resultados devido as diferentes exigências ecológicas dessas espécies quando comparado a espécies de zonas temperadas.

Palavras-chave: Atropelamentos; evitação de estradas; evitação de ruídos; evitação de carros; atração por rodovias.

RESUMEN

REVISIÓN DE LOS FACTORES QUE SUBYACEN LOS MECANISMOS Y EFECTOS DE CARRETERAS SOBRE LOS VERTEBRADOS. La ecología de carreteras es una disciplina emergente que pretende entender los patrones y procesos relacionados con las interacciones entre carreteras y ecosistemas, para establecer medidas efectivas de mitigación de los efectos negativos de las carreteras sobre la vida silvestre. Aunque se ha avanzado bastante en los últimos 10 años, varias preguntas siguen sin responder o la información está incompleta. Nuestro objetivo fue discutir los factores (características de las carreteras) involucrados en los mecanismos y efectos de las carreteras sobre los vertebrados y las lagunas en el conocimiento. Los factores evaluados fueron la densidad de la malla vial, el mantenimiento con sustancias químicas, la presencia de vehículos y el volumen del tráfico. Identificamos cinco mecanismos que derivan de estos factores: evitación de los carros, evitación del ruido, evitación de la superficie de la carretera, atracción por la carretera y colisiones entre vehículos y animales silvestres (WVC). La densidad de las vías causa la evitación de la superficie de la carretera, la atracción por la carretera y colisiones con vehículos; el mantenimiento de carreteras con productos químicos causa la evitación del ruido, la atracción por la carretera y colisiones con vehículos; la presencia de vehículos causa la evitación del ruido, la evitación de carros y las colisiones con vehículos; y el volumen del tráfico causa evitación del ruido y colisiones con vehículos. Las colisiones son el único mecanismo relacionado con todos los factores mencionados y puede ocurrir en combinación con otro mecanismo (la atracción por la carretera); por lo tanto creemos que éste es el mecanismo que afecta a la mayor parte de los animales. Identificamos varias lagunas en el conocimiento, relacionadas principalmente con la identificación de los mecanismos causados por varios factores, particularmente para organismos tropicales. Sugerimos que estudios que incluyan especies tropicales podrían generar nuevos resultados debido a su mayor demanda ecológica, comparada con la de especies de regiones templadas.

Palabras clave: Muerte en carretera; evitación de la superficie de la carretera; evitación del ruido; evitación de los vehículos; atracción por la carretera.

INTRODUCTION

At the end of the 20th century, road ecology was consolidated to be a discipline dedicated to understanding the processes involved in road-ecosystem interactions for creating effective mitigation measures (Forman & Alexander 1998, Forman *et al.* 2003). The growing global road networks and the need to assess the impacts of road implementation and expansion have generated an increased demand for research in the field of road ecology.

Reviews have defined the scope of road ecology research and describe many advances in understanding the effects of roads on wildlife and ecosystems, particularly over the last 10 years (e.g., Forman & Alexander 1998, Laurance *et al.* 2009). The main road effects are the barrier effect, when the organisms can't cross the road surface, and the edge effect, when occur an alteration of ecology, biology or behavior of organisms in vicinity of roads (Fahrig & Rytwinski 2009). These effects can be negative, neutral or positive. They are negative when we can see a reduction in individual fitness, population size, loss and alteration of species composition; neutral when there is no significant effect on the individual, population or community; positive when it leads to increased fitness, population size and number of species (Saunders *et al.* 1991, Cushman 2006).

These effects occur due to mechanisms triggered by factors (or characteristics) of the road (e.g. density, traffic volume, road verge). The main mechanisms are wildlife-vehicle-collisions (WVC), road surface avoidance, noise avoidance, car avoidance and road attraction. The WVC mechanism is related to collisions between vehicles and animals. Road surface avoidance depends on factors such as traffic volume and was related to aversion of individuals to the immediate edge of road surface due to paving, changes in the microclimate and vegetation at the edge. Noise avoidance is related to the individuals' aversion to traffic emissions, such as sound, light and chemical pollutants, and is therefore related to traffic volume.

