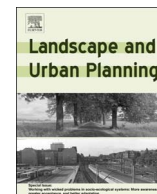




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Research Paper

Species-specific movement traits and specialization determine the spatial responses of small mammals towards roads

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ABSTRACT

The barrier effect is a pervasive impact of road networks. For many small mammals individual avoidance responses can be the mechanism behind the barrier effect. However, little attention has been paid to which species and road characteristics modulate road avoidance and mortality risk. We measured the strength of the barrier effect imposed by the road on three rodent species with different body sizes and habitat specializations: Southern water vole (*Arvicola sapidus*), Mediterranean pine vole (*Microtus duodecimcostatus*) and Algerian mouse (*Mus spretus*). We analysed the effect of traffic intensity on use of space and direction of movement and the effect of road type (4-lane highway, 2-lane paved road and 1-lane unpaved road) on crossing rates with simulations of roads bisecting each home range. Finally, we estimated annual mortality risk from collision based on individual speed, crossing rates, body length, traffic volume and road width. Individual mobility and ecological preferences were assumed as two hypotheses to explain species' responses towards roads. The effects were species-specific, with traffic intensity having a negative influence on the use of space and movement directionality only for water voles and with avoidance of paved roads being evident for the Algerian mouse. Road-kill mortality risk was high in pine voles. Habitat specialization, individual mobility and home-range location were identified as important factors of species' responses towards roads. This study draws attention to the role of behaviour and ecological requirements as well as road characteristics on the strength of the barrier effect imposed by roads for different species.

1. Introduction

Roads are a major concern in conservation biology as they limit the mobility of individuals in search of food, refuge, mates or any other requirement affecting individual survival and the long-term population persistence (van der Ree, Smith, & Grilo, 2015). The overall barrier effect imposed by roads is a result of habitat loss, road avoidance behavioural responses and the mortality toll that results from collisions with vehicles, all of which can inhibit the interchange of individuals and depress population abundance (Jackson & Fahrig, 2011). Therefore, it is essential to evaluate the spatial response of individuals towards roads and traffic in order to fully understand the impacts of these structures and consequently devise effective mitigation measures (Lima, Blackwell, DeVault, & Fernández-Juricic, 2015). Based on the available

information, which is restricted to a small set of species mostly in North America and Europe, managers are forced to make a priori predictions on the expected impact of roads on many species for which no data were available. Typically, it is assumed that body size is the best indicator of barrier effect by assuming that smaller species will have a lower probability to cross roads (e.g. Siers, Reed, & Savidge, 2015). Nevertheless, there are other potential indicators (e.g. behavioural and ecological) that may generate predictions contradicting those from body size (e.g., Jacobson, Bliss-Ketchum, Rivera, & Smith, 2016). For example, diet preferences seemed to explain the lack of response of barn owl to traffic volume (Grilo et al., 2012) whereas Chen and Koprowski (2016) found that roads restricted movements to native forest-dependent species while creating habitat used by an exotic edge-tolerant species.

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Generally it is assumed that small mammals avoid roads. The main inhibitors of their movements are wide paved surfaces and areas with no cover due to avoidance responses to predation risk (McLaren, Fahrig, & Waltho, 2011; Richardson, Shore, & Treweek, 1997). In fact, studies on several small mammals including bank voles (*Myodes glareolus*), western harvest mice (*Reithrodontomys megalotis*), hispid cotton rats (*Sigmodon hispidus*) and Eastern chipmunks (*Tamias striatus*) found that they crossed paved roads with a lower probability than unpaved roads (Adams & Geis, 1983; Bakowski & Kozakiewicz, 1988; Clark, Clark, Johnson, & Haynie, 2001; MacPherson, MacPherson, & Morris, 2011; Mader, 1984). However, the probability of crossing may not necessarily be related only with an avoidance of paved roads per se. Although traffic intensity does not seem to inhibit road crossings of some small mammals (Ford & Fahrig, 2008; Goosem, 2002), it may have a role by reducing the movements in the vicinity of roads, thus reducing the number of road crossing attempts. Additionally, a literature review (Porto-Peter, Molina-Vacas, Rodriguez & Grilo, 2013) showed that home range size may be a key factor in the small mammals' road avoidance behaviour: no crossings were found for species with an average home range of 1000 m² and the high crossing rates were observed in species with an home range size between 10000 and 20 000 m², suggesting that species with home ranges that cannot completely include the road surface are less likely to cross. In fact, the boundaries of small mammal home ranges tend to follow the roads and therefore low road crossings rates may be explained by the expected low frequency of movements across home range boundaries (Feldhamer, Drickamer, Vessey, Merritt & Krajewski, 2007).

The impact of mortality due to vehicle collisions on small mammal populations has received little attention. Some studies provide raw estimates of the number of victims (Clevenger, Chruszcz, & Gunson, 2003; Ramp, Caldwell, Edwards, Warton & Crofta, 2005), but the actual road-kill rates are difficult to measure due to the low detectability of casualties and the high removal rates (Santos, Carvalho, & Mira, 2011). Consequently, the effect of road mortality on small mammals may be severely underestimated. Alternative approaches aimed at overcoming the limitations of road casualty surveys have been proposed (e.g. Langeveld & Jaarsma, 2004; Litvaitis & Tash, 2008). Hels and Buchwald (2001) developed a predictive model incorporating traffic-related and species-specific features to estimate the likelihood of collision during the crossing event. This information combined with the estimated number of road crossings can provide an estimate of the annual collision mortality risk.

