

EFFECTS OF ROADS ON SPATIAL BEHAVIOUR AND ABUNDANCE OF SMALL MAMMALS: GAPS IN KNOWLEDGE

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ABSTRACT

The main goal of this study was to update the current understanding of the spatial behaviour and abundance of small mammals in the vicinity of roads through a complete literature review to identify knowledge gaps. We also examined spatial patterns of small mammals taking into account the biological and road-related factors to provide recommendations for future research. We found 38 papers documenting effects of roads on small mammals during 1974-2013, located mainly in North America and Europe. Results were obtained for 56 species in three mammalian orders considered. We found a high diversity of individual behaviours towards roads within the same species in different studies. Nevertheless, we can summarize some general patterns found in the review: 1) roads may not represent a barrier to movements because individuals are able to cross the roads; 2) although road verges with herbaceous cover favour the small mammal's abundance, there is no clear relationship between road verges and their abundance; 3) as expected, home range size and body mass are positively related with road crossing rates; 4) pavement is the road related feature that seems to limit road crossing rates. Based on our review, we found four key knowledge gaps: 1) absence of detailed information related with habitat and climate conditions in the studies; 2) lack of representativeness of small mammals with different ecological traits; 3) missing data on the effects of roads on species dispersal; and 4) scarce data on the role of crossing structures to maintain population connectivity and which features favour their use.

Keywords: rodents; marsupials; insectivores; road impacts.

RESUMO

EFEITOS DAS ESTRADAS SOBRE O COMPORTAMENTO ESPACIAL E ABUNDÂNCIA DE PEQUENOS MAMÍFEROS: AS LACUNAS NO CONHECIMENTO. O objetivo principal deste estudo foi realizar uma atualização do conhecimento sobre o comportamento espacial e abundância de pequenos mamíferos ao redor das estradas, através de uma revisão completa dos estudos realizados até o atual momento, para identificar lacunas no conhecimento. Foi examinada a associação entre comportamento espacial e abundância de pequenos mamíferos com os fatores biológicos relacionados às rodovias a fim de fornecer recomendações para futuras pesquisas. Foram encontrados 38 artigos que documentam efeitos das estradas sobre pequenos mamíferos durante 1974-2013, localizados principalmente na América do Norte e Europa. Os resultados foram obtidos para 56 espécies em três ordens de mamíferos. Ao longo dos estudos, encontramos uma grande diversidade de resposta de indivíduos da mesma espécie. No entanto, é possível resumir os principais padrões de resposta encontrados nos estudos: 1) as estradas não funcionam como barreira ao movimento dos pequenos mamíferos, uma vez que estes conseguem cruzar a estrada; 2) apesar da vegetação com herbáceas à beira da estrada favorecer a ocorrência de roedores, não foi encontrado uma relação direta entre a beira da estrada e abundância de pequenos mamíferos; 3) como já documentado, a dimensão da área de vida e tamanho corporal das espécies estão positivamente associados à taxa de cruzamentos na estrada; e 4) o tipo de pavimento é a característica da estrada que mais influencia a taxa de travessias na estrada. Com

base na nossa revisão, encontramos quatro lacunas no conhecimento: 1) falta de representatividade de espécies com diferentes características ecológicas; 2) ausência de informação detalhada sobre as condições climáticas e do habitat; 3) falta de informação sobre os efeitos das estradas na capacidade de dispersão das espécies; 4) desconhecimento dos efeitos das estradas na capacidade de dispersão das espécies; e 5) poucos estudos sobre o papel das passagens na manutenção da conectividade das populações assim como os fatores que promovem a sua utilização.

Palavras-chave: roedores; marsupiais; insetívoros; impacto das estradas.

