Part I
Bats in Anthropogenically Changed Landscapes

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; Lesiñski 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 (Bartonicka 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; Lesiñski 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 (Pottie 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 dependents 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 Funcesi, 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

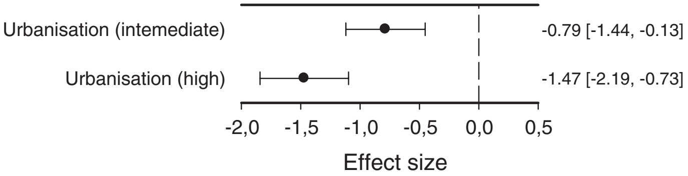

Fig. 2.1 Effect sizes of relative intensity of habitat use by bats in high and intermediate urban development, compared to natural areas. Solid symbols indicate the mean effect size (log odds ratio) and whiskers indicate the estimated standard error. Values of the estimated effect size, including the 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 ($Q_{M(df=86)} = 99.7$, $p > 0.05$).

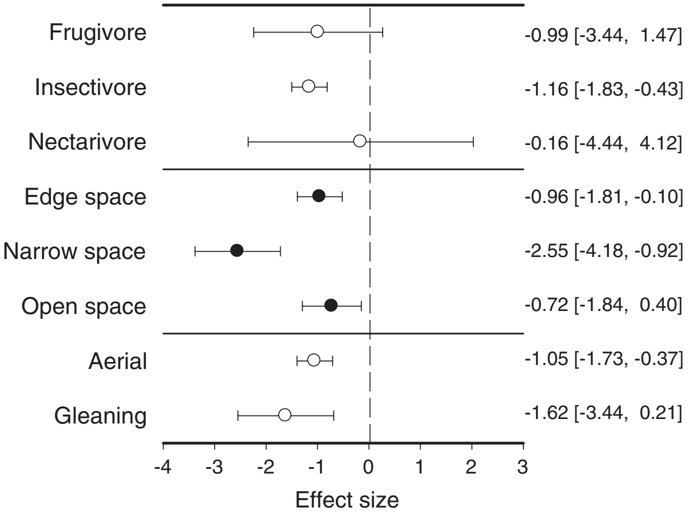

Fig. 2.2 Effect of urbanisation (log odds ratio and the estimated standard error) on relative intensity of habitat use in relation to the predominant food item (**a**), foraging space (**b**), and foraging mode (**c**). Solid symbols indicate the mean effect size (log odds ratio) and whiskers indicate 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).

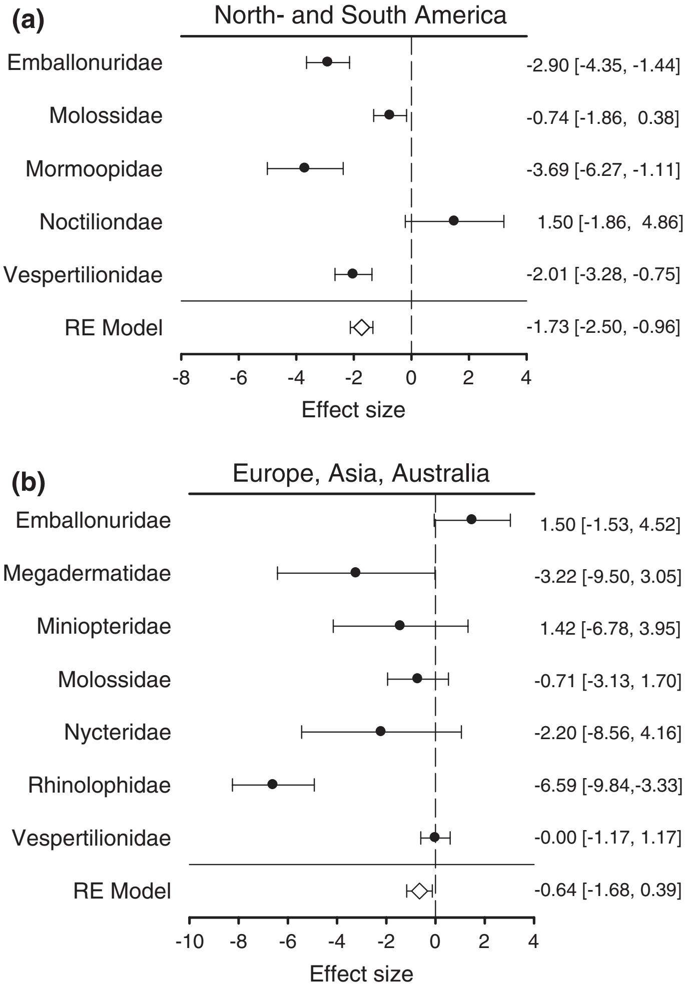

Fig. 2.3 Response of insectivorous bat families to urbanisation in **a** North and South America and **b** Europe, Asia and Australia. A negative effect size reflects a higher association with natural areas, a positive effect size an association with urban areas. Depicted are the mean effect sizes (log 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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Chapter 3
Bats and Roads

