

Chapter 2

Urbanisation and Its Effects on Bats—A Global Meta-Analysis

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Abstract Urbanisation is viewed as the most ecologically damaging change to land use worldwide, posing significant threats to global biodiversity. However, studies from around the world suggest that the impacts of urbanisation are not always negative and can differ between geographic regions and taxa. Bats are a highly diverse group of mammals that occur worldwide, and many species persist in cities. In this chapter, we synthesise current knowledge of bats in urban environments. In addition, we use a meta-analysis approach to test if the general response of bats depends on the intensity of urbanisation. We further investigate if phylogenetic relatedness or functional ecology determines adaptability of species to urban landscapes and if determining factors for urban adaptability are consistent worldwide. Our meta-analysis revealed that, in general, habitat use of bats decreases in urban areas in comparison to natural areas. A high degree of urbanisation had a stronger negative effect on habitat use compared to an intermediate degree of urbanisation. Neither phylogenetic relatedness nor functional ecology alone explained species persistence in urban environments; however, our analysis did indicate differences in the response of bats to urban development at the family level. Bats in the families Rhinolophidae and Mormoopidae exhibited a negative association with urban development, while responses in all other families were highly heterogeneous. Furthermore, our analysis of insectivorous bats

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revealed that the adaptability of individual families, e.g. Emballonuridae and Vespertilionidae, to urbanisation is not consistent worldwide. These results suggest that behavioural and/or morphological traits of individual species may better determine species' adaptability to urban areas, rather than phylogenetic or functional classifications, and that driving factors for species adaptability to urban areas might be regionally divergent. We thus argue that future research should focus on behavioural and morphological traits of bats, to assess if these determine urban adaptability in this species-rich group of mammals.

2.1 Introduction

2.1.1 *The Urban Context*

Urbanisation results in extreme forms of land use alteration (Shochat et al. 2006; Grimm et al. 2008). In the last century, the human population has undergone a transition in which the majority of people now live in urban rather than rural areas (UNPD 2012). The rate of change at which urban areas are evolving due to natural population growth is dramatic, including significant rural-to-urban migration and spatial expansion (Grimm et al. 2008; Montgomery 2008; UN 2012; McDonnell and Hahs 2013). In the last 50 years, the global human population in urban areas increased from 2.53 to 6.97 billion people (UNPD 2012). Yet human pressure resulting from urbanisation is not uniformly distributed on the planet. While urbanisation in the developed countries is slowing down slightly, it is increasing rapidly in developing countries of Asia, Africa, Latin America and the Caribbean, many of which harbour hotspots of biodiversity (Myers et al. 2000). In addition, over half of the urban population growth is projected to occur in smaller towns and cities (UN 2012). This implies that urbanisation is not a locally concentrated event, it is rather a fundamentally dispersed process and a happening worldwide (McDonald 2008).

The ecological footprint of cities reaches far beyond their boundaries (McGranahan and Satterthwaite 2003; McDonald and Marcotullio 2013). Effects of cities operate from local (e.g. through urban sprawl) to global scales (e.g. through greenhouse gas emission) (McDonald et al. 2008), and act both directly, through expansion of urban areas, and indirectly through growth in infrastructure and changes in consumption and pollution (McIntyre et al. 2000; Pickett et al. 2001). Apart from the obvious loss in natural area, expansion of cities also impacts the surrounding rural and natural habitats through increased fragmentation, and edge effects with increasing temperature and noise levels, which together introduce new anthropogenic stressors on fringe ecosystems (Grimm et al. 2008) and nearby protected areas (McDonald et al. 2008; McDonald and Marcotullio 2013). However, despite the radical land transformation and habitat loss incurred through urbanisation, many species (native and introduced) can still persist in urban environments and some even experience population increases (McKinney 2006). This

suggests that urban landscapes can actually provide suitable habitat for a variety of species, albeit an anthropogenically altered habitat. Nevertheless, our understanding of what constitutes a suitable habitat in urban areas and what determines a species' adaptability to an urban environment is currently very limited.

Generally, urban areas are characterised by high quantities of impervious surfaces (McKinney 2002). There are however many additional physical and chemical changes incurred via the process of urbanisation (McDonnell and Pickett 1990), such as increased pollution, eutrophication, increased waste generation, altered hydrology (Vitousek et al. 1997; Grimm et al. 2008), increased urban noise (e.g. Slabbekoorn and Ripmeester 2008) and artificial light (Longcore and Rich 2004). Urban areas can provide a more thermally stable environment via the urban heat island effect (e.g. Zhao et al. 2006); less radiation is reflected during the day and more heat is trapped at night, which can increase minimum temperatures in cities (Grimm et al. 2008). The changed climate profile of cities can benefit some species by making the area more inhabitable year round. In addition, the planting of attractive introduced and native plant species throughout the suburbs and along city roads also changes the resources available to fauna, for example by providing nectar or fruits throughout the year. Altogether these changes can impact local species assemblages within cities and regional biodiversity beyond the municipal boundaries (Grimm et al. 2008).