RESUMEN

EFFECTO DE LAS CARRETERAS SOBRE EL COMPORTAMIENTO ESPACIAL Y ABUNDANCIA DE PEQUEÑOS MAMÍFEROS: LOS VACÍOS EN EL CONOCIMIENTO. El objetivo principal de este estudio fue actualizar el conocimiento sobre el comportamiento espacial y la abundancia de pequeños mamíferos en la vecindad de carreteras, a través de una revisión completa de literatura, para identificar vacíos en el conocimiento. También examinamos los patrones espaciales de pequeños mamíferos considerando factores biológicos y relacionados a las carreteras, con el fin de proporcionar recomendaciones para investigaciones futuras. Encontramos 38 artículos documentando los efectos de las carreteras sobre pequeños mamíferos durante 1974-2013, localizados principalmente en Norteamérica y Europa. Se obtuvieron resultados para 56 especies en tres órdenes de mamíferos. A lo largo de los estudios encontramos gran diversidad de comportamientos individuales hacia las carreteras dentro de la misma especie. Sin embargo, es posible resumir algunos patrones generales encontrados en esta revisión: 1) las carreteras pueden no representar barreras para el movimiento de los pequeños mamíferos, ya que estos consiguen atravesarlas; 2) aunque la vegetación herbácea al borde del camino favorece la ocurrencia de roedores, no se encontró una relación directa entre el borde del camino y su abundancia; 3) como se esperaba, la dimensión del área de vida y el tamaño corporal de las especies están asociados positivamente a la tasa de cruces en la carretera; y 4) el tipo de asfalto es la característica de la carretera que más influye en la tasa de cruces de carretera. Con base en nuestra revisión encontramos cuatro vacíos en el conocimiento: 1) ausencia de información detallada sobre las condiciones climáticas y del hábitat; 2) falta de representatividad de pequeños mamíferos con diferentes características ecológicas; 3) falta de información sobre los efectos de las carreteras sobre la dispersión de las especies; y 4) pocos estudios sobre el papel de las estructuras para el paso de especies en el mantenimiento de la conectividad de las poblaciones, así como los factores que promueven su utilización.

Palabras clave: roedores; marsupiales; insectívoros; impacto de las carreteras.

INTRODUCTION

There is a great amount of literature that examined the effects of roads and traffic on abundance and movements of vertebrates (e.g. Riley *et al.* 2006, Olsson *et al.* 2007, Klar *et al.* 2009). Although direct kills by collision with vehicles is the most explicit effect of roads, the barrier effect through road avoidance may create disruption of demographic connectivity across landscapes which has been shown to be critical for long-term persistence of populations (Forman 2000).

Rytwinski and Fahrig (2011) showed that mammal species with a large body size, high mobility and low

reproductive rate are particularly vulnerable to the negative effects of roads. Although, small mammals in general are small sized, have less mobility and high reproductive rates and several studies show that they are also susceptible to the barrier effect of roads (e.g. Huijser and Bergers 2000, McGregor *et al.* 2008). In fact, small mammals encompass a wide diversity of species with distinct life-history strategies and demographic traits and therefore, exhibit different responses towards roads and traffic. As primary prey for a wide range of raptors and carnivores, as well seed and spore dispersers (Vander Wall 1992, Arosa *et al.* 2009), they play a key role in various ecosystems. This group usually represents a good

model of study because small mammals usually occur in high densities and respond quickly to changes and disturbances due to their short generation times (Steele *et al.* 1984), which have caused a great interest among road ecologist researchers (e.g. McDonald and St. Clair 2004, Rico *et al.* 2009). Several studies have documented that rodents often find suitable habitat close to roads, when there is both high vegetation density and diversity at verges (Rytwinski and Fahrig 2007, Bissonette and Rosa 2009). However, they seem to avoid the pavement itself irrespective of traffic (Rico *et al.* 2007a, McGregor *et al.* 2008) which may promote reproductive isolation, compromising the viability of populations. In addition, gliding species (e.g. *Petaurus norfolcensis*) are not affected directly by the road *per se*, but rather by the gaps in the canopy as a result of road construction (van der Ree *et al.* 2010).

The main goal of this study was to update the current understanding of the spatial behaviour and abundance of small mammals in the vicinity of roads through a complete literature review to identify knowledge gaps. We also examined spatial patterns of small mammals taking into account the biological and road-related factors to provide recommendations for future research.

METHODS

We performed a review of scientific literature that quantified the effects of roads on small mammal (marsupials, marsupialia, insectivores, insectivora, and rodents, rodentia with average weight less than 1kg) spatial behaviour and abundance using Web knowledge, Scopus, Google Scholar and Science direct databases. The terms used for the search were: *small mammal, marsupial, marsupialia, insectivores, insectivora, rodents, rodentia with road, highway, motorway and freeway*. Only studies based on quantitative data were considered. Spatial behaviour studies corresponded to road crossings either at road or existing crossing structures (culverts and under/overpasses). We found studies with two distinct approaches to estimate crossing rates: 1) *Individual Road Crossing (IRC* - proportion of individuals surveyed that crossed the road/day*1000) and 2) *Road Crossing Movements (RCM* - the number of crossings/total individuals surveyed/day*1000). Abundance

was classified into three categories considering the relative abundance/density found in the road verges comparing with landscape matrix: less abundant (-); same abundance (0) and more abundant (+).

For each species identified in at least one publication, we included the average body size and individual home range (*IHRS*) resulting from the PanTHERIA database (Jones *et al.* 2009) and in each study area the road-related features (annual daily traffic, road width/surface, verges vegetation type and land use in the vicinity) (Table 1). We review qualitatively the results and try to find patterns among species with similar biological descriptors or under similar road features.

