



## Heterogeneous road networks have no apparent effect on the genetic structure of small mammal populations



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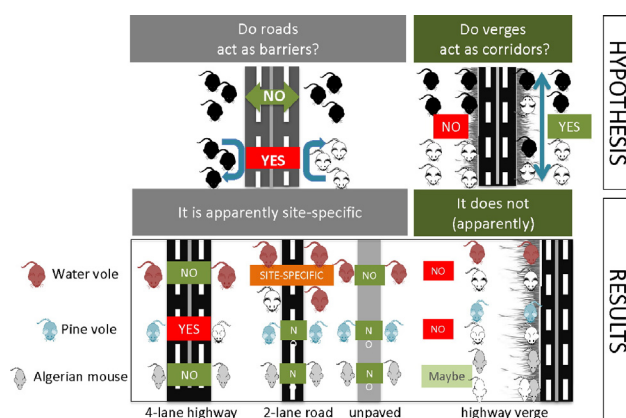
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### HIGHLIGHTS

- Roads are recognized to represent a barrier and a corridor to individual movements.
- We examine these potential effects on the genetic structure of three small mammals.
- No strong evidences were found for an effect of roads on population structure.
- The barrier effect of roads on small mammals seems to be site-specific.
- No corridor effect of verges was found for pine vole and Algerian mouse.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Roads are widely recognized to represent a barrier to individual movements and, conversely, verges can act as potential corridors for the dispersal of many small mammals. Both barrier and corridor effects should generate a clear spatial pattern in genetic structure. Nevertheless, the effect of roads on the genetic structure of small mammal populations still remains unclear. In this study, we examine the barrier effect that different road types (4-lane highway, 2-lane roads and single-lane unpaved roads) may have on the population genetic structure of three species differing in relevant life history traits: southern water vole *Arvicola sapidus*, the Mediterranean pine vole *Microtus duodecimcostatus* and the Algerian mouse *Mus spretus*. We also examine the corridor effect of highway verges on the Mediterranean pine vole and the Algerian mouse. We analysed the population structure through pairwise estimates of  $F_{ST}$  among subpopulations bisected by roads, identified genetic clusters through

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Barrier effect  
Corridor effect

Bayesian assignment approaches, and used simple and partial Mantel tests to evaluate the relative barrier or corridor effect of roads. No strong evidences were found for an effect of roads on population structure of these three species. The barrier effect of roads seems to be site-specific and no corridor effect of verges was found for the pine vole and Algerian mouse populations. The lack of consistent results among species and for each road type lead us to believe that the ability of individual dispersers to use those crossing structures or the habitat quality in the highway verges may have a relatively higher influence on gene flow among populations than the presence of crossing structures per se. Further research should include microhabitat analysis and the estimates of species abundance to understand the mechanisms that underlie the genetic structure observed at some sites.

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## 1. Introduction

Roads are widely recognized to represent a major movement barrier to many species owing to habitat loss, mortality or changes in the behaviour of individuals (Balkenhol and Waits, 2009; Jackson and Fahrig, 2011). By constraining wildlife movements, roads can decrease landscape connectivity and therefore alter community structure through changes in the interspecific competition, predator–prey dynamics, migration or dispersal (Taylor et al., 1993; Wiens, 1996). In fact, roads can cause a direct loss of habitat, which can reduce population size (e.g. Benítez-López et al., 2010) and limit the individual's interchange (Fahrig and Merriam, 1985). Additionally, a substantial source of mortality due to wildlife–vehicle collisions can eliminate movements of either dispersing or breeding individuals (Fahrig and Rytwinski, 2009; Grilo et al., 2009). Likewise, road avoidance behaviour or the presence of physical obstacles like fencing may limit the access to resources (mate, food, refuge) and the dispersal movements (Kostrzewa, 2006; Hepenstrick et al., 2012; Reijnen and Foppen, 1994). All studies argue that these negative effects may lead to changes in demographic patterns of populations, increased genetic structure and decreased genetic diversity, influencing resilience, adaptability and fitness, and jeopardizing population long-term viability (Lande, 1988; Frankham, 2006; Row et al., 2007). Although the long lasting negative effects of roads are empirically well supported, the causal relationships underlying the wildlife population's persistence are still scarce (see van der Ree et al., 2015).

At the same time, other studies show the importance of road-related features as habitat for some species or even their function as corridors (see review in Holderegger and Di Giulio, 2010). Roadsides with vegetation can enhance species richness and abundance of some birds and mammals (Bellamy et al., 2000; Meunier et al., 1999). Particularly in human-dominated landscapes, vegetated roadsides can become key foraging areas for some species due to high food availability and/or strategic refuges for protection and cover from predators (Ascensão et al., 2012; Sabino-Marques and Mira, 2011; Ruiz-Capillas et al., 2013). In some cases, vegetation on roadsides was found to act as habitat corridors by providing a pathway for dispersal between patches (Bennett, 1990).