Anthropogenic changes in urban ecosystems typically occur at rates drastically faster than long-lived organisms are capable of adapting to, and thus disrupt ecological processes that historically governed community structure (Duchamp and Swihart 2008). However, generalisations about the negative effects of urbanisation should not overlook biologically meaningful differences in how taxa respond to human land use (Dixon 2012). Some wildlife species are able to adjust to a life in urban areas. Among vertebrates, a range of birds are relatively abundant in urban environments and bird species richness may peak at intermediate levels of urbanisation because of increased heterogeneity of edge habitats (Blair 2001; McKinney 2002) and changes in resource availability due to provision of artificial feeding stations (Sewell and Catterall 1998). In contrast, only a few mammals have been documented as successful species in urban areas (Macdonald and Newdick 1982; Septon et al. 1995; Luniak 2004). For example, the grey-headed flying fox (*Pteropus poliocephalus*) has established a year-round camp in urban Melbourne, Australia, an area outside of its normal climatic range. Warmer temperatures from the urban heat effect, enhanced precipitation from local irrigation and year-round food resources appear to have facilitated the colony's arrival and persistence (Parris and Hazell 2005). Many animals, however, disappear from cities because they depend on habitat features that no longer exist (Gilbert 1989; McKinney 2002; Luniak 2004; Haupt et al. 2006; McDonnell and Hahs 2008). Declining species often suffer from increased habitat isolation, or face competition from invasive and more dominant species (McDonald and Marcotullio 2013). Some species in urban areas also suffer from additional stress (Isaksson 2010), increased infection and parasitism rates (Giraudeau et al. 2014) and reductions in potential reproductive success (Chamberlain et al. 2009). Urbanisation can also trigger a change

in behaviour (Ditchkoff et al. 2006; Grimm et al. 2008). For example, urban noise alters the pitch at which some birds call (Slabbekoorn and Peet 2003), and affects activity patterns of larger vertebrates (Ditchkoff et al. 2006). Furthermore, increased artificial lighting can potentially disturb the circadian rhythms of nocturnal animals and interfere with the navigation of migrating species (Longcore and Rich 2004; Hölker et al. 2010; see Rowse et al., Chap. 7 this volume).

2.1.2 Urban Wildlife

Persistence of wildlife in urban environments may be linked to opportunism and a high degree of ecological and behavioural plasticity (Luniak 2004). In contrast, species that decline in response to urbanisation are often habitat and resource specialists (McKinney and Lockwood 1999; Jokimäki et al. 2011). Typically this results in altered assemblage structures in urban environments, often with a few highly abundant species, which account for a much higher proportion of the whole community in urban environments than in surrounding wild lands (Shochat et al. 2006). In addition, many native species are replaced by non-native, weedy or pest species (McKinney 2002). The resulting mix of introduced and native species in urban areas can lead to novel species interactions and altered ecosystem functioning (Hobbs et al. 2006). Often these non-native and introduced species are the same species across cities throughout the world. Thus, the flora and fauna of cities are becoming increasingly homogeneous (Hobbs et al. 2006; Grimm et al. 2008), however recent evidence suggests that many cities still retain several endemic species (Aronson et al. 2014).

Multi-scaled and multi-taxa investigations are required to provide detailed information about urban biodiversity (Clergeau et al. 2006). To date, urban ecologists have focused on few taxa, examining the response of conspicuous species to an urbanisation gradient (McDonnell and Hahs 2008). Population- and assemblage-level responses to urbanisation have been examined most prolifically for highly diverse and mobile bird taxa (McKinney 2002; McDonnell and Hahs 2008). Unfortunately, our understanding of how other wildlife, including bats, respond to the complex process of urbanisation is still limited (Barclay and Harder 2003). Research conducted to date provides a general indication that many bats may be declining due to urbanisation, however an understanding of the processes driving these patterns remains largely unknown.

2.1.3 Bats in Urban Environments

Bats likely form the most diverse group of mammals remaining in urban areas (van der Ree and McCarthy 2005; Jung and Kalko 2011). Of the studies conducted in urban landscapes to date, many show that overall bat activity and

species richness are greatest in more natural areas, and decreases with increasing urban influence (Kurta and Teramino 1992; Walsh and Harris 1996; Gaisler et al. 1998; Legakis et al. 2000; Lesiński et al. 2000). However, certain bat species may better be able to adapt to urban landscapes (Avila-Flores and Fenton 2005; Duchamp and Swihart 2008). Coleman and Barclay (2011), however, cautioned that most researchers have worked in forested regions directing less attention to other biomes, including grasslands. They argue that because urban tree cover is fairly constant (<30 %) in all cities (McKinney 2002), urbanisation in tree-rich regions implies deforestation and thus reduced tree cover may cause the negative effect of urbanisation. In contrast, urban areas within grassland regions might enhance structural heterogeneity and thus benefit species richness and relative abundance patterns (see Coleman and Barclay 2011 for more details). This is in accordance with the results of Gehrt and Chelsvig (2003, 2004) investigating the response of bats in and around the highly populated city of Chicago, USA. Here species diversity and occurrence were higher in habitat fragments within urban areas than in similar fragments in rural areas (Gehrt and Chelsvig 2003, 2004). However the large, forested parks in the region may offset the habitat loss caused by urbanisation, and hence they mitigate any negative impacts to bats at the regional scale.