John Altringham and Gerald Kerth

Abstract The effects of roads on bats have been largely neglected until recently, despite growing evidence for profound effects on other wildlife. Roads destroy, fragment and degrade habitat, are sources of light, noise and chemical pollution and can kill directly through collision with traffic. The negative effects of roads on wildlife cannot be refuted but at the same time road building and upgrading are seen as important economic drivers. As a consequence, infrastructure projects and protection of bats are often in conflict with each other. There is now growing evidence that fragmentation caused by roads reduces access to important habitat, leading to lower reproductive output in bats. This barrier effect is associated with reduced foraging activity and species diversity in proximity to motorways and other major roads. The effects of light and noise pollution may add to this effect in the immediate vicinity of roads and also make bats even more reluctant to approach and cross roads. Several studies show that vehicles kill a wide range of bat species and in some situations roadkill may be high enough to lead directly to population decline. Current mitigation efforts against these effects are often ineffective, or remain largely untested. The limited information available suggests that underpasses to take bats under roads may be the most effective means of increasing the safety and permeability of roads. However, underpass design needs further study and alternative methods need to be developed and assessed.

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3.1 Introduction

The global road network gets longer, wider, faster and more complex as existing road systems are upgraded and new roads are built. Despite the widely acknowledged need to reduce our dependence on fossil fuel and growing concerns about the environmental impact of roads, improved communication by road, and even the act of road-building itself, are often seen as essential economic drivers. As road networks expand, traffic volumes increase and congestion remains a problem. A few statistics highlight the pervasive nature of our road networks: only 2 % of Germany is made up of landscape fragments greater than 100 km^2 (Jaeger et al. 2007) and only 17 % of the US landscape is more than 1 km from a road (Riiters and Wickham 2003). In 2012, the UK had 395,000 km of roads, of which over 50,000 km are major roads and 3700 km motorways (Defra 2013). Major roads account for only 13 % of all UK roads, but carry 65 % of the traffic. 50 % of all traffic is on motorways and other major roads in rural areas. Almost 20 % of major road length is dual carriageway. Over 3200 km have been added to the UK network in the last decade and many more have been upgraded.

Roads have several negative impacts on animals. First, building roads and their ancillary structures destroys habitat directly. Secondly, the resulting road network fragments the landscape, potentially restricting animal movements, thereby blocking their access to the remaining habitat. Thirdly, roads are also sources of light, noise and chemical pollution, and so degrade the habitat around them. Moreover, the increased human access provided by roads usually accelerates urban, commercial and agricultural development and increases human disturbance in many ways, e.g. through increased recreational pressure and the introduction of non-native predators and other invasive species. Finally, fast moving traffic kills animals directly. Broad reviews of the effects of roads on vertebrates include Bennett (1991), Forman and Alexander (1998), Trombulak and Frissell (2000), Coffin (2007), Fahrig and Rytwinski (2009), Laurance et al. (2009), Benítez-López et al. (2010), and Rytwinski and Fahrig (2012). Surprisingly, despite the many ways in which roads can impact on wildlife, it is only in the last 20 years that significant attention has been given to what is now often referred to as ‘road ecology’ (Forman et al. 2003). Little of this attention was directed at bats. Moreover, the few existing studies on the impact of roads on bats have all been carried out in North America and Europe.

Globally many bat species are endangered (Racey and Entwistle 2003; Jones et al. 2009), including regions with a dense infrastructure such as North America and Europe (Safi and Kerth 2004). As a consequence, in Europe, for example, bats are of high priority for conservation and all bat species have been strictly protected for two decades by European law (CMS 1994). Despite the importance of bats in conservation, rigorous, peer-reviewed studies on the impact of roads on bats have only begun to be published in the last few years. Only over the last decade it has been widely accepted that roads must have an effect on bats. As a result, mitigation against these effects is becoming increasingly integrated in the road building process and practical mitigation guidelines have been published in a number of countries (e.g. Highways Agency 2001, 2006; Limpens et al. 2005). However, the precise nature and scale of the effects of roads on bats were mostly unknown, and as a consequence mitigation has often been poorly monitored and therefore rarely informed by sound evidence (Altringham 2008; O'Connor et al. 2011).

This review describes the ways in which roads do or may affect bats, discusses the available evidence in relation to each, and where appropriate suggests action for the future, in terms of both research and conservation action. Because work on the impacts of roads on bats is still scarce and biased towards the temperate zone, some work on other animals will be discussed, in particular birds, to help fill important gaps. Roads can affect bats in many ways, and because the mitigation solutions will to some extent be unique to each, the mechanisms will be discussed separately. However, there is considerable interaction between them and the impacts in many cases are cumulative, so some topics will appear under more than one heading.

To our knowledge almost no studies have been published yet that investigated the effects of railways on bats (but see Vandevelde et al. 2014). However, as linear development features, they have the potential to disrupt bats and will be discussed briefly at the end of the review.

3.1.1 Bat Life History

In order to assess the impact of roads on bats, an important consideration is of course the biology of the bats themselves. Bats are small mammals with the life history strategy of very much larger species (e.g. Barclay and Harder 2003; Altringham 2011). They have taken the low fecundity, long life option, often producing only a single pup each year, but frequently living for more than 10 years and not unusually 20 or more (e.g. Barclay and Harder 2003; Altringham 2011). Any external factors that reduce reproductive success, increase mortality, or both, can lead to severe population declines—and recovery will be slow (e.g. Sendor and Simon 2003; Papadatou et al. 2011). Furthermore, bats typically have large summer home ranges compared to other similar sized mammals and many bats migrate over considerable distances between winter and summer roosts (Altringham 2011). Finally, bats are highly gregarious (Kerth 2008). As a result, negative impacts of roads on local bat colonies can affect large numbers of individuals simultaneously. Because of their particular life history, bats are susceptible to a wider range of environmental disturbances than many other small mammals.