Car avoidance is a phenomenon related to a short-range individual aversion to a vehicle that can occur with a single vehicle moving and is independent of traffic volume (Jaeger *et al.* 2005). Road attraction refers to an attraction caused by increased resource availability (carcasses, seeds) (Erritzoe *et al.* 2003, Antworth *et al.* 2005), nesting areas (Aresco 2005) or thermoregulation (Sullivan 1981).

Road surface avoidance, car avoidance, road attraction and WVC cause barrier effect. Individuals with road surface avoidance are tolerant to the microhabitat of road edges but not to road surface. Thus, these species do not cross the road. Car avoidance occurs when animals are tolerant to the microhabitats of road edges and the road surface, but they avoid crossing the road due to immediate presence of vehicles (Jaeger *et al.* 2005). WVC occur when individuals are tolerant of road edge and surface microhabitats, but are killed by vehicles prior to crossing the road, causing barrier effect. The road attraction mechanism is related to the WVC mechanism because individuals are attracted to the surface of road where they are vulnerable to collisions with vehicles (Barrientos & Bolonio 2009) (Figure 1).

Road attraction and noise avoidance cause edge effect. Individuals with noise avoidance avoid the vicinity of roads due to changes in the edge microhabitats (Jaeger *et al.* 2005). On the other hand, the mechanism of road attraction causes a positive edge effect; the animals are attracted to road, so the occurrence and abundance of individuals increases at road edges (Fahrig & Rytwinski 2009) (Figure 1).

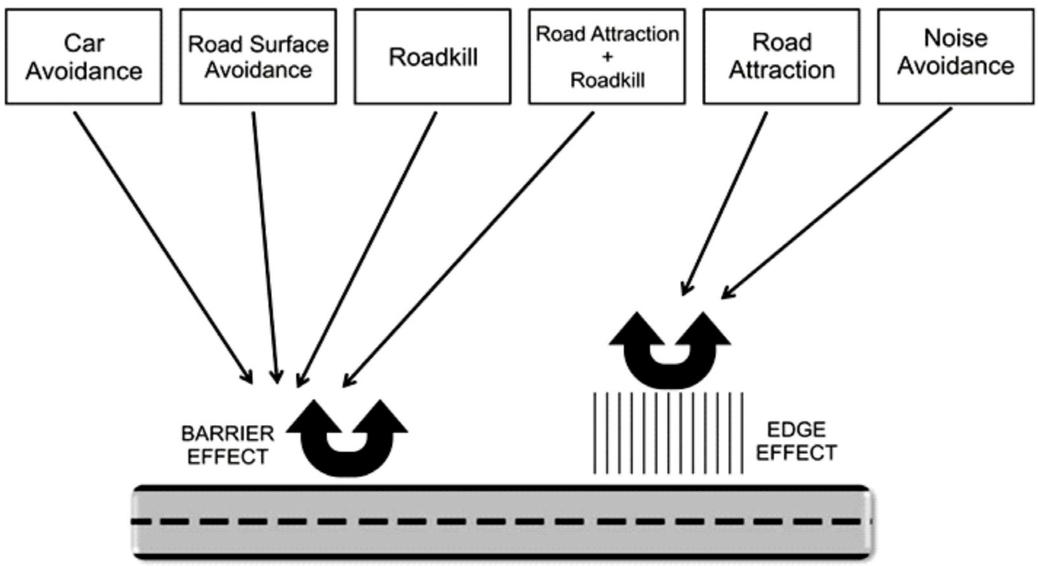

Figure 1. Edge and barrier effects on vertebrates caused either individually or in combination with five road mechanisms.