RESULTS

From 1974 until February 2013, we found 38 papers quantifying the spatial behaviour (n=21) or abundance (n=21) of small mammals towards roads (Table 1). Those studies were mainly located in North America (Canada, USA and Mexico 42%), and Europe (Portugal, Spain, France, Netherlands, Czech Republic, United Kingdom, Germany, Ireland, Poland 42%) followed by Oceania (16%).

Results were obtained for 56 species among the three mammalian orders considered. Rodentia were the most representative group and marsupialia were the least studied. Both the abundant rodent species of eastern woodlands and agricultural field verges of United States (white-footed mouse *Peromyscus leucopus*) and with an extensive range of North America (deer mouse *Peromyscus maniculatus*) were the species most commonly found in these studies (Linzey 2008, Linzey *et al.* 2008). Only three threatened species (Stephen's kangaroo rats *Dipodomys stephensi*, Cabrera vole *Microtus cabrerai* and cozumel harvest mouse *Reithrodontomys spectabilis*) were examined.

Spatial Behaviour

On average the *IRC* rate was 8 ind./day*1000 (range 0-66) and *RCM* was 12 crossings/ind./day*1000 (range 0-118). Species with the highest *IRC* rate were wood mice *Apodemus sylvaticus* (*IRC*=66), bank vole *Myodes glareolus* (*IRC*=61) and field vole *Microtus agrestis* (*IRC*=56). Hedgehog *Erinaceus europaeus*,

wood mice and white-footed mouse were reported with *RCM* above 90 crossings/ind./day*1000. We also found different responses to roads for the same species among studies. For example, eight studies documented that 14 species never crossed the road, but some of them crossed the road in other studies (e.g. yellow-necked mouse *Apodemus flavicollis*), which indicate road avoidance behaviour. Some species never crossed the roads were studied only once (e.g. Merriam's Kangaroo rat *Dipodomys merriami*, meadow vole *Microtus pennsylvanicus*, round-tailed ground squirrel *Spermophilus tereticaudus*, red-tailed chipmunk *Tamias ruficaudus* and southern pocket gopher *Thomomys umbrinus*). In this case, further research is needed to reach a conclusion on the real effect of roads on these species. Methods to record road crossing seems to not affect the results but we found some exceptions for three species (deer mouse, white-footed mouse and, eastern chipmunk *Tamias striatus*). In those cases, we observed higher rates of road crossings using the translocation method than the capture-recapture method. Regarding the use of crossing structures, we detected an average higher use of structures than crossing through the road surface for deer mouse and southern red-backed vole *Myodes gapperi* (McDonald and St. Clair 2004).

Abundance

No records were obtained for marsupials and we found contrast behaviours for the same species among sites and studies. The same species could fall into the three abundance categories with apparently similar type of vegetation in the verges (e.g. water vole *Microtus richardsoni*, deer mouse and western harvest mouse *Reithrodontomys megalotis* (Table 1). In fact, we found 23 species in which their abundance in the road verge was low in relation to the landscape matrix, 25 in which the abundance was higher and 20 species showed no abundance differences.

Spatial Patterns of response to roads regarding biological and road features

Biological features

As expected, we found a slight positive relationship between *IHRS* and road crossing rates (*IRC* and

RCM). In fact, the average *IHRS* was 0.1ha for no crossings (*IRC* and *RCM*). For *IRC* and *RCM* above 50 we found *IHRS* around 2ha and 1ha, respectively. Hedgehog, the species with highest road crossing rate recorded (*RCM*=118.42) had the largest *IHRS*. No relationship was found between *IHRS* and abundance. We found neutral and high abundance in the road verges either for species with low home range sizes (e.g. California vole *Microtus californicus*) and larger home range sizes (e.g. thirteen-lined ground squirrel *Spermophilus tridecemlineatus*) (Adams and Geis 1983). Similarly to *IHRS*, body mass is positively associated to both road crossing rates (*IRC* and *RCM*). We found lower average body mass for no crossings (41g) and higher body mass (131g) for road crossings above 10 (*IRC*). For example, hedgehogs (species with the greatest weight) had an *IRC* of 52 whereas plains harvest mouse *Reithrodontomys montanus* with 11g had the lowest road crossing rate (*IRC*=7.3). No relationship was found between body mass and abundance. The average body mass was similar among the three categories of abundance (40g).