The majority of studies on bats in urban environments come from the temperate regions of Europe and North America. Many studies focus on the response of bats to differently structured areas within the urban environment including historic and newly built city districts (Gaisler et al. 1998; Legakis et al. 2000; Guest et al. 2002; Dixon 2012; Hale et al. 2012; Pearce and Walters 2012), illuminated and non-illuminated areas (Bartoniccka and Zukal 2003), industrial areas (Gaisler et al. 1998) small and larger parklands (Kurta and Teramino 1992; Fabianek et al. 2011; Park et al. 2012) and areas that receive waste water (Kalcounis-Rueppell et al. 2007). Most of these studies report relatively high bat activity and species richness in areas with remaining vegetation such as older residential areas, riverine habitats or parklands. Certain bat species appear to thrive in these urban environments, and success has been linked to species-specific traits (Duchamp and Swihart 2008). In particular, bat species with high wing loadings and aspect ratios, so presumed to forage in open areas (Norberg and Rayner 1987), which also roost primarily in human structures appeared to adjust to urban environments, provided that there is sufficient tree cover (Dixon 2012). Many of these studies imply that protecting and establishing tree networks may improve the resilience of some bat populations to urbanisation (Hale et al. 2012). Population- and assemblage-level responses along gradients of urbanisation reveal that generally foraging activity of bats seems to be higher in rural and forested areas than in urban areas (Geggie and Fenton 1985; Kurta and Teramino 1992; Lesiński et al. 2000). However, it is important to note that some species might be highly flexible in their habitat use. The European bat *Eptesicus nilsonii*, for example, spends a much higher proportion of its foraging time in urban areas after birth of the juveniles than before (Haupt et al. 2006). This raises the importance of repeat observations during different seasons when investigating the response of bats to urbanisation.

In the Neotropics, most studies concerning bats and environmental disturbance have concentrated on fragmentation effects due to logging or agricultural land use (e.g. García-Morales et al. 2013). Persistence of bats in fragmented landscapes has been associated with edge tolerance and mobility in phyllostomids (Meyer and Kalko 2008), and the predominant use of open space as foraging habitat for aerial insectivorous bats (Estrada-Villegas et al. 2010). Of the few studies focusing on urban areas, most report an overall decrease in species richness and relative abundance of bats in urban areas (Avila-Flores and Fenton 2005; Siles et al. 2005; Pacheco et al. 2010; Jung and Kalko 2011) compared to forested areas. Predominantly, insectivorous bats seem to remain in large urban environments (Bredt and Uieda 1996; Filho (2011). Of these, it is typically members of the Molossidae, which are known to forage in the open spaces above the tree canopy that seem to tolerate and potentially profit from highly urbanised areas (Avila-Flores and Fenton 2005; Pacheco et al. 2010; Jung and Kalko 2011). In addition, many buildings in cities provide potential roost sites that resemble natural crevices (Burnett et al. 2001; Avila-Flores and Fenton 2005) and are known to be readily occupied by molossid bats (Kössl et al. 1999; Scales and Wilkins 2007). In a smaller urban setting in Panama, where mature forest meets very restricted urban development, a high diversity of bats occurs within the town and bats frequently forage around street lights (Jung and Kalko 2010). Nevertheless, even in such a low impact urban setting some species of the bat assemblage such as *Centronycteris centralis* revealed high sensitivity and were never recorded within the town, albeit foraging frequently in the nearby mature forest (Jung and Kalko 2010).

Recent investigations from large metropolitan urban centres in Australia show suburban areas can provide foraging habitat for bats (Rhodes and Catterall 2008; Threlfall et al. 2012a), and support greater bat activity and diversity than more urban and even forested areas (Hourigan et al. 2010; Basham et al. 2011; Threlfall et al. 2011, 2012b; Luck et al. 2013). However, studies from regional urban centres in Australia suggest that any urban land cover, even if low-density residential, can decrease bat activity and species richness (Hourigan et al. 2006; Gonsalves et al. 2013; Luck et al. 2013), and can deter some species of clutter-tolerant bats altogether (Gonsalves et al. 2013; Luck et al. 2013). Evidence also suggests that species adapted to open spaces and edges, such as those within the molossid family, do not display the same response to urbanisation in small regional versus large metropolitan urban centres, indicating subtle behavioural differences among species with similar ecomorphology (Luck et al. 2013; McConville et al. 2013a, b). The few studies that have investigated species-specific foraging and roosting requirements, suggest that although bats display high roost site fidelity within urban areas (Rhodes and Wardell-Johnson 2006; Rhodes et al. 2006; Threlfall et al. 2013a), species differ in their ability to forage successfully on aggregations of insects across the urban matrix, reflecting variation in flight characteristics and sensitivity to artificial night lighting (Hourigan et al. 2006; Scanlon and Petit 2008; Threlfall et al. 2013b).