Despite the advances in the field of road ecology, many gaps still exist in our knowledge, like the factors that lead to these mechanisms and effects of roads in the organisms. We understand that evaluate these factors is crucial because it is the object of focus for implementing measures to mitigate the effects of roads on biodiversity. Thus, we had two objectives: (1) to review and discuss the factors modulating the mechanisms and effects caused by roads on the different vertebrate groups; and (2) to identify gaps in our knowledge of the effects of the road factors and mechanisms on vertebrates.

METHODS

To identify the factors involved in the mechanisms and effects of roads on amphibians, reptiles, birds and mammals (excluding bats), we conducted a literature review using seven major databases (Web of Knowledge, Scopus, Elsevier, JSTOR, ScienceDirect, SpringerLink and Wiley Inter Science). We also consulted the references identified in the articles resulting from the database search.

We searched for studies that evaluated the factors road density, traffic volume, presence of vehicles and road maintenance. We consider traffic volume and presence of vehicles as distinct factors because traffic volume is linked to aversion mechanisms that depend on the number of vehicles traveling, while presence of vehicles can be more subtle because depends on the presence of a single car traveling and generates a mechanism aversion of the individual who understands the car as a hostile object, temporarily changing their behavior (e.g. do not cross the road surface until the car have passed) (Jaeger *et al.* 2005). For the road maintenance, we evaluated only studies that examined the effects of road maintenance resulting from the application of chemicals. Mechanical maintenance (e.g., cutting of the vegetation along road edges) was not evaluated. For the search, we used the following keywords in various combinations: road, highway, traffic, noise, flow, impact, chemical, pollutants, pollution, contamination, road density, road effect, road effect zone, mammal, reptile, amphibian and bird.

The present review includes studies at the individual, population and community levels that were selected according to the following criteria: (1) studies that evaluated the effects of roads on wildlife in the vicinity (e.g., abundance near and far from roads) were only included when a quantitative analysis had been performed for at least one of the factors; (2) work involving WVC were only included when the collision rates were related to some of the factors; and (3) factors evaluated in experimental laboratory work (e.g., the evaluation of heavy metal toxicity) were included when linked to the road.

RESULTS AND DISCUSSION

ROAD DENSITY

The density of roads is linked to the process of habitat fragmentation, considering that with higher road density we can see an increased loss of natural areas (Lee *et al.* 2004). Evaluate the mechanisms involved with this factor is difficult because most of studies considered the road density to be another component of the landscape and because of this were not directed to evaluate the effects of road density in organisms. We found many studies that observed road density causing barrier effect, although we cannot evaluate the mechanism behind this effect. These studies shows a reduction in the richness of communities, occurrence, abundance, reproductive success, ecological attributes (e.g., home range, use of space) and life history (e.g., reduction in body size) of numerous species of amphibians, birds and mammals, (medium and large carnivores and herbivores) (Mace *et al.* 1996, Findlay & Houlahan 1997, Nelleman & Cameron 1998, Vos & Chardon 1998, Egan & Paton 2004, Dickson *et al.* 2005, Apps & Mclellan 2006, Fortin *et al.* 2008, Godbout & Ouellet 2008, Liker *et al.* 2008, Crosby *et al.* 2009, Houle *et al.* 2010). In wetland areas, the loss of reptile, amphibian and bird species may reach 20% for each 0.2 km/km^2 increase in roads (Findlay & Houlahan 1997), while ungulates may show a reduction of over 80% in the density of individuals in areas with a road density of 0.6 to 0.9 km/km^2 (Nelleman & Cameron 1998, Apps & Mclellan 2006, Fortin *et al.* 2008).

