



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.

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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.

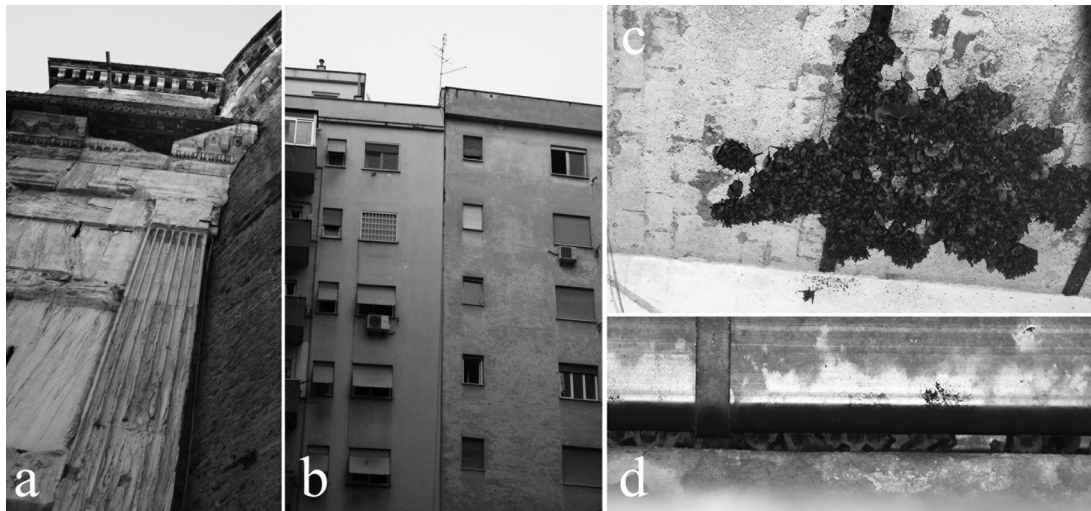


Fig. 1. Examples of urban bat roosts; roosts of European free-tailed bat *Tadarida teniotis* in historical (a: Rome's Pantheon) and modern (b) buildings; mixed-species colony (c) of urban-tolerant (*Myotis emarginatus*) and urban-sensitive (*Rhinolophus euryale*) bats; reproductive colony (d) of a typical synurbic bat (*Pipistrellus pipistrellus*) roosting behind a draining-pipe.

The presence of vegetation has been often advocated as the main factor sustaining insect prey populations (Avila-Flores and Fenton, 2005), whereas lights may attract insects and improve the prey capture success rates by bat species adapted to hunt in artificially illuminated sites (e.g. Furlonger et al., 1987; Tomassini et al., 2014). The distribution and abundance of nocturnal insects preyed upon by bats are largely influenced by factors such as the loss of native vegetation, increased housing densities and artificial lighting. Urbanization may seriously impact insect density, leading to population declines in taxonomic groups of chief importance to bat foraging such as moths (Conrad et al., 2006) and in turn affect bats (Avila-Flores and Fenton, 2005; Geggie and Fenton, 1985; Jung and Kalko, 2011). Scarcity of moths in urban settlements may explain why rhinolophids such as *Rhinolophus euryale* avoid this habitat for foraging (Russo et al., 2002) yet the repulsive effect of artificial lights on bats in this family (Stone et al., 2009) may provide an alternative explanation.

Noticeably, Threlfall et al. (2011) found lowest insect biomass and bat foraging activity in high-density housing areas yet they failed to detect any expected relationship with vegetation cover. The negative relationship between insect biomass and housing density along with an urbanization gradient could be explained from the increase in large impermeable surfaces, leading to low primary productivity – and in turn bat insect prey – in heavily urbanized sites (Threlfall et al., 2011). Other factors potentially affecting bat foraging in urbanized areas independent of prey abundance are wing morphology (Norberg and Rayner, 1987) and echolocation call design (Neuweiler, 1984) which may constrain prey access in open foraging sites such as those found in cities (Avila-Flores and Fenton, 2005; Threlfall et al., 2012). In Europe, pipistrelle bats (*P. kuhlii*, *P. pipistrellus* and *H. savii*) are frequent urban foragers as their FM-QCF echolocation calls (Russo and Jones, 2002) and wing profile (Norberg and Rayner, 1987) perform well in edge habitats including those found in such environments.

