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Review

Sensitivity of bats to urbanization: a review

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ABSTRACT

In this article we review the current knowledge of the effects of urban expansion on bats and assess the potential of these mammals as bioindicators of urbanization. The response of bats to this process is highly species-specific: some species tolerate urban habitat or are even favoured by its roosting or foraging opportunities, others are affected by the loss or fragmentation of key natural habitat, or by the physical and chemical pollution associated with urbanization. Species responses generally translate into altered community structures, with few markedly dominating species. We propose different hypothetical models of bat fitness along an urbanization gradient and discuss why bat population density may not be an effective fitness proxy to assess the reactions of these mammals to urban expansion. We also suggest that urban habitat may act as an ecological trap even for apparently synurbic species. Overall, bat sensitivity to urbanization makes these mammals promising candidates to track the effects of this process of land use change on the biota, but more studies, specifically tailored to explore this role, are needed.

Introduction

Urbanization is a major process of land use change that has considerably transformed habitats and landscapes available to wildlife. The on-going massive growth of urban areas has resulted in the replacement of original habitats in most areas of the world (Baker and Harris, 2007). Many studies have found that urbanization may have detrimental effects on animal species and communities, including: habitat loss and fragmentation (Scolozzi and Geneletti, 2012); road mortality and barrier effects (Baker and Harris, 2007); high density of domestic medium-sized predators such as cats and dogs (Patroneck et al., 1997; Young et al., 2011); effects of chemical and physical pollutants (Perugini et al., 2011), comprising anthropogenic noise and artificial illumination (Francis and Barber, 2013; Stone et al., 2009); and direct human interference (Markovchick-Nicholls et al., 2008). However, it is also known that urbanization may favour some species which succeed in human-altered conditions because they perform well in heterogeneous landscapes (Magle et al., 2012), benefit from the increased temperatures typical of urban areas (Costanza et al., 2001) or use the latter to shelter from large predators (Baker and Harris, 2007). Out of the many species that survive in urbanized areas, some, so-called 'synurbic', are more frequent, or abundant, in urban areas than in other habitats (Francis and Chadwick, 2012). Such species often show behavioural or ecological traits appearing to be tailored to cope with the challenges and opportunities offered by urban environments as a result of phenotypic plasticity or evolutionary processes (Magle et al., 2012). The task of exploiting novel urbanized environments may either lead to species exclusion or adjustment of behaviour and ecology, from foraging patterns to breeding timing and response to stress (Lowry et al., 2013). Successful species often show more "boldness" than others, including a stronger tendency towards risk-taking.

Bats are major contributors to biological diversity (Hutson et al., 2001), with over 1300 species known to date, a number that will most likely increase further thanks to the advances in molecular studies leading to the description of new cryptic species (Mayer et al., 2007). They also form large aggregations and in terms of abundance are among the most numerous living mammals (Jones et al., 2009). Bats are well known to provide a range of key ecosystem services, especially related to their diet and foraging behaviour (Kunz et al., 2011). The large amount of insect prey consumed by

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insectivorous bats – between 25 and 50% of their body mass – makes them excellent pest controllers, whereas nectar-feeding and fruit-eating bats act, respectively, as pollinators and dispersers for economically and ecologically relevant plants (Fujita and Tuttle, 1991).

Bats are also very sensitive to environmental anthropogenic alteration–which threatens the survival of many species (Hutson et al., 2001; Park, 2015)—so they may successfully be employed as bioindicators (Jones et al., 2009). One of the main general properties of a bioindicator is the tendency to show marked and prompt reactions to environmental changes (e.g. McGeoch, 1998). There is growing evidence that bats are profoundly influenced by urbanization exhibiting responses in terms of altered diversity, population size and behaviour. In this article we review the current knowledge of the effects of urbanization on bats and assess the potential of these mammals as bioindicators of this major land use process. As we will see, the response of bats to urbanization is highly species-specific. While some species show a strong degree of adaptation to urban habitat or are even favoured by it, others will decline in response to habitat loss and disturbance. Therefore, a species perspective is essential when assessing the effects of urbanization on bats, although species' differential response will translate into structurally altered bat communities (Threlfall et al., 2012).

We will (1) summarize the effects of urban habitats on roosting, foraging and commuting behaviour, (2) look at habitat or landscape effects on bat communities, (3) discuss whether urban habitat may be regarded as an ecological trap for at least some species, and (4) evaluate the potential importance of bats as bioindicators of urbanization.