However we found studies that identify the mechanisms road surface avoidance, road attraction and WVC triggered by road density and causing barrier effect (Figure 1 and 2). Road attraction and WVC are related and occurs with populations of freshwater turtles and carnivores' mammals. For turtles the species reaches the road surface for dislocate, rest and build nests, because the roads are often the primary (or only) dry areas for these activities. The road surface increased the population of turtles, but at same time makes individuals exposed to WVC (Marchand & Litvaitis 2004, Johnson & Collinge 2004, Aresco 2005, Roe *et al.* 2006, Decatanzaro & Chow-Fraser 2010). Carnivores' mammals are attracted to roads because use the surface as travel routes and forage for carcasses along the roads, being exposed to WVC too (Antworth *et al.* 2005, Coelho *et al.* 2008, Barthelmess & Brooks 2010). When the WVC was eliminated, wolves (*Canis lupus*) are abundant at a road density of 1.42 km/km^2 (Merrill 2000) while in others areas were registered fewer individuals at a road density above of 0.4 km/km^2 (Mladenoff *et al.* 1999, Jedrzejewski *et al.* 2004, Houle *et al.* 2010).

On the other hand, the barrier effect caused by road surface avoidance in the hare *Lepus europaeus* (Roedenbeck & Voser 2008) and the wild rabbit *Oryctolagus cuniculus* (Barrientos & Bolonio 2009) increased the population of these species of preys at road edges. That can induce a mechanism of road attraction and WVC in carnivores' mammals, like observed by Barrientos & Bolonio (2009) between the polecat *Mustela putorius* and the wild rabbit. In the same way several studies suggests that road density increases the abundance of small mammals at the road edge which results in death of their predators (snakes, birds and carnivorous mammals) by WVC (Rytwinski & Fahrig 2007), but this hypothesis was not tested yet.

ROAD MAINTENANCE WITH CHEMICAL SUBSTANCES

Road maintenance can be performed either mechanically or with chemicals such as herbicides and pesticides that facilitate the removal of vegetation from the road edges. In temperate regions, salts are applied (particularly sodium chloride, NaCl, in its ionized form Cl^-) for local road maintenance due to snow (Forman & Alexander 1998, Forman *et al.* 2003). We found many studies that show that chemicals used for road maintenance can adversely affect organisms through the mechanisms of road attraction, noise avoidance and possibly WVC, causing a barrier effect (road attraction and WVC) and edge effect (noise avoidance) (Figure 1 and 2).

Noise avoidance occurs in amphibians because many individuals were death by toxicity of several chemicals substances. The high mortality of individuals results in an edge effect (especially in the first 100 meters), which results in a reduction of richness, changes in species composition and a reduction in population abundance (Scher & Thiery 2005, Sanzo & Hecnar 2006, Collinsa & Russell 2008, Karraker *et al.* 2008). In laboratory experiments with amphibians shows that the lethal effects of Cl^- (up to 100% mortality of individuals) could be observed in embryos and larvae at concentrations between 90 and 945mg/L depending on the species (Sanzo & Hecnar 2006, Karraker *et al.* 2008, Karraker & Ruthig 2009). The effects of Cl^- can be more severe when combined with other substances, such as heavy metals, and UV-B radiation (Snodgrass *et al.* 2008, Marquis *et al.* 2009, Brand *et al.* 2010). In natural environments and including adults in the samples, Collinsa & Russell (2008) found lethal effects ranging from 1,100 to 3,900mg/L of Cl^-. In addition to lethal effects, salts and other substances on roads can affect the behavior of amphibians (reducing the distance traveled and speed of tadpoles) (Denoel *et al.* 2010) and cause morphological and/or physiological abnormalities in embryos and larvae (e.g., a reduction in swimming performance, edema, axial malformations, changes in their rates of metamorphosis) (Sanzo & Hecnar 2006, Karraker 2007, Collinsa & Russell 2008, Snodgrass *et al.* 2008, Karraker & Ruthig 2009, Dorchin & Shanas 2010).

A road attraction mechanism can be observed for Passeriformes and is due to the application of deicing salts that attract to road many species that are naturally attracted to salts, resulting in a increase of individuals and a positive edge effect. However, the attraction of individuals to the road may, at first, increase the abundance of individuals along the edge, but in excess the salt may cause death and sublethal effects, such as symptoms of weakness, slowness, wounds (edema in the gizzard), partial paralysis and disorientation (Bollinger *et al.* 2005, Mineau & Brownlee 2005), resulting in a noise avoidance behavior. Topfer (2010) not tested but believed that the disorientation in birds caused by chemicals from roads led to increased susceptibility of individuals to WVC. These can result in a negative edge effect due the high mortality of individuals in the vicinity of roads by the excess of salt (noise avoidance) or in a barrier effect due the increase in WVC.