3.1.2 Bat Conservation Status

A substantial number of the more than 1200 extant bat species are considered to be endangered (Racey and Entwistle 2003; Jones et al. 2009). Reasons for the decline of bats include habitat loss, pollution, direct persecution and diseases (Jones et al.

2009). Several of these threat factors are also relevant during the construction and maintenance of roads. In Europe, all bats are strictly protected, as all are listed in Annex 4 of the Habitats Directive, and several species have designated protected areas because they are also listed in the Annex 2 of the Habitats Directive (Council Directive 92/43/EEC). As a consequence, whenever bat populations are likely to be adversely affected by the construction of roads, environmental assessments are required and mitigation often becomes a necessity. Thus assessments of bats have been carried out during many recent infrastructure projects (e.g. Kerth and Melber 2009) and this process will continue to be important in the future.

3.2 The Effects of Roads on Bats—Habitat Destruction, Fragmentation, Degradation and Collision Mortality

3.2.1 Loss of Habitat

Road development frequently involves the removal of trees and buildings that hold potential or actual bat roosts. The removal of trees, hedges, scrub, water bodies and unimproved (‘natural’) grassland also reduces available foraging habitat. The road surface alone destroys significant areas of habitat: 7 ha for every 10 km of 7 m wide, two-lane road. Roadside hard shoulders, verges, junctions, service areas and other structures remove yet more potential habitat. As a result, road construction leads to the permanent loss of habitats for bats and thus is likely to reduce population sizes directly.

3.2.2 The Barrier Effect

Roads are potential barriers to flight between roosts and foraging sites and between summer, mating and winter roosts. They could therefore reduce the available home range size and quality and may restrict migration, which could increase mortality and reduce reproductive potential. Roads may act as barriers because they interrupt existing linear flight lines, because some species are reluctant to cross open ground, because some species avoid lit areas (road and vehicle lights) and, at least initially, because they represent sudden changes in the bats’ familiar landscape. Roads may therefore fragment habitat, decreasing its accessible area and quality. Since habitat area and quality are major determinants of population size, then habitat fragmentation will lower the sustainable population size.

Barriers such as roads may also limit the flow of individuals between populations with two major consequences. First, barriers may slow the recovery from local population declines since recruitment of individuals from neighbouring populations (“rescue effect”) will be reduced and this will further increase the probability of local extinction. Secondly, barriers may also reduce gene flow between populations and increase inbreeding, reducing individual fitness and increasing the risk of local extinction. Genetic isolation such as this can only occur with very low levels of dispersal. These factors may only be significant for rare bat species that already have small and fragmented populations. Of course it may be that they are rare because of their susceptibility to these and other anthropogenic pressures.

Genetic isolation as a direct result of roads has not been studied in bats. In several other mammal species an effect of roads on genetic population structure has been found (Frantz et al. 2012). For example, Gerlach and Musolf (2000) have shown that populations of bank vole are genetically different either side of a four-lane highway. However, even in bat species such as Bechstein's bat, *Myotis bechsteinii*, for which barrier effects of motorways haven been shown to occur in the summer habitat (Kerth and Melber 2009), local populations living in an area with several motorways show only weak genetic differentiation (Kerth et al. 2002; Kerth and Petit 2005). In accordance with the findings on Bechstein's bats, population genetic studies on other temperate zone bats typically found no or very little evidence for genetic isolation on the regional scale (Moussy et al. 2013), despite the dense road network in Europe and North America. This suggests that in the temperate zone roads probably have no significant effect on gene flow in most bat species. For tropical bats much less data on population genetic structures are available but the situation may be different from the temperate zone. In general, mammal and bird species living in tropical rainforests are often particularly reluctant to cross open areas (Laurance et al. 2009). Moreover, unlike most bats in Europe and North America, tropical bats often mate close to or at the breeding sites of the females. Both features make tropical bats likely to suffer more from fragmentation by roads by means of restricted gene flow than temperate zone bat species. Clearly, further studies are needed to test this.

There is considerable evidence to suggest that roads act as barriers to bats during foraging and movements between different day roosts (roost switching) in the summer habitat. Bats have been shown to make major detours to avoid roads or to find appropriate crossing points (e.g. Kerth and Melber 2009). This behaviour could lead to longer journeys that consume time and energy or even deny bats access to parts of their habitat. In the study by Kerth and Melber (2009) of 32 radiotracked, female Bechstein's bats, only three individuals, belonging to two different maternity colonies, crossed a four-lane motorway cutting through a German forest to forage (Fig. 3.1). All three bats used an underpass to cross the motorway. Other bats from four nearby colonies did not cross the motorway. Moreover, during roost switching none of the colonies crossed the motorway. In addition, foraging areas of females were smaller in those colonies whose home range was bounded by the motorway, relative to those bounded by more natural forest edges. Importantly, females in colonies bounded by the motorway had lower reproductive success than other females, persuasive evidence for the adverse effects on reproductive output. In the same study, six barbastelle bats, *Barbastella barbastellus*, belonging to one maternity colony, were also tracked and five made several flights