The effects of artificial illumination on bats have recently received great attention and are now better understood (Stone et al., 2015). Although light pollution is a threat to bat conservation (Stone et al., 2009), some species appear to have specialized into artificially illuminated sites (e.g. Rydell and Racey, 1995). By attracting prey – especially moths – from dark, natural habitat, artificial illumination may favour light-tolerant bats such as pipistrelles at the expense of light-sensitive species (e.g. rhinolophids), potentially altering interspecific competition dynamics (Arlettaz

et al., 2000). Recently, Tomassini et al. (2014) described a rapid increase in skull size in Italian populations of *P. kuhlii* recorded after World War II and related it to the boost in artificial illumination associated with urban expansion in the country. *P. kuhlii* largely forages near streetlamps where it may capture moths, including those sensitive to bat ultrasound that are nonetheless caught because their antipredatory manoeuvres are impaired by artificial lighting (Tomassini et al., 2014).

Although generally only a few species may feed in heavily urbanized areas, more may be found foraging in less developed suburbs: the latter are characterised by productive soil sustaining higher insect prey availability (Threlfall et al., 2011). Similarly, although in large cities of Southern Italy bat activity is generally small and limited to few synanthropic species (D. Russo, pers. obs.), Russo and Jones (2003) found it to be intense in rural towns that were mostly illuminated, and generally scattered with small gardens, orchards and fields. Urban parks and rivers crossing cities harbour more bat species, so their presence and correct management are important to preserve bats in large urban settlements (Avila-Flores and Fenton, 2005; Gaisler et al., 1998).

Crossing urbanized landscapes

By replacing natural habitat or interrupting connectivity, urbanized areas and roads may interfere considerably with bat movement (Kerth and Melber, 2009). Generally speaking, biological corridors of different size, from riparian vegetation (Russo et al., 2002; Serra-Cobo et al., 2002) to hedgerows (Verboom and Huitema, 1997; Park, 2015), have been found to be of utmost importance to bat movement. Therefore, a decrease in landscape connectivity caused by urban expansion is likely to affect many species. Interruptions may also be caused by infrastructures associated with urban areas such as roads (Bennett and Zurcher, 2013) or artificial illumination disrupting bat commuting (Stone et al., 2009). Besides causing road kills, roads represent barriers or filters to movement, determining gaps that bats may find difficult to cross, especially in association with higher traffic noise (Bennett and Zurcher, 2013).

Some species do not cross urban matrices and avoid patches of natural habitat if the latter are close to illuminated areas (Threlfall et al., 2013a,b). As with foraging, echolocation and flight performances largely influence the ability of different bat species to cross urbanized mosaics. Species characterized by a fast, high flight such

as molossids (Jung and Kalko, 2011) are generally less sensitive to land cover modifications as their movement is independent from structural features. The barrier effect caused by roads is also species-specific, as slow-flying, manoeuvrable bats foraging by gleaning may be more reluctant to cross roads even if underpasses are available (Kerth and Melber, 2009). Roads seem not to discourage species flying high up, mostly hunting on the wing, from crossing.

Soundscapes

Urban landscapes are typically filled with human-produced sounds (Botteldooren et al., 2004; Raimbault and Dubois, 2005). Urbanization is a major cause of fragmentation of terrestrial acoustic landscapes (Lynch et al., 2011), a process known to affect animal behaviour and distribution (Barber and Crooks, 2010; Francis and Barber, 2013). Acoustics plays a major role in a bat's life so these mammals are potentially affected by human-generated noise (Barber and Crooks, 2010), yet this aspect has been poorly explored. Schaub et al. (2008) showed that under laboratory conditions, the passive-listening performance of greater mouse-eared bats *Myotis myotis* searching for ground-dwelling prey arthropods is impaired by background traffic noise. These bats detect the presence of prey from the rustling noise produced when the insect moves on the substrate, a condition making echolocation of little use to detect a target (Russo et al., 2007). By masking natural prey noise, traffic noise decreased capture success and altered prey search time relative to alternative experimental sets in which either no noise, or natural noise, was broadcast (Schaub et al., 2008).