Despite the organism affected, the edge effects due to chemical substances applied during road maintenance depend on differences in metabolism, diet, quantity of food consumed, home range and longevity (Forman *et al.* 2003). The life stage also seems to influence the susceptibility of individuals to contaminants because we noted that the mortality of amphibians by toxicity is more pronounced following the order embryos > larvae > adults.

VEHICLE PRESENCE

In studies evaluating the effects of roads on biodiversity, vehicles are usually considered within the context of traffic volume. However, vehicles have characteristics such as speed and light (headlamps) that also affect organisms even at low traffic volumes (Forman *et al.* 2003, Jaeger *et al.* 2005). Vehicle presence is a short-range phenomenon that can occurs when the animal habits or travel around the vicinity of roads but avoid crossing the road due to presence of moving vehicles (Jaeger *et al.* 2005). We found studies that show that the presence of vehicles triggers car avoidance, noise avoidance and WVC mechanisms (Figure 2).

The car avoidance mechanism has been observed in snakes, large herbivorous mammals and small mammals that exhibit flight behavior (Andrews & Gibbons 2005, Ford & Fahrig 2008) or increased vigilance (Andrews & Gibbons 2005, St Clair & Forrest 2009) in the presence of moving vehicles. Andrews & Gibbons (2005) observed that snakes react to a moving vehicle in the same way that they react to the presence of a predator (immobility or flight, depending on the species). Bears use road edges and only move onto the road during times of low traffic volume (100 vehicles/day) (Waller & Servheen 2005), especially at night when traffic approaches zero (Gibeau *et al.* 2002, Waller & Servheen 2005, Graham *et al.* 2010). Considering the concepts of Jaeger *et al.* (2005), bears would be classified as exhibiting noise avoidance behavior due to their avoidance of high traffic volumes; however, because no edge effect occurs, the presence of the moving vehicle may be more important than the traffic volume for these animals, triggering a car avoidance mechanism. The absence of bears in areas of high traffic volume may be associated with a WVC mechanism or factors that are indirectly involved with the road, such as hunting and increased human population. In the same way, Seiler (2005) noted that WVC in large herbivorous mammals occurred more frequently in sections of the road that have an intermediate speed limit of 90 km/h compared with speed limits of 50, 70 and 110 km/h. This observation suggests that at lower speed (50 and 70 km/h) the WVC is insignificant, but at 1100 km/h we can't see many roadkills because the WVC already cause an edge effect (many collisions results in fewer individuals in the vicinity of roads) or it is occurring a car avoidance mechanism because animals avoid vehicles moving at high speeds.

Mazerolle *et al.* (2005) conducted an experiment in laboratory in which several species of amphibians were stimulated with lights of the same type and intensity as the headlamps of common cars and observed that after the light stimulus, the animals remained stationary that can increase the WVC vulnerability. According to Jaeger *et al.* (2005), the presence of one vehicle moving is only responsible for the mechanism of car avoidance. In contrast, noise avoidance is related to traffic volume and occurs when individuals do not come close to the edge of the road. However, the results of Mazerolle *et al.* (2005) demonstrate that animals can reach the edges, and in some cases (e.g., headlights), the vehicle can trigger a process of association between noise avoidance and WVC due to avoidance of headlights of vehicle (without a relationship to traffic) that can cause WVC due the stationary state of animals.