Asian bat assemblages comprise a variety of frugivore and insectivore bat species; however, there is limited information on urban impacts to bats in this region

of the world. Many roosting and foraging resources for frugivore species such as *Cynopterus* and *Pteropus* species are provided by exotic trees that grow easily in urban centres in Asia, for example *Ficus*, *Livistona* and *Syzygium* species, which have been studied in Hong Kong (Corlett 2005, 2006), India (Caughlin et al. 2012) and Japan (Nakamoto et al. 2007). Frugivore species in these systems provide critical seed dispersal services and can play a role in regeneration and pollination of some tree species (Mahmood-ul-Hassan et al. 2010; Caughlin et al. 2012). Radio-tracking studies show that some bat species roost in forested areas (Nakamoto et al. 2012) or in-built structures (Nadeem et al. 2013), however many frugivore species appear to profit from the density of planted exotic vegetation and both frugivore and insectivore bats can benefit from increased foraging resources in urban areas (Corlett 2005; Nakamoto et al. 2007; Utthammachai et al. 2008; Caughlin et al. 2012; Nakamoto et al. 2012). However, it appears that Asian bats, particularly large pteropodids, are also under threat from direct human impacts via hunting (Thomas et al. 2013), in addition to human land use alteration, and hence, any impact of urbanisation may be confounded by direct human impacts. However, increasing land use change and growing urban populations have been stated as a likely cause of dramatic declines of many bat species (including pteropodids) in Singapore (Pottier et al. 2005; Lane et al. 2006), where it is suggested the reported declines may reflect the declining status of bats in Southeast Asia more broadly (Lane et al. 2006). The only study to our knowledge that has examined bat species distribution in relation to increasing urbanisation was conducted in Pakistan, where greater bat capture success was recorded in urban areas in comparison to suburban and rural areas (Nadeem et al. 2013), and in line with other studies worldwide, the urban bat assemblage was dominated by a few common species. However, it is unclear whether these results were influenced by trapping success, and as such, should be interpreted cautiously.

The co-location of biodiversity and high human population densities raises the importance of conservation-related studies in urban areas where anthropogenic growth directly interacts with the highest levels of biodiversity (Rompré et al. 2008). In these landscapes, it is especially important to identify the underlying mechanisms determining the potential of different species to adjust to urban environments. Currently, our general understanding of what influences a species success and details of urban foraging and roosting habitat selection is incomplete. Yet, arguably the conservation of species such as bats in urban areas depends upon this knowledge (Fenton 1997).

2.2 Evidence-Based Evaluation of the Effect of Urbanisation on Bats Worldwide Using a Meta-Analysis

Within this book chapter, we were in particular interested in the general conclusions concerning the potential of bats to adjust to urban environments. We thus synthesised pre-existing data of published literature with a focus on bats in urban

versus natural environments in a worldwide meta-analysis. Meta-analysis has been previously used in ecology and conservation because results can lead to evidence-based environmental policies.

Here, we investigated the general response of bats to urbanisation and tested whether this is consistent across cities differing in the intensity of urban development. In addition, we address the question of whether adaptability of species to urban landscapes correlates with phylogeny or rather functional ecology. Functional ecology of species can be linked to species traits, where traits refer to morphological, behavioural or physiological attributes of species (Violle et al. 2007). Using such functional traits can improve understanding of and help predict how species respond to environmental change (Didham et al. 1996; Flynn et al. 2009), such as increasing urbanisation. A key challenge is to develop frameworks that can predict how the environment acts as a filter by advantaging or disadvantaging species with certain traits. Urbanisation has been demonstrated to select for, or against, species with specific response traits within flora and fauna communities, including remnant grasslands (Williams et al. 2005), bat communities (Threlfall et al. 2011) and bird communities (Evans et al. 2011). To more fully understand and predict the impact of increasing urban land cover on urban bat communities, the identification and investigation of traits across a variety of studies in urban landscapes worldwide may prove useful. To do this, we investigated the response of bats to urbanisation using a functional ecology approach and further investigated if these mechanisms are consistent worldwide and thus separately analysed the compiled literature for America (North and South America combined) versus Europe, Asia and Australia. Based on previous studies in urban and other human disturbed landscapes, we expected that predominant food item (fruits, nectar and insects), foraging mode (aerial, gleaning) and foraging space (narrow, edge and open, following Schnitzler and Kalko (2001)) may impact upon a species ability to adapt to urban environments, as suggested by (e.g. Avila-Flores and Fenton 2005; Jung and Kalko 2011; Threlfall et al. 2011)