Bat social calls typically exhibit lower frequencies than do echolocation calls, sometimes being at least partly audible (Pfalzer and Kusch, 2003); in this way they may travel longer distances and prove to be more effective for communication. For *P. kuhlii* social calls recorded in two areas of Southern Italy characterised by a different degree of urbanization, Russo and Jones (1999) found that bats from the more urbanized area emitted social calls at lower frequencies and hypothesised that this might be a result of an acoustic adaptation process aimed to reduce attenuation and degradation of calls propagating in the more complex habitat.

Exciting and practically unexplored research topics, with important implications for bat conservation, are also offered by the potential effect of habitat-specific structural constraints – comprising walls and other artificial surfaces – on the propagation of echolocation calls and whether acoustic responses to this habitat structure exist.

Influence on patterns of richness and diversity

Bats make no exception to the general rule that by replacing or fragmenting natural habitats, urban expansion alters community structure and dynamics, with inevitable consequences for species richness and diversity. Generalist, flexible species will dominate at the expense of more sensitive or specialized ones. Changed roosting and foraging conditions will translate into altered richness or diversity as a result of strongly species-specific, or at least guild-specific mechanisms (Luck et al., 2013).

Studies done in different regions (Australia: Luck et al., 2013; North America: Coleman and Barclay, 2011; Central America: Avila-Flores and Fenton, 2005; South America: Hourigan et al., 2010, 2006; Europe: Hale et al., 2012) found that urbanization may have different effects upon bat abundance and diversity, yet all showed altered species assemblages, with one or two species markedly dominating in the community. In some cases, bat abundance was found to increase in urbanized areas because synurbic species were overrepresented and even biased sampling. This is the case

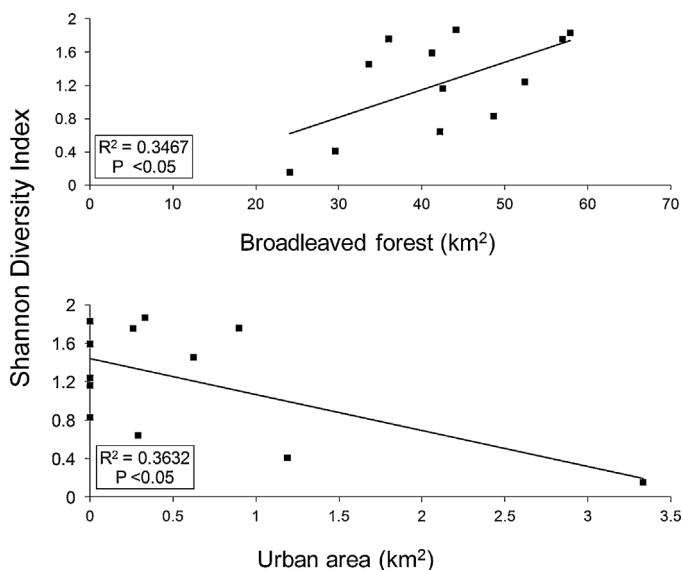


Fig. 2. Relationship between bat diversity (expressed as Shannon's index values) and, respectively, the availability of forest (above) and urban habitat (below) in 5-km radius circular "landscapes" of central and southern Italy ($n=12$). Diversity was estimated from mistnetting data and adjusted for unequal sample effort by rarefaction analysis.

with synurbic molossids (e.g. *Tadarida brasiliensis*, *T. teniotis* and *Mormopterus* spp.). Peaks in richness or abundance have been found in suburban areas rather than strongly urbanized ones (e.g. Coleman and Barclay, 2011; Luck et al., 2013). It is important to remark, however, that abundance may not be a reliable proxy for fitness, as discussed later. The richness peaks in suburban areas would be expected according to the intermediate disturbance hypothesis (Connell, 1978), as they would be located halfway along a polarisation (from natural to urban habitat) gradient. This condition would produce "optimal" levels of disturbance intensity and frequency, maximising biodiversity.