TRAFFIC VOLUME

Traffic volume is a principal factor in habitat degradation in areas traversed by roads through noise, light and chemical pollution (Forman *et al.* 2003). Many studies have shown that amphibians, reptiles, birds and mammals (medium and large carnivores and herbivores) living in areas close to roads exhibit an edge effect caused by traffic volume that can vary between 50 and 2800 meters depending on the organism and traffic volume. This edge effect results in behavioral changes (e.g. changes in the rate of displacement), reduced reproductive success and declining populations of these organisms. However, the given sampling design does not allow for the evaluation of the mechanism responsible for this effect (Mclellan & Shackleton 1988, Beringer *et al.* 1990, Reijnen *et al.* 1995, Yost & Wright 2001, Forman *et al.* 2002, Gibeau *et al.* 2002, Chruszcz *et al.* 2003, Bautista *et al.* 2004, Pellet *et al.* 2004, Waller & Servheen 2005, Gagnon *et al.* 2007, McCown *et al.* 2009, Graham *et al.* 2010).

Other studies indicate that audible traffic noise triggers noise avoidance mechanisms in amphibians and birds in temperate and tropical zones. These organisms exhibit changes in their vocalization patterns (primarily frequency and amplitude of the sounds) when exposed to traffic noise. These changes may be related to an increase or decrease in the number of calls depending on the organism (Sun & Narins 2005, Lengagne 2008, Kaiser & Hammers 2009, Parris & Schneider 2009, Parris *et al.* 2009, Cunnington & Fahrig 2010, Hoskin & Goosem 2010, Kaiser *et al.* 2011). A decrease in vocalization sound levels can cause a masking of communication signals (Sun & Narins 2005), while an increase in vocalization sound levels comes at a high energy cost and alters the time available for other activities such as foraging (Oberweger & Goller 2001). Edge effects occur in the individual level because direct changes are not observed in populations at road edges, but changes in individual behavior at the edges are observed. Nevertheless, the individual effects may be reflected in the population; acoustic communication in birds and amphibians is extremely important for reproductive success because it is through this communication that attraction occurs during courtship. These animals also use acoustic communication for territorial defense, predator detection and parental care (Habib *et al.* 2007, Bee & Swanson 2007, Leonard & Horn 2008, Kaiser & Hammers 2009, Parris *et al.* 2009, Kaiser *et al.* 2011).

For amphibians, vocalization is primarily used to attract females and defend territories (Vilaca *et al.* 2011) and may be related to the size of the males in some species. Given a choice, females prefer lower frequency calls, indicating larger and/or more experienced males (Wollerman 1998). Although Parris *et al.* (2009) found no relationship between male size and vocalization in areas affected by traffic noise, Hoskin & Goosem (2010) demonstrated that smaller males are concentrated closer to roads (with the loudest noise) and have higher frequency calls. Thus, these individuals may become less attractive to females (Wollerman 1998).

In birds, a reduction in the nest density has been observed in a variety of forest and open-area bird species along road edges (Reijnen *et al.* 1995, Rheindt 2003, Halfwek *et al.* 2011). However, some traffic volume studies found neutral effects for Falconiformes and Passeriformes that are common in areas with human presence (Reijnen *et al.* 1995, Richardson *et al.*1997, Kuitunen *et al.* 2003, Bautista *et al.* 2004). Peris & Pescador (2004) also observed that some bird species exhibit a positive edge effect, preferring to reproduce in areas exposed to noise (*Passer domesticus* and *Passer petronia*). Traffic volume appears to have a neutral effect on small mammals (Ford & Fahrig 2008, McGregor *et al.* 2008).

Another way in which traffic volume triggers a noise avoidance mechanism is the contamination by substances from the vehicles. Lethal and sublethal effects have not been observed in Falconiformes and small mammals; however, accumulation of these chemicals can occur with age and were observed in various tissues (Sures *et al.* 2003, Ek *et al.* 2004, Marchellesi *et al.* 2010, Rautio *et al.* 2010). Ek *et al.* (2004) found a temporal increase of 150% in palladium (Pd) concentrations in the eggs of *Falco peregrines* (comparing the 1970s with the 1990s), which was not statistically significant, but requires monitoring given that vehicle catalysts, which are the main sources of Pd contamination, were only introduced into the study area in 1986. Palladium is one of the contaminants that accumulate in the tissues of organisms living near roads. Ek *et al.* (2004) observed a mobility gradient in the direction of palladium, (Pd) > platinum (Pt) > rhodium (Rh), for Falconiformes, and Marchellesi *et al.* (2010) found a gradient in the order of Pd > Rh > Pt for small mammals. However, these studies evaluated only the relationship between the concentration of substances and their effects on the organisms. A gap remains in our knowledge about the relationships between the substance concentrations and traffic volume.