Road features

Road crossing rates were not affected by traffic. In roads with very low traffic volume the *IRC* and *RCM* average was 8.08 and 15.85, respectively. No crossings were detected for an average daily traffic of 2.600 whereas high crossing rates (*IRC* and *RCM*>50) occurred in roads with 2.873 and 2.194 vehicles/day, respectively. Equally, we found no relationship between road width and road crossing rates. Rico *et al.* (2007a) recorded similar road crossing rates for bank vole at one-lane and two-lanes roads. We found for the same species (white-footed mouse *Peromyscus leucopus*) higher road crossing rates for 4-lanes (Richardson *et al.* 1997) than 2-lanes roads (McGregor *et al.* 2008) whereas eastern chipmunk *Tamias striatus* had an opposite response (higher crossings in 1-lane and no crossings in 4-lanes). As expected, type of pavement affected the species behaviour. We found an average *IRC* of 12 in unpaved roads and a lower *IRC* in paved roads (*IRC*=6). We observed a positive association between abundance and road verges with herbaceous and shrub cover. When agriculture dominates the surrounding landscape, the road verges tend to have higher small

mammal abundance than when the surrounding landscape is mainly forest.

DISCUSSION

The main finding of this review is that species show high variability in their populations regarding the behaviour towards roads. Thus, it is not clear to what extent those findings are applicable to species. We believe that microclimate conditions, microhabitat availability, predation pressure, and population density may explain variation among behaviour responses and therefore may limit the prediction of the road impact on species. Nevertheless, we can summarize some general patterns found in the review: 1) roads may not represent a barrier to movements because individuals are able to cross the roads; 2) although road verges with herbaceous cover favour the small mammal's abundance, there is no clear relationship between road verges and their abundance; 3) as expected, home range size and body mass are positively related with road crossing rates; 4) pavement is the road related feature that seems to limit road crossing rates.

The primary goal of this review was to search for spatial behaviour responses of small mammals towards roads taking into account some biological and road-related features. The majority of studies were more focus on the estimation of road crossing rates and abundance (e.g. Adams and Geis 1983, Ford and Fahrig 2008, Bissonette and Rosa 2009) rather than analysing the features that explain those responses. However, we found some exceptions that should be highlighted in this review. For instance, Fuentes-Montemayor *et al.* (2009) analysed the effect of life history and social variables on the rodents abundance whereas Bellamy *et al.* (2000) assessed the importance of width, density and size of verge, vegetation and ditch, respectively on rodents abundance. Additionally, Santos *et al.* (2007) and Sabino-Marques and Mira (2011) analysed the effect of floristic composition and vegetation structure of road verges on insectivores and rodents abundance.

Although, we found a high number of publications, the target species were mainly in North America and Europe. Further, these studies focus mainly in species with similar ecological requirements, which limit the

analysis of the impact of roads on functional groups and therefore, the prediction of impacts in other less known species with similar traits.

A relevant finding confirming the road avoidance of small mammals suggested by several authors was the general negative effect of pavement on road crossings rates. Unpaved roads have been documented to be more permeable to small mammal movements than paved roads (Mader 1984, Bakowski and Kosakiewicz 1988, Rico *et al.* 2007a). In our review, we also observed a higher tendency of avoiding paved roads, suggested by Jaeger *et al.* (2005) as road surface behaviour, which have implications on the population connectivity. However, we found interesting exceptions. For instance, wood mice showed high road crossing rates for paved and unpaved roads. Similarly, field vole show high rate of crossings on paved roads. Fortunately, species use existing crossing structures regularly and apparently the smaller structures seem to promote the crossing of several species (e.g. deer mice *Peromyscus maniculatus*, meadow voles *Microtus pennsylvanicus* and red-backed voles *Clethrionomys gapperi*) (McDonald and St. Clair 2004), perhaps because these ones may provide more protection from predators.

Although, there is a close association between pavement and road width, no relationship was found between road width and road crossing rates. One good example of this finding occurred with the white-footed mouse that has similar road crossings rate either in 1-lane and 4-lanes road (Oxley *et al.* 1974, Richardson *et al.* 1997). This is an unexpected result because there are several studies that document more restricted movements on wide roads than on narrow roads (e.g. Conrey and Mills 2001, Rico *et al.* 2007). In line with our results, research has been documented that an increase traffic volume did not affect small mammal movements; rather, the road itself had a larger impact (Goosem 2002, Rico 2007a, Ford and Fahrig 2008). However, Macpherson *et al.* (2011) found that the RCM of wood mouse decreased when the traffic increased. This finding is supported by Richardson *et al.* (1997) which detected that traffic intensity alone is a barrier to movement. Nevertheless, they pointed out that traffic and road width are usually positively correlated and in general studies hardly analyse one factor and controlling for the other (e.g. van der Ree 2006).