An important point to make is that urbanization grows at the expenses of other habitats, so when analyses are carried out at landscape scale it is difficult to disentangle the relative community effects of disappearing natural habitat from those of increasing urbanization. For example, in a study done in Central and Southern Italy, the effects of the occurrence of woodland and urban habitat on bat diversity (different sample sizes were adjusted by rarefaction analysis) were tested for 12 rural landscapes within a 5-km radius from capture points (D. Russo, unpublished). Two opposite trends were found: bat diversity increased along a positive gradient of woodland cover, yet decreased as urbanization increased (Fig. 2). The two effects, however, are dependent on each other: urban areas have expanded replacing woodland, so that a strong negative correlation occurred between the two habitat types ($r = -0.758$; $P < 0.005$). The higher species richness typical of forest bat communities may explain the observed pattern.

Urban areas and fitness in bats

Based on what we have seen so far, a somewhat simplistic synthesis of the effects of urbanization on bats is represented by a winner-or-loser model: some more opportunistic species would become synurbic and exploit the novel ecological conditions found in urban sites whereas most others, being less flexible, would be affected by the loss of habitat and/or the altered environmental conditions.

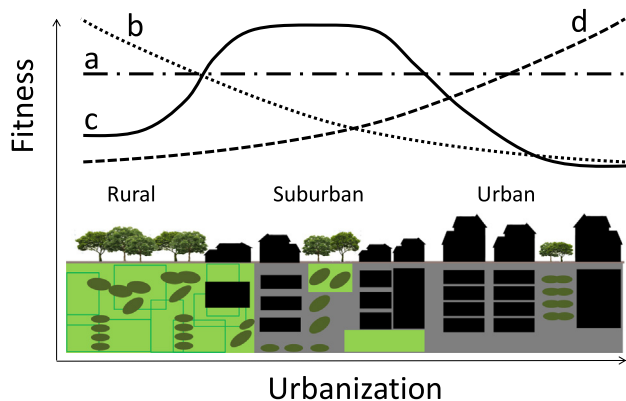


Fig. 3. Hypothetical species-specific responses of bat fitness to an increasing gradient of urbanization; (a) urban-tolerant species; (b) urban-sensitive species; (c) suburban-habitat specialist; (d) synurbic species. In the bird's eye view map of landscape (below) the change in background colour from left to right corresponds to a decrease in cultivated fields, replaced by impervious surfaces, whereas ellipses represent trees and black rectangles buildings.

We suggest that individual fitness follows different paths along an urbanization gradient according to the species considered. Provided that an effective way to estimate individual fitness is established, this might be used to test different predictions such as those outlined in Fig. 3, corresponding to hypothetical fitness paths in a range of species, from highly affected to favoured (synurbic) by urbanization (Luck et al., 2013). Species maximizing individual fitness in suburban areas, laying half way along the gradient, might help explain the richness peak found in such habitats by several studies (Duchamp et al., 2004; Lumsden and Bennett, 2005; Threlfall et al., 2012).

There are reasons to believe that the high population density some species reach in urban areas may be a misleading proxy of increased fitness so their synanthropy may have been at least overestimated. Although not explicitly addressed by most of the available scientific literature, urban biotopes might in fact act as ecological traps (Schlaepfer et al., 2002) for bats, i.e. a habitat “low in quality for reproduction and survival that cannot sustain a population, yet preferred over other available, high-quality habitats” (Battin, 2004; Donovan and Thompson, 2001) as demonstrated for other synanthropic taxa (Sumasgutner et al., 2014). To our best knowledge, the only study that has clearly addressed the impact of urbanization on bat fitness is a 3-year work done in the city of Calgary (Canada) and its surroundings on *Myotis lucifugus* (Coleman and Barclay, 2011). It tested whether the increase of habitat complexity linked with urbanization in the North American Prairies would benefit this synanthropic bat by making more resources (day-roosts, tree cover and insect food) available thus improving its fitness. The study targeted urban vs. non-urban riparian sites. Bats that did best were located in transition habitat comprised between genuinely urban and rural areas. High-density urban populations exhibited decreased body condition and smaller production of juveniles, perhaps due to the higher competition for food, stress, disease transmission or acoustic pollution, suggesting that this habitat may represent an ecological trap. The Calgary case is instructive as it shows that high population density is not an effective indicator that urban sites constitute population sources for synanthropic bats (Coleman and Barclay, 2011).

Why might urban sites act as ecological traps for bats?

The reasons to support the hypothesis that urban sites may act as ecological traps for apparently tolerant or synanthropic species are summarized as follows.