2.2.1 Data Acquisition and Meta-Analysis

We used the Web of Knowledge (Thomson Reuter) to search for publications containing the following key words “bats” AND, “urban”, “urbanis(z)ation”, AND “gradient”, “community”, “assemblage”, “species composition”. This resulted in 99 studies reporting bat responses to urbanisation. In addition, we searched the reference list of these publications for further relevant articles. We compiled all studies focusing on bats in urban areas in our primary dataset. This selection also including different bat inventory methods such as acoustic monitoring, mist net and harp trap sampling as well as visual observations and roost surveys. In many of these articles however, quantitative data on bats were missing, sampling effort was not standardised, or studies did not reciprocally sample bats in urban versus natural areas. We excluded all of these studies from our final dataset, as it

was impossible to calculate a standard effect size of urbanisation. We thus only included studies into our final meta-analysis that reported species-specific data on capture success, roosting individuals, occurrence counts or activity per sampling time in both urban and natural areas (Table 2.1). In a few cases, we extracted data from graphs. We considered all of these measures as indicators of the relative intensity of habitat use and thus assumed comparability of these datasets and hence eligibility to be combined in a meta-analysis. Our final data set for the meta-analysis consisted of 23 articles (Table 2.1) and 96 bat species. Within this dataset we discriminated between studies with high ($N = 5$) and intermediate intensity ($N = 5$) of urbanisation following the individual authors' statements in their articles (Table 2.1). Our designation of 'high' and 'intermediate' was qualitative and based on descriptions of the urban study area from the original papers. For example, Avila-Flores and Fenton (2005) state that their study area of Mexico City is one of the "largest and most populated cities in the world", hence we assigned this study a 'high' urban intensity. Gonsalves et al. (2013) state that no quantification of urban intensity was made in their study, however they suggest that housing density in their study area was low and could be classified as suburban, hence we assigned this study an 'intermediate' urban intensity. This classification is by no means comprehensive, however we believe for comparative purposes these two classifications give some indication and context of the intensity of urban development in the study area for each study used. Some articles ($N = 13$) reported the response of bats to multiple intensities of urbanisation; here we extracted data on the highest, the lowest and the intermediate degrees of urbanisation. Data from urban parks, suburbia or small towns we considered as intermediate degrees of urbanisation.

For each species reported in an article we compared the relative intensity of habitat use in urban (treatment group) versus natural areas (control group) and calculated the log odds ratio as a standardised effect size (Rosenberg et al. 2000). A positive log odds ratio > 0 indicated species that showed a higher intensity of habitat use in urban areas, while a negative log odds ratio < 0 indicated higher intensity of habitat use in natural areas. For multiple reports on a species' response to urbanisation in distinct articles we averaged the log odds ratios to avoid pseudoreplication. Species with incomplete identifications were deleted from the dataset, except for *Mormopterus species 2* (Australia) which has not yet been formally named (Adams et al. 1988) and *Eumops* sp. (Panama) which most likely includes the two species *Eumops glaucinus* and *Eumops auripendulus* (Jung and Kalko 2011). For our analysis we thus considered each bat species ($N = 96$) as a study case for our final meta-analysis models. For all statistical analysis, we used the statistical software package R Version 2.1.4. (R Development Core Team 2011), package "metafor" (Viechtbauer 2013) (version 1.6-0).

In a first approach, we focused on the general response of bats to urbanisation and investigated if the overall response of bats depends on the degree of urbanisation. Hereby we distinguished between high and intermediate intensity of urbanisation (see above) and calculated log odds ratios for the respective contrast to natural areas. We then conducted a random effect model meta-analysis for the

Table 2.1 List of publications included in the meta-analyses

Reference	Country	Urban intensity	Study type	N species urban	N species suburban	N species forest	Survey method	Considered habitat types
Avila-Flores and Fenton (2005)	Mexico	High	Urban gradient	2	3	4	Acoustic monitoring	Residential areas, large parks, forest
Basham et al. (2010)	Australia	Intermediate	Urban/forest	NA	11	13	Acoustic monitoring	Backyards, natural bushland
Bihari (2004)	Hungary	High	Urban/forest	1	NA	1	Roost survey	Residential area, forested park
Chirichella (2004)	Italy	High	Urban gradient	1	1	1	Public survey	Urban, suburban, forest
Duchamp et al. (2004)	USA	High	Urban/forest	2	NA	2	Captures/telemetry	Urban, woods
Fabianek et al. (2011)	Canada	Intermediate	Urban gradient	NA	3	3	Acoustic monitoring	Urban parks < 100 ha, urban parks > 100 ha
Gaisler et al. (1998)	Czech Republic	High	Urban gradient	2	2	2	Acoustic monitoring	Historical city centre, old suburbs, outskirts
Gehrt and Chelsvig (2004)	USA	High	Urban gradient	5	NA	4	Acoustic monitoring	Urban index: 0 (urban) urban index: -5 (rural)
Gonsalves et al. (2013)	Australia	Intermediate	Urban/forest	NA	9	13	Acoustic monitoring	Small urban, forest
Hale et al. (2013)	United Kingdom	High	Urban gradient	2	2	2	Acoustic monitoring	Dense urban, suburban, rural
Haupt et al. (2006)	Germany	High	Urban/forest	1	NA	1	Captures/telemetry	Urban areas, forest (before and after birth of juveniles)
Hourigan et al. (2006)	Australia	Intermediate	Urban gradient	NA	8	8	Acoustic monitoring	Intermediate suburbs, woodland
Hourigan et al. (2010)	Australia	High	Urban gradient	13	13	13	Acoustic monitoring	High and low-density residential, bush land

(continued)

Table 2.1 (continued)