Urban roosts

Roosts are resources playing a central role to the natural history of bats (e.g. Kunz, 1982). Their availability has implications for both bat geographical distribution and the diversity of bat communities (e.g. Findley, 1993). Roost structure, microclimate and degree of protection from predators critically influence bat survival and reproductive success (Kunz and Lumsden, 2003). Since the onset of urbanization, with the appearance of buildings and other human constructions such as bridges, tunnels etc., the ecology of bat roosting must have undergone dramatic changes, judging from the number of species that today roost either dominantly or exclusively in such structures. As natural roosts have become scarcer because of habitat loss and land use change, buildings have acquired a great value for bats (Kunz, 1982). Human constructions may simulate the structural and functional properties found in cliffs, caves or trees, all important natural roosts, so bats may have easily learnt to exploit the new artificial roosting environment. For example, the molossid *Tadarida teniotis*, naturally roosting in cliff crevices, is often found in vertical cracks or other narrow fissures in the walls of tall buildings, thus mimicking the kind of roosts available in non-urban environments (Arlettaz, 1990; Fig. 1). Other species, including some of major conservation importance such as *Rhinolophus ferrumequinum*, reproduce in large spaces such as attics (Ransome, 1998). However, it is important to remark that only some bat species may roost in buildings, whereas those more specialized into natural roosts, including those most strictly cave-dwellers or tree-dwellers, may not adapt. As urbanization often increases at the expense of natural habitats such as forests, the latter species are likely to be affected by the associated loss of suitable roosts. Rarely, buildings may offer conditions suitable even to bats specialized for cave-roosting (Fig. 1).

A first clear advantage offered by urban settlements to bats that adapt to roost in buildings is the large availability of roosting habitat, particularly for bats that may use narrow spaces of recent buildings (Fig. 1). This may be one of the main factors explaining why some species, such as Kuhl's pipistrelle *Pipistrellus kuhlii* in Southern Europe, have become so abundant and are expanding their range (Bogdanowicz, 2004). Besides, roosts in buildings may provide a warmer microclimate for reproductive females reducing homeothermy costs (Kerth et al., 2001), advancing the timing of reproduction and improving the growth of young, which will reach a larger body size (Lausen and Barclay, 2006; Ransome, 1998). Roosts in buildings may also host larger colonies. Although climate change has often been advocated as a cause for the range expansion of some house-dwelling bats, indeed increasing urbanization offers an alternative or complementary hypothesis worth testing to explain the process. In certain cases urban roosts have been suggested to offer effective protection from predators (Lausen and Barclay, 2006), but as we will see ahead this does not appear to be a general rule (Ancillotto et al., 2013). There is also one documented case of bats apparently benefiting from insecticides. In two roost buildings of synurbic *Eptesicus fuscus* in Colorado, residents sprayed insecticides to counter the spreading of *Cimex* sp., and the chemical was suggested to reduce the rate of ectoparasitism affecting bats at those sites (Pearce and O'Shea, 2007).

Urban sites are also preferred targets for the installation of bat boxes (Agnelli et al., 2011), which in such cases are mostly colonized by opportunistic, synanthropic species—in southern Europe, especially *P. kuhlii* or *Hypsugo savii*. The ecological implications of these initiatives are poorly understood. It would be worth testing whether the resulting increased population density of these bats could lead to competitive exclusion of more sensitive species from areas where the latter would otherwise occur, especially suburban sites hosting remnants of natural vegetation (Arlettaz et al., 2000).

Water availability in urban habitat

Because of their distinct morphology and physiology, bats are often exposed to dehydration: they lose much water through their body surface, particularly via the respiratory system and the wing membranes (Chew and White, 1960; Thomas and Cloutier, 1992). Especially in arid, semiarid or Mediterranean areas, where water is permanently or seasonally limiting, human-made water bodies created within or near urban sites such as artificial ponds, water reservoirs, cattle troughs or swimming pools may provide vital drinking opportunities (Razgour et al., 2010; Russo et al., 2012; Korine et al., 2015). For example, in small Mediterranean islands, where bats exhibit marked foraging flexibility to feed in habitats that differ profoundly from those used on the mainland (Ancillotto et al., 2014; Davy et al., 2007), swimming pools of resorts and villas often provide them with otherwise rare or absent drinking water.

Urbanization and foraging behaviour

Urbanization has often been described as detrimental to bat foraging, yet the reaction of foraging bats to it varies according to species. Although some species may successfully exploit urban roosting sites, their flexibility may not extend to foraging behaviour too. Markedly generalist species (in Europe, for example *P. kuhlii*, *Pipistrellus pipistrellus* and *H. savii*) are often those most likely to roost and forage near urban settlements (Duchamp et al., 2004). However, bats roosting in cities may not find suitable foraging grounds near their roosts and thus must travel longer distances to reach them (Geggie and Fenton, 1985).

From studies conducted in many geographic areas it can be generalized that (1) bat activity declines as urban density increases, (2) some species take advantage of street lamp foraging but most will not, and (3) natural or semi-natural habitat within urban areas support more bat activity.