Urban habitat may lure large numbers of bats and expose them to opportunistic predators

Roosting in buildings may expose bats to opportunistic predators (Threlfall et al., 2013a,b) which reach especially high densities in urban environments, including crows, kestrels, seagulls, rats, possums, dogs and especially domestic cats (Ancillotto et al., 2013; Mikula, 2013; Mikula et al., 2013; Threlfall et al., 2013a,b): these may potentially lead to the disappearance of entire colonies. In Italy, Ancillotto et al. (2013) found that predation by domestic cats was stronger in rural, low-density urban sites. In such areas, where owned cats are often kept outdoor, a high capture rate of adult female bats by cats was recorded. Owls have also been found to catch more bats in human settlements than in natural habitats, probably because of the proximity between owl and bat roosts as well as the easier access to bats in non-forested urban habitats (Lesiński et al., 2009). Predators may detect acoustic and olfactory cues. Even in small amounts, odours that accumulate from roosting in human-made structures, such as those due to droppings, act as strong predator attractors (Threlfall et al., 2013a,b).

Conflict with humans in urban habitat may lead to increased mortality

Bats may be excluded from houses because of damage resulting from dropping accumulation, and, when bats enter human living areas, due to concerns over possible transmission of diseases to humans (Streicker et al., 2013) or simple psychological intolerance to bat proximity (exclusion is illegal in some countries, legal in others). O'Shea et al. (2011) found that 35% of colonies roosting in buildings were excluded over a period of 4 years, so this conflict may represent a serious conservation issue. Colony displacement can lead to disruption of social groups, increased individual mortality (Aguar et al., 2012; Neilson and Fenton, 1994) and decrease of reproductive success (Agosta, 2002). Unsustainable alteration of roosts, including building modification or demolition (O'Shea et al., 2011) is another major conflict factor. Although easy to mitigate by appropriate strategies (e.g. Mitchell-Jones and McLeish, 2004), conflicts may be locally frequent, go unnoticed and bring about serious conservation consequences on bat populations particularly when they affect large colonies.

Competition with alien species

Urban areas often represent the places where alien species are first introduced (Menchetti and Mori, 2014). Although the effects of exotic species on bats roosting in urban areas have been long assumed to be negligible, recent work suggests that alien taxa (specifically, introduced parakeets) competing for roosts may represent a problem and even kill bats (Hernández-Brito et al., 2014; Menchetti et al., 2014).

Bats may experience increased mortality as road kills

Roads are ubiquitous in urban areas (Di Giulio et al., 2009) and may affect bats living there by increasing the risk of collisions with vehicles (Lesiński, 2007; Medinas et al., 2012; Russell et al., 2009) or, indirectly, by interrupting commuting routes and fragmenting foraging areas (Russell et al., 2009; Wray et al., 2005). Species that fly low over ground seem to be more affected.

Bats may get trapped in buildings

Data from wildlife rescue centres in Greece (Kalpakis et al., 2005), Spain (Monsalve-dolz, 2014) and Italy (LIPU, pers. comm.) document cases of *T. teniotis* mass mortality: 43–600 bats have

been observed to get trapped in small balconies or courtyards in city centres. Episodes of high accidental mortality of bats trapped inside buildings have been also reported during swarming by pipistrelle (Dietz et al., 2009) and noctule bats (Mühldorfer et al. 2011). Breathable roofing membranes, insulating textiles used in buildings in lieu of roofing underlay such as bitumen felt, have been found to entangle bats and cause significant mortality as the threads they are made of are pulled loose through contact with bats (Waring et al. 2014). There is also anecdotal evidence that in certain building roosts newborns find fewer opportunities to cling on walls, or encounter slippery surfaces, especially when mothers are out to forage (A. Tomassini com. pers.), so they fall frequently and die of starvation, dehydration or are taken by predators.

Higher competition for food may occur in urban areas

Increased roost availability may support unusually high densities of synanthropic species: this condition might result in increased competition for food, especially given the low insect productivity of urban biotopes (Coleman and Barclay, 2011). Passive (unintended) information transfer via echolocation calls or feeding buzzes (Fenton, 2003) may be frequent in urban areas. Although eavesdropping on conspecific calls favours bats from the same social unit (Dechmann et al., 2009), under high population densities it might lead to strong intra- or interspecific competition at feeding sites, concentrating large numbers of bats above optimal foraging density.