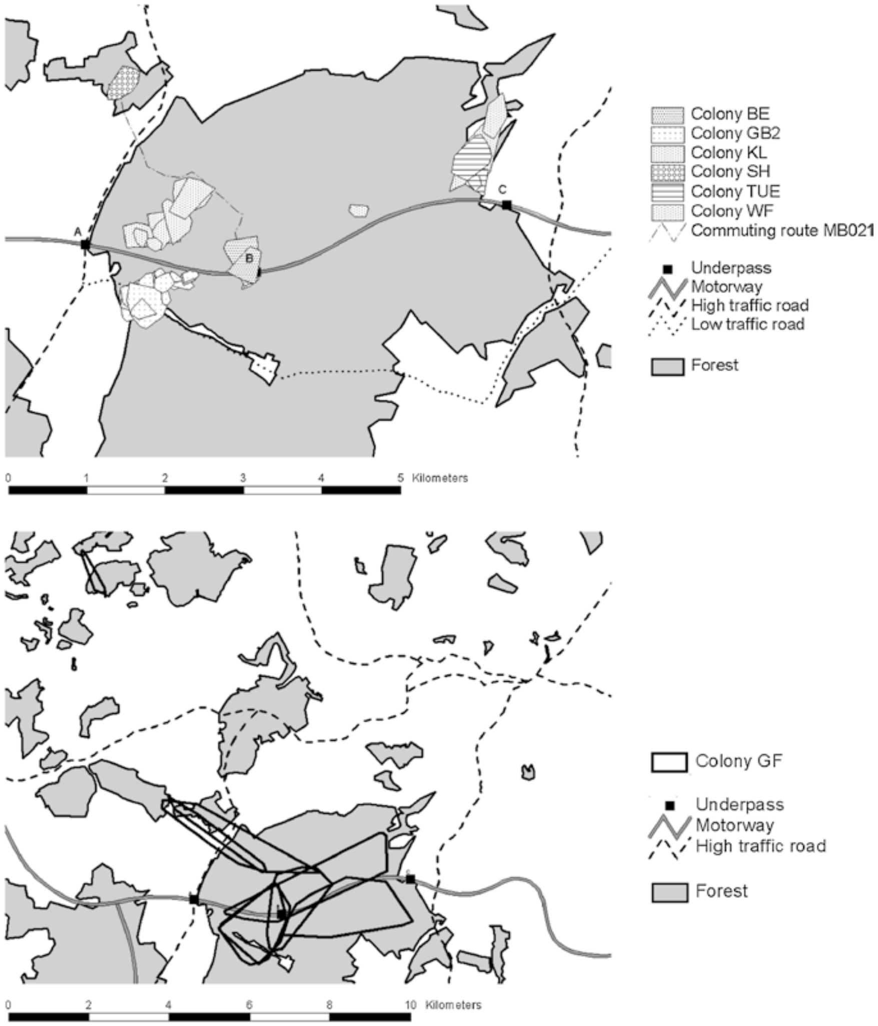

Fig. 3.1 Home range use of two forest bat species living close to a motorway in Germany. The *upper picture* shows the polygons depicting the individual foraging areas of 32 Bechstein's bats belonging to six different colonies living in a German forest that is cut by a motorway. The *lower picture* shows the polygons depicting individual foraging areas of six barbastelle bats belonging to one colony living in the same forest as the Bechstein's bat colonies. From Kerth and Melber (2009)

over the road itself (Fig. 3.1). Moreover, the barbastelle bat colony used roosts on both sides of the motorway. These findings highlight the fact that the effects of roads are species-specific, as will be discussed in more detail later. Berthinussen and Altringham (2012a) observed only three bats flying over a six-lane motorway, all belonging to *Nyctalus* species, at heights above 20 m. *Nyctalus* species are known to fly high and to forage in open spaces (e.g. Jones 1995), behaviour that is likely to make them less susceptible to the barrier effects of roads and to collision mortality. The absence of other species of bat flying over the road in this study suggests that the severance of linear elements by the road may have caused the abandonment of previous flight lines.

Roads may be perceived as barriers by bats for several reasons: open spaces and artificial light expose them to predation, and moving traffic and noise may be seen as threats. Small gaps (<5 m) in cover along flight routes can interrupt commuting bats (e.g. Bennett and Zurcher 2013), but many species will cross open spaces, even those adapted to forage in woodland (e.g. Kerth and Melber 2009; Abbott 2012; Abbott et al. 2012a; Berthinussen and Altringham 2012b), although they will typically do so close to the ground (e.g. Russell et al. 2009; Abbott 2012; Abbott et al. 2012a; Berthinussen and Altringham 2012b). Abbott et al. (2012a) observed low-flying species crossing at sites where mature hedgerows had been severed by the road, even when the gap was >50 m. However, Abbott (2012) found that the rate of bat crossing decreased with increasing distance between mature hedgerows on opposite sides of the road, suggesting a greater barrier effect. Russell et al. (2009) reported that reduced cover at the roadside reduced the number of crossing bats.

That some bats will cross roads is not an indicator that open roads are not a problem—the proportion of bats that do cross may be very small and they are at risk of collision with traffic. The presence of traffic does appear to have a direct effect on the likelihood of crossing, since Indiana bats, *Myotis sodalis*, reverse their flight paths and exhibit anti-predator avoidance behaviour in response to approaching vehicles (Zurcher et al. 2010; Bennett and Zurcher 2013). No specific study has been made of crossing behaviour in relation to traffic volume and road width but anecdotal evidence suggests that it matters. For example, in the study of Kerth and Melber (2009) an individual Bechstein's bat that flew over a two-lane road did only cross a four-lane highway through an underpass. Light and noise are discussed below.