Indeed, dispersal movements that result in successful breeding is the underlying mechanism for gene flow, the movement and integration of alleles from one population to another, which introduce and maintain genetic variability to populations (see Clobert et al., 2012). Lack of gene flow can lead to the loss of genetic diversity by drift, which increases the risk of range contractions and local extinctions (Markert et al., 2010). Population genetics is being increasingly used in road ecology because of its higher power to detect functional barrier/corridor effects of roads, since not all movement behaviours can be translated into dispersal and gene flow (e.g. Riley et al., 2006; Simmons et al., 2010; Blair et al., 2012; Hartmann et al., 2013). Thus, quantifying gene flow is a crucial step to determine to which extent genetically effective dispersal is limited or promoted by roads (Balkenhol and Waits, 2009; Lesbarrères et al., 2006; Sunnucks and Balkenhol, 2015; Ascensão et al., 2016).

Genetic studies show that highways and high-traffic roads promote genetic structure in a wide range of vertebrate species with diverse life-history traits: low mobile species such as red-backed salamander

*Plethodon cinereus* (Noel et al., 2007; Marsh et al., 2008), moor frog *Rana arvalis* (Vos et al., 2001), wood frog *Rana sylvatica* (Crosby et al., 2009), timber rattlesnake *Crotalus horridus* (Clark et al., 2010), bank vole *Clethrionomys glareolus* (Gerlach and Musolf, 2000) and white-footed mouse *Peromyscus leucopus* (Marrotte et al., 2014); from habitat specialists like koala *Phascoglossus cinereus* (Dudaniec et al., 2013), grizzly bear *Ursus arctus* (Proctor et al., 2005), desert bighorn sheep *Ovis canadensis nelsoni* (Epps et al., 2005), and roe deer *Capreolus capreolus* (Hepenstrick et al., 2012) to habitat generalists like coyote *Canis latrans* (Riley et al., 2006), Eurasian badger *Meles meles* (Frantz et al., 2010) and bobcat *Lynx rufus* (Riley et al., 2006). Other studies show that highways and roads apparently do not cause genetic structure in populations of the same species or in species with similar habitat specialization and movement ability, like bank vole *Microtus arvalis* in France (Gauffre et al., 2008), bank voles in Denmark (*Myodes glareolus*) (Redeker et al., 2006), the bank vole and yellow-necked mouse *Apodemus flavicollis* in the Czech Republic (Rico et al., 2009), or bobcat in Michigan and Iowa (Millions and Swanson, 2007; Reding et al., 2013). This fact indicates that some populations are more vulnerable to roads than others and the relationship between gene flow and species traits are complex and determined by a combination of road- and landscape-related features. On the other hand, several studies hypothesized that road verges may act as potential dispersal corridors (e.g. Vermeulen, 1994; Huijser and Clevenger, 2006), but few confirmed the functional effect of road verges as corridors using the genetic structure analysis (e.g. Prunier et al., 2013; Vilemeyer et al., 2016).

To clarify the role of road features on patterns of gene flow, it is thus important to analyse multiple species in the same landscape by using identical methods (Schwenk and Donovan, 2011; Engler et al., 2014). Such multiple species approach should consider species with different ecological features to evaluate how they influence the species response towards roads. Moreover, when landscapes exhibit considerable heterogeneity, the effect of roads on gene flow may be masked by other factors, producing biased results. Thus, we argue that a multiple species approach should compare populations along the same road system to analyse the role of species features on gene flow across and along roads.

The main goal of this study was to examine the effect of different types of roads on the genetic structure of three small mammal species with varying habitat specializations: southern water vole *Arvicola sapidus*, the Mediterranean pine vole *Microtus duodecimcostatus* and the Algerian mouse *Mus spretus*. The Southern water vole is a habitat specialist, which is mainly associated with patches of low vegetation on muddy soils along the border of water bodies (Román, 2007; Palomo and Gisbert, 2005). The Mediterranean pine vole is a fossorial habitat specialist with preference for patches of Mediterranean grassland (Santos et al., 2009). The Algerian mouse is widespread in Iberian Peninsula and seems to be abundant in Mediterranean regions like southern Spain. It is a habitat generalist and can be found in grasslands, dry shrubland, cereal fields and open woodlands (Gray et al., 1998). More specifically, we aim to analyse the barrier effect of different type of roads (4-lane highway, 2-lane roads and single-lane unpaved road) on the three small mammals species and the effect of highway verges on the Mediterranean pine vole and the Algerian mouse as potential dispersal corridors within and along the verges.

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