Effects of urbanization on bat health

Pollutants and pesticides are more abundant in urbanized habitats where they often affect wildlife. Frugivorous bats in urban areas of South America were found to be more subject to an alopecic syndrome than those occurring in natural habitats, probably as a consequence of pollution and poor-quality foraging sites (Bello-Gutiérrez et al., 2010). Some species are also affected by chemicals employed to protect roof timbers against wood-boring insects and fungi, when these products are used at roosting sites (e.g. Racey and Swift, 1986).

Urban life also leads bats to change some aspects of their ecology and behaviour, with negative consequences for their health. Bats in buildings form larger colonies than in natural roosts (Lausen and Barclay, 2006) and may alter roost switching patterns in response to human disturbance (Streicker et al., 2013), both factors which seemingly increase the spreading of diseases. Mühldorfer et al. (2011) detected an unusually high presence of infectious diseases in urban bats, particularly in maternity roosts. The sedentary behaviour by flying foxes in urban parks of Australia, a new roosting habitat associated with human settlements, has been related with pathogen outbreaks and a decline in population immunity (Plowright et al., 2011).

Although a comprehensive coverage of this subject would be beyond the scope of this review, we mention that bats carry several viral diseases harmful to humans such as Nipah (Luby et al., 2009), Hendra (Smith et al., 2011), Ebola (Leroy et al., 2005), Marburg (Townner et al., 2007) and Sars (Wang et al., 2006) whose spread is indirectly associated with urbanization. In the last 50 years, especially in the tropics, these viruses have caused recurrent outbreaks among people. Deforestation and the expansion of urban areas have dramatically increased the likelihood that people come into contact with bats carrying viruses. Forests hosting bats are fragmented and interspersed with progressively more numerous human settlements. A good example is provided by a recent study into the spread of Nipah virus in Bangladesh (Hahn et al., 2014). It has shown that the likelihood for a village to have an outbreak doubles for every 10 percent tree cover loss. Bats scattered in small colonies across

the fragmented forest landscape get closer to the villages and are more likely to drink from the pots attached to date palm trunks by villagers to collect date palm sap (a sweet syrup largely consumed by people), contaminating it with saliva, urine or droppings.

Bats may be disturbed by artificial light or anthropogenic noise

Bats may persist in roosts whose surroundings are artificially illuminated or disturbed by human-generated noise but this may disrupt their natural behaviour and potentially lead to a drop in fitness (Shirley et al., 2001).

Interference with artificial smooth surfaces

Recent experiments carried out in the laboratory (Greif and Siemers, 2010) and in the field (Russo et al., 2012) have shown that bats recognize water surfaces by echolocation and that any horizontal smooth surface may be mistaken as water. Bats may then be lured by artificial surfaces of this kind which trigger unsuccessful drinking attempts (Russo et al., 2012), but it is unknown whether these effects may be energetically costly for bats, particularly at physiologically demanding times such as pregnancy and lactation. Preliminary work has shown that bats perceive an extended vertical mirror as an open flyway and may collide with it (Zsebök et al., 2011). Again, it is unknown whether vertical smooth surfaces such as window glasses may lead to a significant number of bat casualties, but this impact cannot be ruled out.

Bats as bioindicators of urbanization

Overall, bats prove very sensitive to urbanization, although the magnitude and direction of the effects depend on the scale of analysis and are species-specific. The general pattern is that as urbanization expands, a reduction in richness of bat communities is recorded, associated with the decline or disappearance of urban-sensitive species and the population increase in urban-tolerant, or synurbic, species. Bats are thus promising candidates to track the effects of urbanization on wildlife physiology, behaviour and ecology, but more studies, specifically tailored to explore this role, are needed.

From a practical perspective too, bats appear to be suitable urbanization indicators because in urban habitats they can be easily recorded. The tendency of bats to roost in human-made structures makes them conspicuous and easy to survey in urban areas, offering exciting options to carry out citizen-science campaigns. Besides, most bat species occurring in such areas broadcast loud calls and their presence may be easily recorded by acoustic surveys. Further aids in urban bat research are being offered by the noticeable expansion of automatic bat detector systems and the development of classification algorithms (Walters et al., 2012).

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