In addition to the noise avoidance mechanism, increased traffic volume results in increased of WVC. The roadkill rates for amphibians, birds, reptiles and large mammals (including herbivores and carnivores) are directly associated with increasing traffic volume (Fahrig *et al.* 1995, Clarke *et al.* 1998, Carr & Fahrig 2001, Hels & Buchwald 2001, Kuitunen *et al.* 2003, Mazerolle 2004, Seiler 2005, Roe *et al.* 2006, Colino-Rabanal *et al.* 2011).

We observed two patterns related to traffic volume: (1) the increase in traffic noise causes an avoidance mechanism that results in edge effects by altering species abundance and distribution in areas closest to roads, and (2) species move along roads in any traffic volume and became expose to WVC, generating a barrier effect. These patterns are related to dispersal ability. Amphibians, reptiles and large mammals (carnivores and herbivores) with greater dispersal ability constantly cross roads, leading to an increase in roadkill rates proportional to the increase in traffic volume (Fahrig *et al.* 1995, Clarke *et al.* 1998, Carr & Fahrig 2001, Hels & Buchwald 2001, Yost & Wright 2001, Mazerolle 2004, Roe *et al.* 2006, Eigenbrod *et al.* 2008, Barrientos & Bolonio 2009, Bouchard *et al.* 2009, Colino-Rabanal *et al.* 2011). Species with lower dispersal capacities are subject to edge effects, with reduced abundances close to roads due to traffic noise and chemical contamination (Carr & Fahrig 2001, Eigenbrod *et al.* 2008).

Without a well-planned sampling design, distinctions between the different mechanisms involved in the effects caused by traffic volume may be impossible. Summers *et al.* (2011) reported an increase in the richness of birds with increasing distance from the road (less noisy areas) that was not related to traffic noise. The authors believe that the decrease in richness and abundance of birds near the road may be caused by WVC, which have been identified as a major cause of adult bird mortality (Bujoczek *et al.* 2011). Likewise, Kuitunen *et al.* (2003) observed that although the passerine *Ficedula hypoleuca* selected forest-road edges for breeding in any traffic volume, juveniles living in nests near roads were less likely to survive, indicating a high rate of parent roadkill.

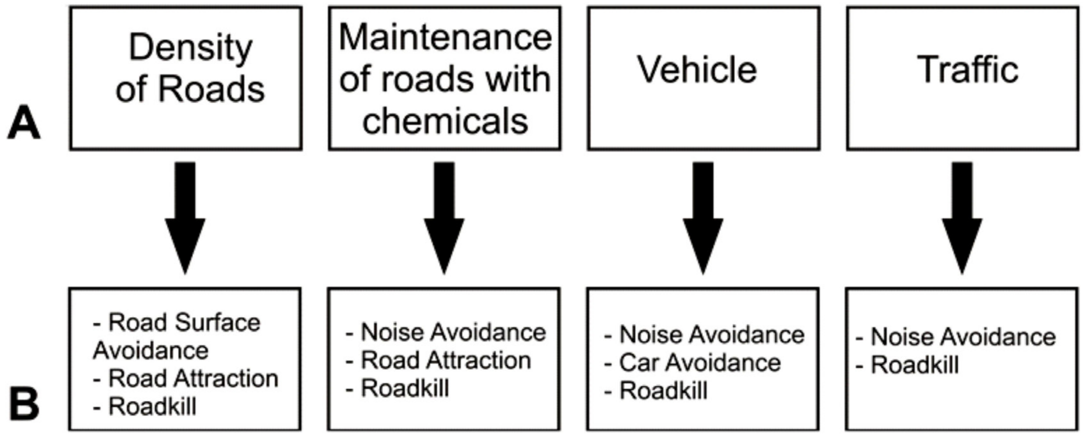

Figure 2. Road factors (A) and mechanisms (B) on vertebrates.