Surprisingly, we found contrast results between species abundance and road verges which may be explained by the lack of detailed information on verge features. Based on several studies, we expected that verges favour the small mammals abundance because they can be grazing exclosure areas when fenced, are likely to concentrate water which promote the vegetation growth, and consequently decrease the exposure to predators (Ascensão *et al.* 2012). In fact, we found a close association between rodent abundance and the herbs and shrubs presence when there is agriculture in the vicinity. This is consistent with Sabino-Marques and Mira (2011) that show roadside verges in intensively grazed Mediterranean landscapes act as important refuges, being crucial for their survival where suitable habitat in the vicinity is scarce. Moreover, Adams and Geis (1983) have documented that grassland species generally preferred road verges and many less habitat-specific species occurred both in road verges and adjacent landscape. In fact, Bellamy *et al.* (2000) compared several types of road verges for rodents and insectivores and show the importance of width and type of vegetation depend on the species-specific traits and the availability of their habitat in the verges.

In line with Rytwinski and Fahrig (2011), small mammal species with greater mobility (higher home range sizes) are more vulnerable to the negative effects of roads. We found that species with greater home-ranges tend to cross the roads more often which may increase the risk of being hit by vehicles. However, the movements between both sides of the road prevent the fragmentation between populations and therefore, limit genetic differences as observed by Rico *et al.* (2009). In this case, the road mortality may be compensated by the high reproductive rate of small mammals (Adams and Geis 1983), and consequently the high population densities and research should focus on the barrier effect due to road surface avoidance.

Based on our review, we found four key knowledge gaps: 1) absence of detailed information related with habitat and climate conditions in the studies; 2) lack of representativeness of small mammals with different ecological traits; 3) missing data on the effects of roads on species dispersal; and 4) scarce data on the role of crossing structures to maintain population connectivity and which features favour their use.

Suggestions for Further Work

Our results imply that priority should be directed towards improving three key issues in knowledge: a) extend the range of ecosystems analysed to include species with different ecological requirements; b) examine the ability of dispersing juveniles to cross the roads and c) analyse the relationship between road-related features and how this can be translated in the degree of isolation. In those research studies several questions should be addressed: 1) what is the role of micro-habitat and climate on small mammals response towards roads and of existing crossing structures to maintain road permeability to small mammal movements should also be addressed? 2) do road crossings even in high traffic roads occur when decreases the traffic intensity? and 3) are road crossing rates between subpopulations are large enough to avoid genetic differentiation? Radio-tracking data can provide further information on where and when the road crossings occur, whereas genetic analysis will help to understand the genetic differentiation and isolation degree between populations of both sides of the road.

ACKNOWLEDGMENTS: This study was conducted in the framework of a research project “Interacções entre os mamíferos e as estradas: implicações no comportamento e na estrutura genética” PTDC/BIA-BIC/110097/2009 funded by Fundação para a Ciência e Tecnologia. Additional fund was provided by Fundação para a Ciência e a Tecnologia through Post-doctoral (CG SFRH/BPD/64205/2009) grant. We thank Marcello D’Amico for constructive and insightful comments on an earlier version of the manuscript.

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Submetido em 16/07/2012

Aceito em 30/04/2013

Table 1. Review of biological features, region, method (CMR – capture-mark-recapture; IC – identification of colonies; MF – means of footprints; P – pigments; RT – radio-tracking; SP – sand pads; T – translocation), abundance in road verges in relation to landscape matrix (less abundant (-); same abundance (0) and more abundant (+)), spatial behaviour (IRC/RCM), road features: traffic (Annual daily traffic volume was classified in four categories: (1) very low (<1000 vehicles/day); (2) low (1000-10000 vehicles/day); (3) intermediate (10000-30000 vehicles/day) and (4) high (>30000 vehicles/day)), road width/surface (4-lane paved road, 2-lane paved road, 1-lane paved road and 1-lane unpaved road), verge vegetation structure (herbs, shrubs and trees), land use (forest, agriculture) and references for each study. Numbers separated by “;”, “;” refer to different study areas in the same research study; * crossing structures use; ** (ind./passage/day*1000).