Evidence for a barrier effect is seen in other studies. Berthinussen and Altringham (2012a) found that total bat activity, the activity of the most abundant species (*Pipistrellus pipistrellus*) and the number of species, were all positively correlated with distance from a 40 year-old, six-lane, unlit motorway in rural north-west England (30–40,000 vehicles/day). Total activity increased more than threefold between 0 and 1600 m from the road. These effects were consistent over the two years of study and similar results were obtained on a rural motorway in south-west England (25–90,000 vehicles/day) (Berthinussen 2013). Unpublished work (A. Berthinussen and J.D. Altringham, in preparation) shows that this effect can extend to single carriageway (two-lane) roads. The most likely explanation for this spatially extensive reduction in bat activity is a long-term barrier effect, possibly in combination with increased mortality, driving colonies away from the road, and this is discussed further below.

3.2.3 Roadkill

Bats that attempt to cross roads risk collision, and hotspots for mortality have been found where flyways cross roads and where there is favourable habitat for bats on both sides of a road (e.g. Lesiński 2007; Russell et al. 2009; Medinas et al. 2013). Although agile and manoeuvrable in flight, most bat species fly at low speeds (<20 km/h) and many fly close to the ground (0–4 m: e.g. Russell et al. 2009; Berthinussen and Altringham 2012b), particularly when crossing open spaces. In contrast to the majority of birds, most bats also spend most of the time they are out of the roost in flight. They make extensive use of linear landscape features, such as woodland edges and hedgerows along roads, for foraging and as navigational aids when commuting and several recent studies have shown how important these linear elements are to bats (e.g. Boughey et al. 2012; Frey-Ehrenbold et al. 2013; Bellamy et al. 2013). Flying close to such edges may also reduce predation risk. In combination, these behavioural traits make bats highly vulnerable to moving vehicles when either foraging along roads or when attempting to cross roads on commuting flights. Being small, bats can probably be pulled easily into the slipstream of passing vehicles. Russell et al. (2009) watched over 26,000 bat crossings (primarily little brown bats, *Myotis lucifugus*) on a highway in the USA. Bats approached the road using tree canopy cover and fewer bats were recorded crossing where cover was absent. The lower the cover, the lower the bats crossed the road. Where bats were forced to cross an open field on leaving the roost most did so at a height of less than 2 m. Berthinussen and Altringham (2012b) recorded bats of four or more species crossing roads at mean heights well below 5 m (Fig. 3.2).

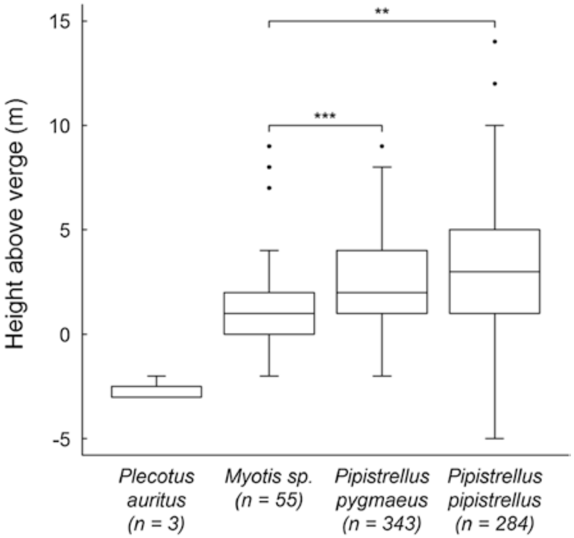

Fig. 3.2 Boxplot of flight height above verge height of identified crossing bats. Median with upper and lower quartiles. Significant differences shown for *Myotis* and *Pipistrellus* species $**P < 0.0005$, $***P < 0.0001$. Verges are elevated on either side of the road and are above road height, therefore negative values indicate bats flying across the road below the height of the verge. From Berthinussen and Altringham (2012b)

Lesinski (2007) recorded bat casualties on an 8 km section of two-lane highway by weekly searches for carcasses over four summers. Casualties ranged from 0.3 bats/km/year in built-up areas to 6.8 bats/km/year where roads were bordered by trees. However, a study by Slater (2002) of the rate of removal of 'carcasses' (small pieces of chicken!) by scavengers on Welsh roads, suggests that a census of this kind may underestimate wildlife road kills as much as 12–16 fold, since dawn scavengers typically removed small carcasses within 30 min. More recently Santos et al. (2011) have also shown that bat carcasses persist on roads in Portugal for a similarly brief period due to scavenging. Teixeria et al. (2013) studied roads in Brazil and found that roadkill estimates increased 2–40 fold when scavenging and low detectability were accounted for. This wide variation was due to taxonomic differences and bats would be at the high end of this range. In addition, small bat carcasses are difficult to spot and many will be thrown clear of the road or carried some distance on the vehicle, suggesting that underestimates will be even greater. Arnett (2006) found that humans (in the absence of scavengers) were able to find only 14 and 42 % of bat carcasses placed at two wind farm sites and Mathews et al. (2013) reported that humans found only 20 % of bat carcasses at wind farms, relative to 73 % found by dogs. Road mortality studies will therefore inevitably under-estimate true mortality rates.