Reference	Country	Urban intensity	Study type	N species urban	N species suburban	N species forest	Survey method	Considered habitat types
Jung and Kalko (2010)	Panama	Intermediate	Urban/forest	NA	21	22	Acoustic monitoring	Small town, forest
Jung and Kalko (2011)	Panama	High	Urban gradient	16	21	25	Acoustic monitoring	Urban, small town, forest
Kurta and Teramino (1992)	USA	High	Urban/forest	4	NA	5	Captures	Urban/rural
Lesinski et al. (2000)	Poland	High	Urban gradient	3	3	3	Acoustic monitoring	Central, suburban(III), suburban(V)
Nadeem et al. (2013)	Pakistan	High	Urban gradient	4	4	3	Roost surveys	Urban, suburban, rural dwelling
Pottie et al. (2005)	Malaysia/Singapore	High	Urban gradient	5	5	12	Roost surveys/captures/acoustic monitoring	City/urban, suburban, primary forest
Silva et al. (2005)	Brazil	High	Urban gradient	7	8	9	Acoustic monitoring	Small farm, campus Fences, forest
Threlfall et al. (2011, 2012)	Australia	High	Urban gradient	10	15	7	Acoustic monitoring	Urban, suburban, forest
Utthammachai et al. (2008)	Thailand	High	Urban gradient	1	1	1	Acoustic monitoring	Forest patch, village/others, urban
Walters et al. (2007)	USA	High	Urban/forest	1	1	1	Captures	Woodlots, low-density residential, commercial lands

Given are the reference, the country where the study was carried out, the urban intensity (large or small) the study type (gradient, paired design), the number of bat species reported by each author for each habitat type, the survey methodology of the original data and the considered habitat types included in the meta-analysis. NA indicates that the corresponding study had no record of bats for the specified habitat type

effect of high and intermediate urban development, respectively. Random effect models provide an unconditional inference of a larger set of studies from which only a few are included in the meta-analysis and assumed to be a random sample (Viechtbauer 2010). We compared both models based on the reported effect size and assessed the proportion of heterogeneity of bat responses between high and intermediate urban development (τ^2 highly urban- τ^2 small urban/ τ^2 highly urban).

In a second approach, we pooled data from high and intermediate urbanisation categories to investigate if the potential of bats to adjust to urban environments is determined by phylogeny or rather functional ecology using a mixed model meta-analysis. For this analysis we classified bats according to their taxonomic family and genus, their predominant food item (fruits, nectar and insects), foraging mode (aerial, gleaning) and foraging space (narrow, edge and open, following Schnitzler and Kalko (2001)) and included these classifications as moderators in our mixed model meta-analysis. We further investigated in detail how each of the categorical moderators influences effect size. Further, focusing on aerial insectivores, the majority of study cases in our dataset, we then investigated if moderators influencing the adaptability to urban areas are consistent between North and South America versus Europe, Asia and Australia. P-levels for all models were assessed using a permutation test with 1000 randomizations. In none of our models did the funnel plot technique (Viechtbauer 2013) reveal any significant publication bias or asymmetry in our dataset (function: regtest, package metaphor).

2.2.2 High Versus Lower Levels of Urbanisation

Our random effect meta-analysis revealed that in general, urbanisation negatively affects bats, and areas with high (deviance = 453.14, z -value = -3.9 , $p < 0.001$) and intermediate (deviance = 439.73; z -value = -2.4 , $p < 0.05$) degrees of urban development reveal significantly lower intensity of habitat use across species compared to natural areas (Fig. 2.1). A high degree of urbanisation had a stronger negative effect on the general intensity of habitat use (estimate: -1.47) than an intermediate degree of urban development (estimate: -0.79). However, in both high and intermediate urban development, we found significant variation in the

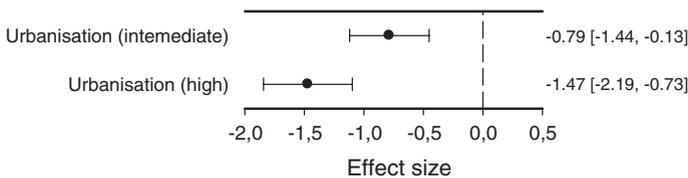


Fig. 2.1 Effect sizes of relative intensity of habitat use by bats in high and intermediate urban development, compared to natural areas. Solid symbols indicate the mean effect size (log odds ratio) and whiskers indicate the estimated standard error. Values of the estimated effect size, including the 95 % confidence intervals are listed on the right side of the figure

effect sizes (high urban development: $Q_{(df=84)} = 641.2, p < 0.0001$; intermediate urban development $Q_{(df=85)} = 989.9, p < 0.0001$), indicating a high variability in the response of bat species to urbanisation. This species-specific variability in the intermediate degree of urbanisation ($\tau^2 = 7.74$) accounted for 21 % of the variability in the areas with high urban development ($\tau^2 = 9.80$). This suggests that although intermediate urban development clearly has a negative influence on bats it still permits the use of this habitat by more species showing fewer extremes in the species-specific response to urbanisation, compared to high urban development.