SPECIES	BIOLOGICAL FEATURES		REGION	METHOD	ABUNDANCE	SPATIAL BEHAVIOR			ROAD FEATURES		LAND USE	REFERENCES
	BM (g)	HR (ha)				IRC	RCM	Traffic	Road width/surface	Road verge		
Marsupialia												
<i>Isodon obesulus</i>	825	0.01		SP	-	-	-	250**	-	-	-	Harris <i>et al.</i> 2010
<i>Petaurus norfolcensis</i>	230	2	Australia	RT	-	51	-	2	4-lanes	herb/tree	-	van der Ree (2006)
						17	-	2			-	
						-	33	3			agriculture	van der Ree <i>et al.</i> (2010)
Insectivora												
<i>Crocodyra russula</i>	10	0.02	Portugal	CMR	(+)	-	-	1	4-lanes	herb/shrub/tree	agriculture	Ascensão <i>et al.</i> 2012
			France		(0)	-	-	-	2-lanes	herb/shrub/tree		Sabino-Marques & Mira (2011)
			Spain		(+)	-	-	?	4-lanes	-	-	Meunier <i>et al.</i> 1999
			USA		(+);(-)	-	-	2	paved	herb/shrub	-	Ruiz-Capillas <i>et al.</i> 2013
<i>Cryptotis parva</i>	5	0.17	Netherlands	MF	(-)	-	-	2	2-lanes	herb/shrub/tree	-	Adams & Geis (1983)
			UK	RT	-	53	118	1			-	Huijser & Bergers 2000
<i>Erinaceus europaeus</i>	778	7			-	0	0	1	unpaved	herb/shrub/tree	forest	Rico <i>et al.</i> (2007b)
<i>Sorex araneus</i>	9	5.24	Czec. Rep.	CMR	-	0	0	1	2-lanes			
<i>S.trowbridgii</i>	5	-	USA		(-)	-	-	-	paved	herb/shrub	-	Adams & Geis (1983)
<i>S. vagrans</i>	6	0.20			(+)	-	-	-	paved	herb/shrub	-	
Rodentia												

Continuation Table 1

SPECIES	BIOLOGICAL FEATURES		REGION	METHOD	ABUNDANCE	SPATIAL BEHAVIOR			ROAD FEATURES		LAND USE	REFERENCES
	BM (g)	HR (ha)				IRC	RCM	Traffic	Road width/surface	Road verge		
<i>Amospermophilus leucurus</i>	104	5	USA		(0)	0.7	-	2	4-lanes	herb/shrub	-	Garland & Bradley (1984)
			Germany		-	0;0	0	1;2	2-lanes	-	-	Mader (1984)
<i>Apodemus flavicollis</i>	32	0.16	Czech Rep.		-	-	22;22	1	unpaved	herb/shrub/tree	forest	Rico <i>et al.</i> (2007a)
			Portugal		-	7	-	3	2-lanes	herb/shrub/tree	-	Rico <i>et al.</i> (2007b)
<i>A. sylvaticus</i>				CMR	(+)	-	-	1	4-lanes	herb/shrub/tree	agriculture	Ascensão <i>et al.</i> 2012
	22	0.71	UK		-	67	-	-	-	herb	-	Richardson <i>et al.</i> (1997)
			France		-	-	67;100	1	unpaved	shrub	agriculture	Macpherson <i>et al.</i> (2011)
			Spain		(+)	-	-	2	2-lanes	-	-	Meunier <i>et al.</i> 1999
<i>Chaetodipus formosus</i>	20	-	USA		(0)	0	0	2	4-lanes	herb/shrub	forest	Ruiz-Capillas <i>et al.</i> 2013
					(0)	0	0	2	4-lanes	herb/shrub	-	Garland & Bradley (1984)
<i>Chatodipus hispidus</i>	37	-			(+);(-);(-)	18; 18;0	18;18;0	1	unpaved;2-lanes;2-lanes	herb/tree	agriculture	Kuykendall & Keller (2011)
<i>Dipodomys heermanni</i>	63	-	USA		(0)	-	-	-	paved	herb/shrub	-	Adams & Geis (1983)
<i>D. merriami</i>	38	0.21			(0)	0	0	2	4-lanes	-	-	Garland & Bradley (1984)
<i>D. stephensi</i>	69	0.10			(+);(-)	-	-	-	unpaved	herb	agriculture	Brock & Kelt (2003)
<i>Melomys cervinipes</i>				CMR/T	(0)	-	-	-	-	-	-	Burnett (1992)
	71	-	Australia		(+)	-	-	1	2-lanes	shrub	forest	Goosem (2000)
					(+)	0.2	0.2;3	1	-	-	-	Goosem (2001)
<i>Microtus agrestis</i>	36	0.08	UK		(0)	-	-	1	-	tree	-	Goosem (2002)
<i>M. arvalis</i>	27	0.05	France		(+)	56	-	-	4-lanes	herb	-	Richardson <i>et al.</i> (1997)
<i>M. cabreræ</i>	53	-	Portugal		(-)	-	-	1	paved	herb	agriculture	Meunier <i>et al.</i> (1999)
<i>M. californicus</i>	57	0.01			(0);(+)	-	-	-	-	-	-	Santos <i>et al.</i> (2007)
<i>M. montanus</i>	43	0.01			(0);(+)	-	-	-	-	-	-	-
<i>M. ochrogaster</i>	42	0.03	USA		(+)	-	-	-	paved	herb/shrub	-	Adams & Geis (1983)
<i>M. oregoni</i>	20	0.07			(0);(+)	-	-	-	-	-	-	-