A significant proportion of European bat species, occupying a range of ecological niches, have been documented as roadkill (e.g. Billington 2001–2006; Lesiński 2007; Lesiński et al. 2010). Woodland-adapted species should be most affected due to their characteristic low and slow flight, but this prediction was not supported by Lesiński et al. (2010), as noctules (*Nyctalus noctula*) were killed in significant numbers. Clearly other factors can play an important role locally. Forman et al. (2003, pp 120–122) show that wildlife collisions increase as vehicle speed and traffic volume increase, and with proximity to wildlife habitat and wildlife movement corridors. There are no data on bats relating mortality to speed and traffic volume, but there is no reason to believe they will be different from that of other taxa. There are data from bats to show that roadkill is greater in good habitat and at natural crossing points (Lesiński et al. 2010; Medinas et al. 2013). The effects of traffic speed and volume, road width and height, habitat characteristics, and bat species on rates of roadkill should be explored in greater depth to help us understand how best to mitigate against the effects of roads.

Collection of roadkill carcasses by Russell et al. (2009) led to a conservative estimate of an annual mortality of 5 % of the bats in local roosts. Altringham (2008) arrived at a similar estimate, based on conservative calculations for a road in the UK crossed by lesser horseshoe bats from a large roost (data from Billington 2001–2006). Theoretical studies (e.g. Lande 1987; With and King 1999; Carr and Fahrig 2001) show that populations of animal species with low reproductive rates and high intrinsic mobility, such as bats, are more susceptible to decline and ultimately extinction by the additional mortality caused by roads.

3.2.4 Habitat Degradation—Light, Noise and Chemical Pollution

Light Several studies (e.g. Rydell 1992; Blake et al. 1994; Stone et al. 2009, 2012) have shown that road lighting deters many bat species, notably slow-flying, woodland-adapted species such as members of the genera *Rhinolophus, Myotis* and *Plecotus*, from approaching the road. Lighting will probably exacerbate the barrier effect of roads, since those species reluctant to cross open spaces are also those most likely to avoid light. Both high-pressure sodium and white LED light deter woodland-adapted species, even at low intensity (Stone et al. 2009, 2012). Because light intensity drops rapidly away from the source and will often be blocked by vegetation, the effects of isolated sources are not likely to be far reaching in the landscape, but large arrays of high intensity lights will have a significant effect close to roads.

Light can also attract some bat species, in particular open air foragers such as *Nyctalus* and generalists like *Pipistrellus* (e.g. Rydell 1992; Blake et al. 1994), since short wavelength light attracts insect prey, concentrating them around lights and increasing bat foraging efficiency. This may be not be all good news, since bats exploiting insect swarms around lights may be at greater risk of collision with traffic.

As discussed above, many woodland-adapted bats avoid all forms of visible light, so insects around lights are not available to them. Many insects may indeed be drawn out of woodland towards lights, reducing prey availability to woodland specialists. This could effectively enhance the edge effect around woodland. This has yet to be demonstrated but is worth investigation. The chapter by Rowse et al. discusses the detrimental and beneficial effects of artificial lights on bats in detail.

Noise Most insectivorous bats rely on hearing the returning echoes of their ultrasonic echolocation calls to orientate, detect prey and even communicate. Some species locate and capture prey by listening for sounds generated by their prey, such as wing movements or mating calls. Traffic noise may mask prey-generated sounds and the lower frequency components of echolocation calls. During indoor flight room experiments, simulated traffic noise reduced the feeding efficiency of the greater mouse-eared bat, *Myotis myotis*, which typically hunts by listening for sounds made by its prey on the ground (Siemers and Schaub 2011). It is likely that habitats adjacent to noisy roads would therefore be unattractive as feeding areas for this and other species that glean their prey from the ground or vegetation by listening to rustling noises. Vehicle noise may also exacerbate the barrier effect: bats become less likely to fly across a road as traffic noise increases (Bennett and Zurcher 2013). Currently, there are no published field studies that have assessed the effect of traffic noise on bat diversity, abundance or breeding success. However, as described below, traffic noise, like light, is only likely to have a significant effect over relatively short distances.

Pollution Chemical pollution is another significant factor potentially affecting bats close to roads: transport is the fastest growing source of greenhouse gases. In the USA, over 50 % of domestic CO_2 emissions come from cars, putting 1.7 billion tonnes into the atmosphere every year—a major contributor to climate change. In addition there are the local effects of other chemical pollutants. Automobile exhaust gases close to a road have been shown to be associated with a decline in arthropod diversity and abundance (Przybylski 1979). Motto et al. (1970) and Muskett and Jones (1980) found significant effects on invertebrates of lead and other metals from cars up to 30 m from roads.