2.2.3 Phylogeny Versus Functional Ecology

Neither phylogeny ($Q_{M(df=3)} = 11.57, p > 0.05$) nor functional ecology ($Q_{M(df=3)} = 12.18, p > 0.05$) explained the heterogeneity in bat response to urbanisation. However, a different pattern emerged when investigating the effect of single moderators in detail. Response to urbanisation differed between families ($Q_{M(df=10)} = 32.4, p = 0.05$) with bat species in the Rhinolophidae being negatively affected by urban development ($p < 0.01$). In addition, bat species in the Mormoopidae tended to respond negatively towards urbanisation, as the 95 % confidence interval did not overlap with zero. All other families revealed a high heterogeneity in the response to urbanisation. Effect size was neither genera— ($Q_{M(df=46)} = 81.4, p > 0.05$) nor species-specific ($Q_{M(df=86)} = 99.7, p > 0.05$).

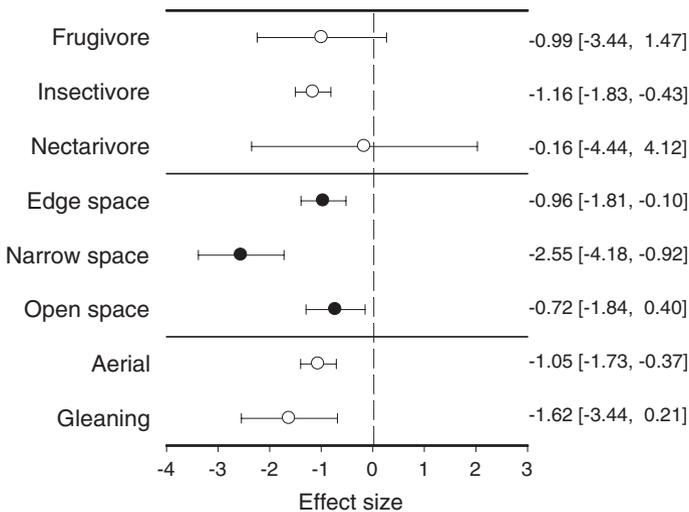


Fig. 2.2 Effect of urbanisation (log odds ratio and the estimated standard error) on relative intensity of habitat use in relation to the predominant food item (a), foraging space (b), and foraging mode (c). Solid symbols indicate the mean effect size (log odds ratio) and whiskers indicate the estimated standard error. Values of the estimated effect size, including the 95 % confidence intervals are listed on the right side of the figure

None of the functional classifications, food item, foraging mode and foraging space, revealed a significant association with the persistence of bats in urban areas. However narrow space foragers (estimate -2.55 ± 0.83 , $p = 0.06$) revealed a tendency to be associated with natural areas (Fig. 2.2).

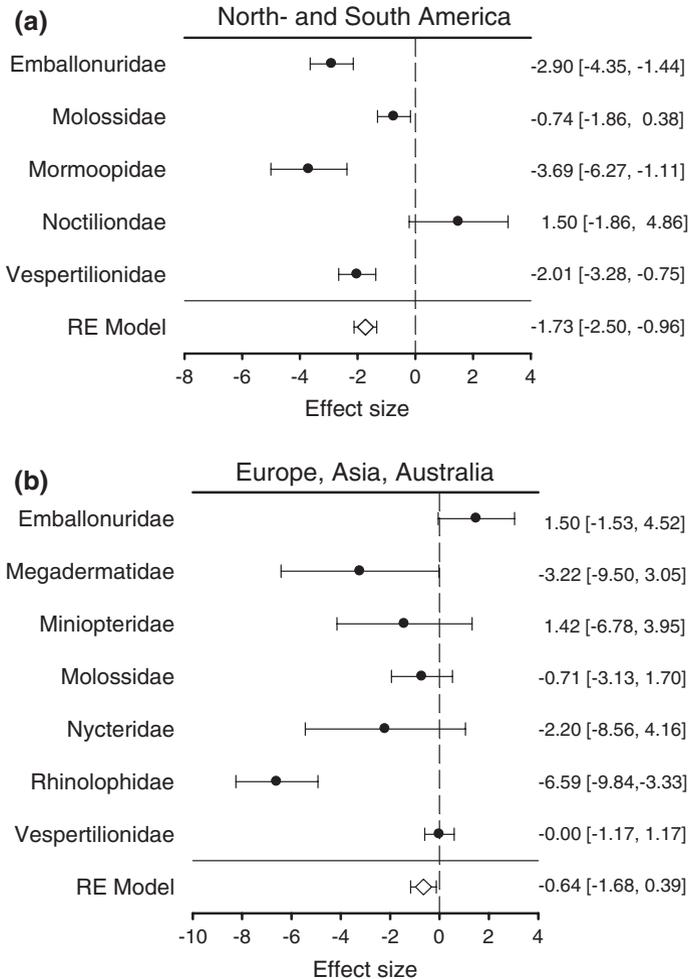


Fig. 2.3 Response of insectivorous bat families to urbanisation in **a** North and South America and **b** Europe, Asia and Australia. A negative effect size reflects a higher association with natural areas, a positive effect size an association with urban areas. Depicted are the mean effect sizes (log odds ratio) and the estimated standard errors by family. Values of the estimated effect size, including the 95 % confidence intervals are listed on the right side of the figure. The overall effect of urbanisation on insectivorous bats, based on the random effect model (RE Model), is given at the bottom of the respective figure