Continuation Table 1

SPECIES	BIOLOGICAL FEATURES		REGION	METHOD	ABUNDANCE	SPATIAL BEHAVIOR			ROAD FEATURES		LAND USE	REFERENCES
	BM (g)	HR (ha)				IRC	RCM	Traffic	Road width/surface	Road verge		
<i>M. pennsylvanicus</i>	42	0.03	Canada	CMR	(+)	-	-	-	-	herb	forest	Douglas (1977)
				CMR/T	-	0*	3	4-lanes		herb/tree	-	McDonald & St. Clair (2004)
<i>M. richardsoni</i>	86	0.03			(-);(0);(+)	-	-	-	-	-	-	
<i>M. townsendii</i>	52	0.06	USA	CMR	(0);(+)	-	-	paved		herb/shrub	-	Adams & Geis (1983)
					(-);(0);(+)	-	-	-	-	-	-	
<i>Mus musculus</i>	19	0.06		CMR/ RT/P	-	100	-	Paved/unpaved		herb	agriculture	Clark <i>et al.</i> 2001
			Portugal		(+)	-	1	4-lanes		herb/shrub/ tree		Ascensão <i>et al.</i> 2012
<i>M. spretus</i>	17	0.02	Spain		(+)	-	2			tree	forest	Ruiz-Capillas <i>et al.</i> 2013
<i>Myodes californicus</i>	18	0.12	USA	CMR	(-);(0)	-	-	paved		herb/shrub	-	Adams & Geis (1983)
			USA		(-)	-	2	2-lanes		tree	forest	Conrey & Mills (2001)
<i>M. gapperi</i>	20	0.06	Canada	T	-	42*	-	3	4-lanes	herb/tree	-	McDonald & St. Clair (2004)
			Canada		-	1	-	3		tree	forest	McLaren <i>et al.</i> (2011)
			Germany	CMR	(-)	-	-	-	-	herb		Douglas (1977)
					-	0	1;2	2-lanes		-	-	Mader (1984)
<i>M. glareolus</i>	21	0.12	Poland	CMR/T	-	61	-	1	unpaved	herb/shrub/ tree		Bakowski & Kozakiewicz (1988)
			Czech Rep.		-	-	17;0;6;13	1;2;2;1	unpaved;2-lanes;2-lanes	herb/shrub/ tree	forest	Rico <i>et al.</i> (2007a)
<i>M. rutilus</i>	20	-	Canada	CMR	(-)	-	53;67	1	unpaved	shrub	agriculture	Macpherson <i>et al.</i> (2011)
<i>Neotoma fuscipes</i>	213	0.19			(-)	-	-	-	-	herb	forest	Douglas (1977)
<i>N. lepida</i>	144	0.14	USA		(+)	0	0	2	4-lanes		-	Adams & Geis (1983)
<i>Ochrotomys nuttalli</i>	23	0.41			(-)	-	-	-	paved	herb/shrub	-	Garland & Bradley (1984)
<i>Onychomys torridus</i>	22	1			(0)	0	0	2	4-lanes		-	Adams & Geis (1983)
											-	Garland & Bradley (1984)