3.2.5 Species-Specific Effects

Body size, wing form, echolocation call structure and feeding and roosting ecology all determine how bats fly and use the landscape. Thus, it is not surprising that the effects of roads on bats are to a significant extent species-specific. Larger, fast-flying species, adapted to foraging in the open, appear from most studies to be less affected by roads (e.g. Kerth and Melber 2009; Abbott et al. 2012a; Berthinussen and Altringham 2012a), as they typically fly high above the ground. Their greater flight efficiency and speed relative to woodland-adapted species mean that even if they are forced to make long diversions to find safe crossing points or to avoid roads altogether, the consequences are likely to be less important. Smaller, slower flying, woodland-adapted species are more manoeuvrable and typically capable of gleaning and hovering but this necessarily makes them less efficient flyers (Altringham 2011). Woodland species are also more reluctant to fly in the open and tend to commute along linear features in the landscape such as treelines, waterways, and woodland edges. These features provide protection from weather and predators, are sources of insect prey, and provide conspicuous acoustic and visual landmarks for orientation. Figure 3.3 shows schematically the main patterns of flight and habitat use by insectivorous bats. It is unfortunate that the species most likely to be affected by roads, the slow-flying, woodland-adapted bats, such as *Rhinolophus* and some *Myotis* species, are also those that have suffered most from human activity in Europe and North-America and are at highest risk of extinction there (Safi and Kerth 2004).

3.2.6 Road Class and Speed

The greater width of motorways may make them more effective barriers (Berthinussen and Altringham 2012a) than most other roads. However, traffic density may be equally important (Russell et al. 2009; Zurcher et al. 2010; Bennett and Zurcher 2013) and many major non-motorway roads carry similar or greater traffic volumes, at comparable speed, to rural motorways.

Even minor roads are avoided by many bat species. In a habitat suitability modelling (HSM) study in northern England based on extensive acoustic surveys,

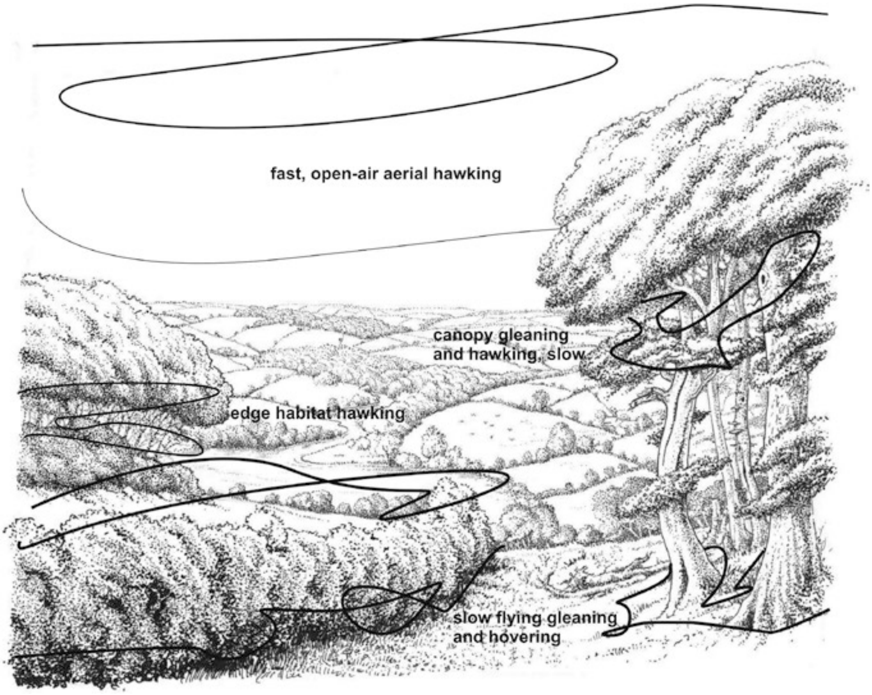

Fig. 3.3 Flight style and habitat use by insectivorous bats. Drawing by Tom McOwat

Bellamy et al. (2013) found that only *Nyctalus* and *Pipistrellus* species showed a positive association with roads and then only when roads were at low densities and in close proximity to woodland. This association is likely due to the use by bats of hedgerows along roads that connect to woodland. Other species, particularly woodland specialists, such as *Myotis* and *Plecotus* species, avoided roads and all species avoided roads when they became dense around settlements. All road classes were combined in this study, but minor roads predominate in the region, so the effects of major roads were probably underestimated. Studies of birds support these conclusions: Develey and Stouffer (2001) and Laurance et al. (2004) have shown that even narrow, unpaved forest roads can act as barriers to tropical forest birds.

In the absence of further work on bats we can look at other animals. Forman et al. (2003) demonstrated that roads act as significant barriers to a variety of mammals from voles to grizzly bears, that primary roads are significantly more effective barriers than secondary roads, and the barrier effect increases with increasing traffic volume. The effects in some cases are severe. Gerlach and Musolf (2000) have shown that populations of bank vole are genetically distinct either side of a busy four-lane highway (50 m wide, 30,000 vehicles/day), but not either side of a two-lane country road (10 m, 5000 vehicles/day) or a railway. Highways can be major genetic barriers even to large and mobile animals such as coyotes and lynx (Riley et al. 2006) or red deer (Frantz et al. 2012).

3.2.7 Cumulative Effects, Extinction Debt and the Importance of Scale

Most of the factors discussed above will be cumulative. The effects of each individually need not therefore be great for the combination to have a profound effect on a bat population. Furthermore, in many cases there will be a lag, known as the extinction debt, between cause and effect (e.g. Tilman et al. 1994; Loehle and Li 1996). This is illustrated in Fig. 3.4.