KNOWLEDGE GAPS

Considering each factor, the density of roads has been widely studied, especially within the context of landscape ecology. However, we do not know the road density mechanisms for many groups of vertebrates, like amphibians, reptiles and birds. For road maintenance performed using chemicals, we found only studies with amphibians and birds. Therefore, we do not know how salts and other substances used for road maintenance affect reptiles and mammals. Vehicle presence is known to trigger car avoidance in snakes and mammals (small and large) and should be evaluated for other groups. Traffic volume and WVC mechanism has been studied for all groups; however, gaps exist in understanding the effects of audible noise on reptiles and mammals and the effects of chemical contamination due to traffic for amphibians, birds (only Falconiformes have been studied) and reptiles.

Considering the mechanisms, the most neglected are the road surface avoidance and road surface attraction. The road surface avoidance mechanism requires work to assess road versus other fragmentation agents or to assess road width, the presence of paved surfaces and the presence of vegetation on the edge. As for the mechanism of road attraction, determining whether animals are attracted to or only use the road as a part of their normal dispersal route is difficult. Therefore, studies with specific designs are required to assess whether resources provided by roads (carcasses, grain, insects, nesting sites) and the ease of movement cause this mechanism in different groups. We know that scavengers are affected by the mechanism of road attraction due to the presence of carcasses (Antworth *et al.* 2005) and that other birds are attracted by insects and seeds (Erritzoe *et al.* 2003), but we were unable to find any study that evaluated the relationship between the resources of road surface and the mechanisms of road attraction and WVC.

In addition to gaps in the road factors and mechanisms, we identified two other areas lacking in information: (1) how all factors and mechanisms affect tropical organisms and (2) how roads affect individual fitness. A few studies have been conducted to evaluate traffic volume × traffic noise for some species of tropical birds and amphibians (Kaiser & Hammers 2009, Parris & Schneider 2009, Hoskin & Goosem 2010, Kaiser *et al.* 2011). Studies in the area of individual fitness have shown that although reptiles and terrestrial mammals do not use acoustic communication strategies such as those found in amphibians and birds (Zug *et al.* 2001, Pough *et al.* 2008), they may perceive noisy areas as less desirable, affecting the individual without necessarily affecting the population in the short and medium term.

CONCLUSION

Based on our revision we found studies that show that density of roads causes road surface avoidance, road attraction and WVC; maintenance of roads with chemical causes noise avoidance, road attraction and WVC; vehicle presence causes noise avoidance, car avoidance and WVC; and traffic volume causes noise avoidance and WVC. We can't evaluate the importance of each factor or mechanism to loss of biodiversity caused by roads, but we believe that WVC is a mechanism of particular concern because it is the only linked to all of the road factors and the only that can be influenced by another mechanism (road attraction). Jackson & Fahrig (2011) already show that WVC causes continuous loss of genetic diversity, while other mechanisms that lead to the barrier effect caused by roads are most prominent immediately after road construction with the initial loss of genetic diversity stabilizing in the first generations.

Some vertebrate groups are clearly more susceptible than others to specific mechanisms. Amphibians and birds, in particular, experience noise avoidance and WVC. However, birds can also suffer road attraction, and amphibians can suffer road surface avoidance. Reptiles are the most neglected group in the studies. Turtles are known to experience road attraction and WVC, while snakes experience WVC and car avoidance. Medium and large mammals are primarily affected by WVC, car avoidance and possibly road attraction. Small mammals are affected by car avoidance and road surface avoidance mechanisms. Many conclusions are limited to temperate regions, and we believe that new findings will result from studies in tropical environments.

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