In this study we aimed to estimate the strength of the barrier effect imposed by roads on small mammals through the simultaneous evaluation of road avoidance behaviour and mortality risk. We addressed the effect of traffic intensity on individuals' use of space and movement directionality, and then we compared road crossing events with similar movements within each home range without roads. Finally, we estimated the risk of road-related mortality once they attempted to cross. Because it is crucial to identify a priori which species are most likely to be affected by roads in order to define the most appropriate mitigation measures for their populations, we selected three species representing different body sizes (potential degree of mobility) and habitat specializations: Southern water vole (*Arvicola sapidus*), Mediterranean pine vole (*Microtus duodecimcostatus*) and Algerian mouse (*Mus spretus*). The water vole, with a mean body weight of 275 g, is a semi-aquatic species associated with patches of low vegetation on muddy soils along the border of water bodies (Palomo & Gisbert, 2005; Román, 2007). Native to Portugal, Spain and France, it has undergone a marked reduction in its range and is classified as Vulnerable (IUCN, 2008). The pine vole has a mean adult body weight of 21 g; it is a fossorial species present in Mediterranean grassland patches (Santos, Mira, & Matthias, 2009). Pine voles are common across their range (western Mediterranean) and are classified as Least Concern (IUCN, 2008). The Algerian mouse, with a mean adult body weight of 17 g, is a habitat generalist that can be found in grasslands, dry shrubland, cereal fields and open woodlands

(Gray et al., 1998). Endemic to the Mediterranean region, it is common across its range and is classified as Least Concern (IUCN, 2008).

We developed two sets of a priori hypotheses generated by assuming different indicators of barrier effect as relevant. The first comes from the assumption that individual mobility is the main driver of crossing attempts: we predict that the larger species, the water vole, will have larger home ranges and an associated higher mobility, increasing the likelihood of crossing any type of road and therefore, increasing mortality risk. Under this hypothesis body size would be a good indicator of the expected barrier effects (see Clader, 1983; Haskell, Ritchie, & Olff, 2002). The second set of hypothesis came from the assumption that ecological preferences play a major role in shaping behavioural responses towards roads: we predict that habitat specialist species should avoid including roads within their home ranges. Therefore, generalist Algerian mouse should have the capacity to move in nearly any kind of cover and, therefore, it should be the species with the highest crossing rates and road-kill risk. The water vole should move only within or next to water bodies and the pine vole should be heavily constrained by the availability of pasture remnants and by the presence of adequate soils to dig burrows, thus reducing crossing rates. Under this second hypothesis habitat specialization should be a better a priori indicator of barrier effects.

2. Methods

2.1. Study area

Live trapping and radio tracking took place in southern Spain (provinces of Huelva and Seville) (Fig. 1). The area includes two 4-lane highways (A-49 and the A-483) and a network of 2-lane paved roads and 1-lane unpaved roads, with an average width of 27.6 and 3 m, respectively. The A-49 highway has a median section covered with natural shrubby vegetation and therefore can be viewed as two parallel 2-lane roads. Additionally, the A-49 highway has one unpaved road on each side, at varying distances, acting as service roads. The average daily traffic in 2011 was 31 842 vehicles for the highway, with maximum values during summer weekends of 140 000 vehicles, while traffic intensities ranged between 1500 and 3500 vehicles on the 2-lane paved roads present in the study area (sources: Ministerio de Fomento, España and Consejería de Fomento y Vivienda, Junta de Andalucía). On unpaved roads the average daily traffic ranged between 0 and 20 vehicles (E. Revilla, personal communication, September 15, 2011). This region is characterized by intensive agriculture, mainly by olive tree plantations, which allow for the existence of small remnants of non-tilled pasture around the trees, interspersed with vineyards and cereal crops.

2.2. Small mammals and traffic data

We surveyed in the vicinity of A-49, 2-lane roads and unpaved roads to search for suitable habitat and signs of activity of the three species (trails, latrines close to water bodies for water vole, fresh burrow openings for pine vole, and high density patches of herbaceous vegetation for Algerian mouse). All unpaved roads surveyed were located parallel to highways at a distance from five to 20 m. A confounding effect may be expected for the species response towards unpaved roads in two contrasting forms: the presence of the highway may lead individuals to cross the unpaved road or the presence of the unpaved road may lead individuals to avoid both the unpaved and the highway. We found suitable habitat and signs of activity in the vicinity of the A-49 and on parallel unpaved roads for the three species. Unfortunately, suitable habitat with signs of activity was found near the two lane-roads only for the Algerian mouse. Thus, a total of eight sites were selected to perform radio tracking: one site at the A-49 highway with a parallel unpaved road for water vole; two sites in the vicinity of the highway and unpaved roads for the pine vole; and two other sites near the

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