



Original investigation

Different responses of attic-dwelling bat species to landscape naturalness

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ABSTRACT

Although the general role of bats and the tolerance of many species to urbanized areas is well known, the relationship between urban roosts and their surrounding landscapes having different degrees of naturalness still requires our attention, mainly in species that are the most adapted to human-made structures. We used extensive data from attic-dwelling bat surveillance conducted throughout Slovakia to assess species responses to the degree of naturalness of the landscape surrounding their anthropogenic roosts. Using generalized linear mixed-effects modelling, we found that some bats established their nursery colonies in either a habitat with a higher proportion of forests mostly at sub-mountain/mountain altitudes (*R. hipposideros*, *P. auritus*, *M. emarginatus*), or they preferred lowlands with a predominance of arable land (*E. serotinus*, *P. austriacus*). Furthermore, higher habitat heterogeneity and the proportion of grassland were positively associated with the occurrence of *P. auritus*; however, negative associations with these habitat variables were found in *E. serotinus*. The predicted suitability of an area for bats to establish nursery colonies suggests the existence of two regions with different bat species composition in the study area: a region of the Pannonian Lowlands and a less urbanized mountain region of the Carpathian Mountains. Our study thus showed that landscape naturalness is a determining factor for roost-site selection by bats preferring anthropogenic roosts; however, some bat species did not express specific preferences according to the tested environmental variables, and other ecological traits in the evaluated species should be considered.

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Introduction

Landscape urbanization is, among other human impacts, considered to be one of the most important factors influencing, either positively or detrimentally, ecological traits in many animal species (e.g. Baker and Harris, 2007; McKinney, 2006, 2008). Species' responses to specific conditions of urbanized areas as complex ecosystems are various and seem to be species-specific. We may classify taxa according to urban tolerance as urban avoiders, urban adapters or urban exploiters (Blair, 1996; Fischer et al., 2015; Germaine and Wakeling, 2001; Kark et al., 2007). Thus, different species, although closely related, may avoid such areas

or may utilize and colonize them as dwellers through the process of synurbanization (e.g. Francis and Chadwick, 2012). Among mammal species, bats represent the largest group inhabiting a variety of human-made structures within a wide urbanization gradient (Kunz, 1982). In detail, they could be characterized as urban-tolerant, urban-sensitive, suburban-habitat specialists or as adapted synurbic species (Russo and Ancillotto, 2014). However, depending on the different landscapes, habitat or climate of a region, variability in this trait has been observed between even closely related species as well as among distinct populations of the same species (e.g. Dietz et al., 2009; Lintott et al., 2015a,b; Rodrigues et al., 2003; Uhrin et al., 2010).

The influence of urbanized areas on bat communities in temperate zones was emphasized in a series of studies showing several functions of settlements for bats. Bats can find hibernacula, swarming sites, maternity roosts, foraging grounds or transient roosts in such areas (e.g. Gehrt and Chelvig, 2004; Jung and Threlfall, 2016;

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Loeb et al., 2009; Neubaum et al., 2007; Oprea et al., 2009; Rydell, 1992). Furthermore, particular species can benefit from utilization of urbanized structures in various respects, including reduced predation risk, energetic benefits and/or the presence of social or mating partners. On the other hand, several negative consequences, such as human-biased threats, buildings as ecological traps and the presence of predators and pathogens, should also be considered (Voigt et al., 2016). Thus, from a conservation point of view, the contribution of urbanized areas in hosting viable populations of endangered bat species requires our attention (Shwartz et al., 2014).

Naturalness as a visual concept of the landscape character used in modern nature conservation practices can be measured by different indicators (level of succession, number or shape of habitat patches, shape or length of edges, etc.) and it describes how close a landscape is to a perceived natural state (e.g. Ode et al., 2009). Although the occurrence of bats in urbanized sites is well known, the relationship between urban roosts and surrounding landscapes with different degrees of naturalness is not yet fully understood in such species. Radio-tracking studies have suggested that almost all European bat species roosting in urbanized sites use adjacent woodlands and to some extent also arable land as foraging habitats (e.g. Arlettaz, 1999; Ashrafi et al., 2013; Bontadina et al., 2002; Catto et al., 1996; Dekker et al., 2013; Dietz et al., 2013; Entwistle et al., 1997; Flanders and Jones, 2009; Fonderflick et al., 2015; Krull et al., 1991; Robinson and Stebbings, 1997). Landscape analyses have shown a significant impact of the foraging habitat on roost selection by a species. In a heavily deforested landscape of the British Isles, the roost location of six urban-roosting bat species was positively associated with either the extent or proximity of broadleaved woodlands (Boughy et al., 2011). Certain house-dwelling bats depend on the availability of wooded elements near their roosts (Bellamy and Altringham, 2015; Moussy, 2011; Tournant et al., 2013), while others were found to forage in areas with a significantly higher cover of arable land and grassland (Tink et al., 2014). On the other hand, some well adapted city specialists benefit even from foraging in hostile urban areas (Ancillotto et al., 2016; Maxinová et al., 2016). Furthermore, the spatial integration of maternity roosts into a connected network allowing the exchange of individuals among roosts in a heterogeneous landscape was another factor explaining bat presence (Tournant et al., 2013). The degree of landscape urbanization or naturalness influences populations of bats in many aspects (Coleman and Barclay, 2011; Hale et al., 2012); however, the influence of landscape composition surrounding roost sites is scale-dependent (Gorresen et al., 2005; Mehr et al., 2011), and highly urbanized areas may thus represent a natural refuge (represented by gardens, orchards, parks) for some bat species within landscapes dominated by unsuitable types of land cover (Fabianek et al., 2011; Gehrt and Chelsvig, 2004; Jung and Threlfal, 2016; Li and Wilkins, 2014; Smith and Gehrt, 2010; Tink et al., 2014).