Continuation Table 1

SPECIES	BIOLOGICAL FEATURES		REGION	METHOD	ABUNDANCE	SPATIAL BEHAVIOR			ROAD FEATURES		LAND USE	REFERENCES
	BM (g)	HR (ha)				IRC	RCM	Traffic	Road width/surface	Road verge		
<i>Oryzomys couesi</i>	69	-	Mexico		(+)	-	-	-	-	-	forest	Fuentes-Montemayor et al 2009
<i>Peromyscus eremicus</i>	23	0.27	USA		(-)	0	0	2	4-lanes	herb/shrub	-	Garland & Bradley (1984)
<i>P. gratus</i>	27	-			(-):(0)	-	-	-	-	paved	-	-
					-	0;17	0;10	1	unpaved			
					-	4	4	1				
			Canada	CMR	-	0;3	0;3	2	2-lanes	tree	forest	Oxley et al. (1974)
					-	3	3	1				
					-	0	0	1				
					-	0	0	3	4-lanes			
<i>P. leucopus</i>	18	0.10	USA		(-):(0);(+)	-	-	-	paved	herb/shrub	-	Adams & Geis (1983)
					-	18	-	-	4-lanes	herb	-	Richardson et al. (1997)
			UK		-	38	-	2	-		forest	McGregor et al. (2003)
					-	0.18/-	2.98	2	2-lanes	tree	-	McGregor et al. (2008)
			Canada	T	-	4	-	3	4-lanes		forest	McLaren et al. (2011)
					-	0	0	0	4-lanes		agriculture	Archer (2003)
				CMR/ RT/P	-	18	-	-	Paved/unpaved	herb		Clark et al. 2001
					-	4	-	-	unpaved	herb/shrub	-	Kozel & Fleharty (1979)
			USA	CMR	(-):(0)	-	-	-	paved		-	Adams & Geis (1983)
<i>P. maniculatus</i>	20	0.26			(-)	-	-	2	2-lanes	tree	forest	Conroy & Mills (2001)
					(-)	-	-	-	4-lanes			
			Canada	T	-	222*	-	3		herb/tree	-	McDonald & St. Clair (2004)
			USA		(-):(0);(+)	-	28;10;31	1	unpaved;2-lanes; 2-lanes		agriculture	Kuykendall & Keller (2011)
					(-)	-	-	1				Goosem (2000)
<i>Rattus</i> sp.	-	-	Australia	CMR	(+)	-	4;6	1	2-lanes	shrub	forest	Goosem (2001)
					(-):(0);(+)	-	-	1				Goosem (2002)

Continuation Table 1

SPECIES	BIOLOGICAL FEATURES		REGION	METHOD	ABUNDANCE	SPATIAL BEHAVIOR			ROAD FEATURES		LAND USE	REFERENCES
	BM (g)	HR (ha)				IRC	RCM	Traffic	Road width/surface	Road verge		
<i>Reithrodontomys fulvescens</i>	12	0.1		CMR/ RT/P	-	0.02	-	-	2-lanes/ unpaved	herb	agriculture	Clark <i>et al.</i> 2001
<i>R. humulis</i>	8	0.38		CMR	(0)/(+)	-	-	-	2-lanes	herb/shrub	-	Adams & Geis (1983)
					(-)/(0)/(+)	-	-	-				
<i>R. megalotis</i>	11	0.11	USA		(-)/(+)	-	13/5	1	unpaved			
					(-)	-	0	1				
<i>R. montanus</i>	11	0.25		CMR	(-)	8	8.	1	2-lanes	herb/tree	agriculture	Kuykendall & Keller (2011)
					(-)/(+)	7;-	7/19	1				
<i>R. spectabilis</i>			Mexico		(0)	-	-	-	-	-	forest	Fuentes-Montemayor <i>et al.</i> 2009
<i>Sigmodon hispidus</i>	111	0.2		CMR/ RT/P	-	80	-	-	2-lanes / unpaved	herb	agriculture	Clark <i>et al.</i> 2001
					(+)	-	-	-	paved	herb/shrub	-	Adams & Geis (1983)
<i>S. hispidus</i>	111	0.28	USA		(-)	0	0	1	unpaved	herb/tree	agriculture	
					(-)/(+)	7;-	7;14	1		herb/tree		Kuykendall & Keller (2011)
					(+)/(+)	-	-	-	2-lanes	herb/tree	-	
<i>Spermophilus tereticaudus</i>	148	1			(-)	0	0	2	4-lanes	herb/shrub	-	Garland & Bradley (1984)
<i>S. tridecemlineatus</i>	148	2			-	9	-	-	unpaved	herb	agriculture	Kozel & Fleharty (1979)
					(0)/(+)	-	-	-	2-lanes	herb/shrub	-	Adams & Geis (1983)
<i>Tamias ruficaudus</i>	60	-	USA		(-)	0	0	2	4-lanes	tree	agriculture	Comrey & Mills (2001)
					-	23;8	11;8	1	unpaved			
<i>T. striatus</i>	-	-	Canada		-	0	0	1	2-lanes	tree	forest	Oxley <i>et al.</i> (1974)
					-	0	0	2				
					-	0	0	3	4-lanes			
					-	32	-	2	-			McGregor <i>et al.</i> (2003)
					-	-	12	2	2-lanes			McGregor <i>et al.</i> (2008)
<i>Thomomys umbrinus</i>	125	-	USA		(+)	0	0	2	4-lanes	herb/shrub	-	Garland & Bradley (1984)
<i>Uromys caudimaculatus</i>	644	-	Australia		(-)	-	5/7	1	2-lanes	shrub	forest	Goosem (2001)
					(+)	-	-	1		shrub	-	Goosem (2002)
					(+)	-	-	1		shrub	forest	