2.2.4 Contrasting the Effects between North and South America and Europe, Asia and Australia Focusing on Insectivores

The general response of insectivorous bats differed between the Americas and Europe, Asia and Australia. While insectivorous bats in the Americas revealed a significant negative response to urbanisation (deviance = 171.18, z -value = -4.4 , $p < 0.001$) the overall response of insectivorous bats to urbanisation in Europe, Asia and Australia was insignificant (deviance = 258.9, z -value = -1.2 , $p > 0.05$, Fig. 2.3a, b).

However, in both the Americas ($Q_{M(df=5)} = 35.1$, $p < 0.05$) and Europe, Asia and Australia ($Q_{M(df=7)} = 18.7$, $p < 0.05$) the response to urbanisation differed significantly across families. Interestingly this family-level response was inconsistent between the Neo- and Paleotropics. While Neotropical bats in the Emballonuridae showed a strong tendency to be associated with natural areas (estimate: -2.9 ± 0.7 , $p = 0.06$), emballonurids in the Paleotropics (estimate: 1.5 ± 1.5 , $p > 0.05$) occurred frequently in urban areas. We found a similar trend in the globally distributed family of Vespertilionidae, which showed a higher association with natural areas in the Americas (estimate: -2.0 ± 0.6 , $p > 0.05$) but did not reveal any clear association in Europe, Asia and Australia (estimate: -0.0 ± 0.6 , $p > 0.05$) (Fig. 2.3a, b).

2.3 Adaptability of Species to Urban Areas: General Trends, Species-Specific Differences and Future Research

Urban areas can provide suitable habitat for a variety of species, albeit an anthropogenically altered habitat (McKinney 2006). However, our general understanding of what influences a species' success in urban environments is limited. Arguably the conservation of species such as bats in urban areas is dependent upon this knowledge (Fenton 1997). Within this book chapter, we reviewed the existing literature on bats in urban areas. In addition, we combined published data in a meta-analysis to evaluate and derive general patterns in the response of bats to urban development.

Our meta-analysis revealed that, in general, habitat use of bats decreases in urban areas. A high degree of urbanisation had a stronger negative effect on overall habitat use of bats compared to an intermediate degree of urban development. However, habitat use in intermediate urban development was much lower compared with natural areas. This is alarming, as it is generally thought that small towns and suburban landscapes could potentially provide suitable habitat for a wide range of species (McKinney 2006), including bats. The combination

of habitats with different complexity in smaller urban developments should lead to greater complementarity at a local scale and should favour species diversity and abundance. Some of the publications in our meta-analysis dataset indeed report a higher bat diversity, activity (Hourigan et al. 2010; Threlfall et al. 2011, 2012b) and feeding activity (Jung and Kalko 2011; Threlfall et al. 2012a) at intermediate levels of disturbance compared to natural or urban habitats. Other studies reported that any urban land cover, even if low-density residential, can decrease bat activity and species richness (Hourigan et al. 2006; Gonsalves et al. 2013; Luck et al. 2013), and even deter individual species (Jung and Kalko 2010; Gonsalves et al. 2013; Luck et al. 2013). Altogether, this strongly suggests regional differences in the intensity of urban development and points towards an interacting effect of the surrounding landscape (see Coleman and Barclay 2011).

Results from recent urban bat studies suggest that bats of some families (e.g. molossids Jung and Kalko 2011) are better pre-adapted for life in an urban environment compared to others (e.g. rhinolophids Stone et al. 2009; Threlfall et al. 2011). Our analysis also indicated a family-specific effect of urbanisation and confirmed the negative response of Rhinolophidae to urban development across the Old World. However, the responses of Molossidae and Vespertilionidae, which are known to frequently roost in man-made structures in North and South America, did not reveal consistent associations with either urban or natural areas across continents. This might be due to the high morphological and behavioural heterogeneity within these families. We believe that the likely explanation for our results is that the response to urbanisation is dictated by the behavioural and morphological traits of species, regardless of geographic region or phylogeny. In particular, species foraging in open space seem to persist in urban areas, as due to their wing morphology (high aspect ratio and wing loading) they might be able to commute large distances between roosting sites and feeding areas (Jung and Kalko 2011). Thus traits predicting species mobility have been associated with urban tolerance (Jung and Kalko 2011; Threlfall et al. 2012a), and the ability to forage around street lights (see Rowse et al., Chap. 7 this volume). In addition, traits that allow for flexible roost and foraging strategies confer an advantage for urban-tolerant species. Our current results support these findings and thus suggest that adaptability of bats to urban environments (or disturbance in general) might be correlated with, and reflected by, species behavioural flexibility. Advancement of knowledge in this area will assist with conservation efforts of bat species globally, and potentially allow development of a predictive framework for assessing the impacts of urban development on bats.

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