In Central Europe, there is wide spectrum of bat species that use man-made structures for roosting, however, as house-dwelling species are considered to be mainly those bats that occupy similar anthropogenic roosts in the urbanized areas of towns and villages, mostly spacious attics in large and old sacral buildings, where they establish nursery colonies (Dietz et al., 2009). Nowadays, these several species roost only in such anthropogenic roosts (exceptions in underground shelters are very rare; reviewed by Krištofik and Danko, 2012) and thus, from the point of view of roosting site, they can be considered as attic-dwelling bats. To answer how habitat composition and spatial heterogeneity influence roost-site selection by these species, a large scale study within a landscape with different degrees of naturalness may be helpful. Since all of the target species express strong roost-site fidelity (evidence gathered over decades is common), information about their occurrence could

be suitable for effective spatial analysis and predictive modelling. For this purpose, we used extensive data from attic-dwelling bat surveillance conducted in urban-located roosting sites over the whole area of Slovakia. We aimed to assess the occurrence of nursery colonies in such a type of roosts and the specific responses of bat species to different naturalness of the landscape that is considered to be their expected foraging area. Furthermore, on the basis of their habitat selection, we attempted to predict potential of the landscape for bats to establish their nursery colonies in areas where they were not yet recorded. In a landscape that offers suitable foraging habitats for some species but does not have suitable roosts available, such information could provide an effective and relevant conservation tool for attic-dwelling bats.

Material and methods

Study area

This study covers the whole territory of Slovakia (49,035 km², 94–2655 m a.s.l.). The main part of the area belongs to the Carpathians; the lowlands in the south-west and south-east belong to the Pannonian Lowlands. The area is in the Atlantic climatic region and has a long-term average temperature of -3.9°C in January and 17.4°C in July, with yearly precipitation of about 740 mm. The region is characterized by various vegetation zones divided into eight forest vegetation levels (oak, beech-oak, oak-beech, beech, fir-beech, spruce-beech-fir, spruce and dwarf pine) with a natural timber line at 1450–1700 m a.s.l. More than 42% of the country's area is forested. Although the area is relatively densely populated by humans (110 inhabitants per km²) living in 138 towns and 2885 villages, settlements are concentrated in rural landscapes. There are only three larger towns – that is heavily build-up sites – that have 100–500 thousands inhabitants.

Data collection

We collected all available data (ca. 2700 records collected during 1960–2009), both published (compiled by Uhrin and Polakovičová, 2000; Uhrin, 2006; Uhrin and Ševčík, 2011) and unpublished, on attic-dwelling bats occurring in the attics of buildings in Slovakia. From this large source of data, we selected records on bat species that dominate in this type of building roost in Slovakia and that establish nursery colonies for reproduction almost exclusively in them (Krištofik and Danko, 2012). Bats roosting in other parts of buildings (e.g. behind gutter pipes and claddings, in wall crevices, etc.) were thus omitted from our survey. Using this criterion we analysed the occurrence of the greater horseshoe bat *Rhinolophus ferrumequinum* (Schreber, 1774), the lesser horseshoe bat *Rhinolophus hipposideros* (Borkhausen, 1797), the greater mouse-eared bat *Myotis myotis* (Borkhausen, 1797), the lesser mouse-eared bat *Myotis blythii* (Tomes, 1857), Geoffroy's bat *Myotis emarginatus* (Geoffroy, 1806), the serotine bat *Eptesicus serotinus* (Schreber, 1774), the brown long-eared bat *Plecotus auritus* (Linnaeus, 1758) and the grey long-eared bat *Plecotus austriacus* (Fischer, 1829).

Statistical analysis

In order to identify the factors influencing the presence of nursery colonies of attic-dwelling bats in landscapes of different degree of naturalness, we used seven environmental variables which characterise the habitat surrounding bat roosts. We recorded altitude and calculated the relative proportion of main habitat types (forest, arable land, gardens [including hop-gardens, vineyards and orchards], grassland, and urban land) within a circle of 5-km radius around each roost (78.5 km²). We then estimated the landscape heterogeneity as the length of the boundaries between the five

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