The effects of habitat loss and reduced habitat quality on the distribution of flying bats may be seen quickly, as bats alter their foraging and commuting behaviour to adapt as best they can to the altered landscape. Collision mortality, unless very high, may not have a significant and detectable effect for several generations. The barrier effect may take several more generations to show itself, since it is likely to involve the decline and/or relocation of nursery and other roosts, but it too may be rapid, for example when bats are completely excluded from key foraging areas. Although no data exist for bats, a study of the effects of roads on wetland biodiversity (birds, mammals, reptiles, amphibian and plants) suggests that the full effects may not be seen for several decades (Findlay and Bourdages 2000). This has important implications for monitoring the effects of roads and assessing the effectiveness of mitigation, as discussed later.

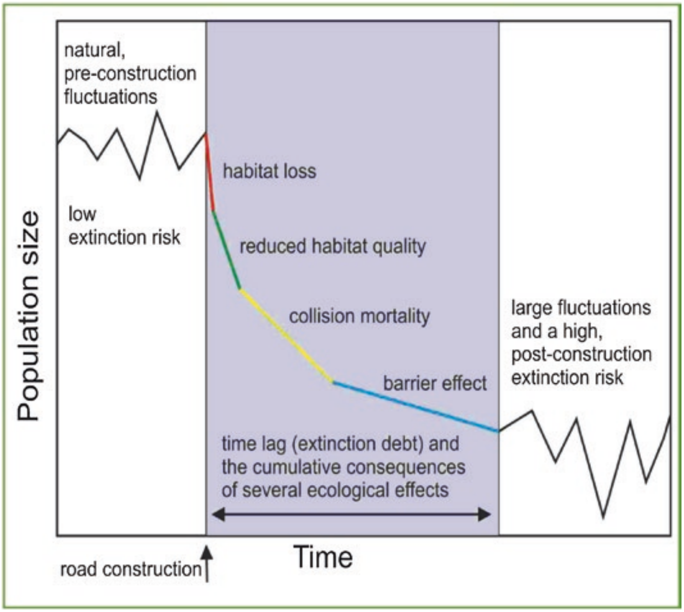

Fig. 3.4 The multiple causes of bat population reduction by roads and the delayed response (extinction debt). Adapted from Forman et al. (2003)

Berthinussen and Altringham (2012a) found that the decline in diversity and abundance of bats extended to at least 1.6 km from a motorway. Which of the above mechanisms contribute to this extensive effect? Low activity and diversity close to the road may be due to most or all of the factors identified: habitat degradation resulting from light, noise and chemical pollution, a barrier effect, or increased mortality due to roadkill. Noise pollution can contribute only to short-range effects, since noise levels in the study fell rapidly over the first 200 m and were close to ambient thereafter. Lab studies on the gleaning greater mouse-eared bat *Myotis myotis* (Schaub et al. 2008; Siemers and Schaub 2011) show that even species that hunt by listening for prey-generated noise are not likely to be affected by roads more than 60 m away. Light pollution was not considered by Berthinussen and Altringham, since the road sections studied were unlit. However, any effect of light pollution from road and vehicle lights is also likely to operate over relatively short distances, due to the inverse square relationship between distance and light intensity. In addition vegetation alongside of roads will further reduce the effect of light and noise pollution quickly. Road developments can disrupt local hydrology and polluted run-off may degrade wetland foraging habitats (Highways Agency 2001), but the scale of such effects will be very variable. As discussed above, chemical pollution is likely to be a factor only over relatively short distances unless dispersion is facilitated by drainage. The many processes that may be degrading roadside habitats need further study, but none of those discussed are likely to explain changes in bat activity over 1.6 km.

Reduced activity over long distances can however be explained by the combination of a barrier effect and increased mortality due to roadkill. The home ranges of temperate insectivorous bat species typically extend 0.5–5 km from their roost (e.g. Bontadina et al. 2002; Senior et al. 2005; Davidson-Watts et al. 2006; Smith and Racey 2008), and most species show high fidelity to roosts, foraging sites and commuting routes (e.g. Racey and Swift 1985; Entwistle et al. 2000; Senior et al. 2005; Kerth and van Schaik 2012; Melber et al. 2013). A major road built close to a nursery roost has the potential to reduce the home range area of a colony through both destruction of habitat and the severance of commuting routes that reduces access to foraging areas. The bats have several options. One is to continue to use the roosts close to the road with a reduced foraging area, reduced resources and reduced reproductive potential (Kerth and Melber 2009). The colony is therefore likely to decline. Alternatively bats may cross the road to maintain their original home range area. Local habitat loss and degradation and increased roadkill will compromise the colony, which may therefore decline. Mortality from roadkill is likely to be high since most species cross at heights that put them in the paths of vehicles (e.g. Verboom and Spoelstra 1999; Gaisler et al. 2009; Russell et al. 2009; Berthinussen and Altringham 2012b). Bats may waste time and energy by commuting greater distances, either away from the road to find new foraging sites, or to find 'safe' crossing points along the road to commute to their original foraging sites. All of these outcomes will reduce the reproductive output of nursery colonies (e.g. Tuttle 1976; Kerth and Melber 2009). Alternatively the colonies may relocate away from the road, into habitat that is presumably already fully exploited by other colonies. All ‘solutions’ will lead to a fall in bat density near to the road. The overall fall in habitat quality will most likely lead to reduced reproductive success and increased adult mortality and in long-lived bats these will have a profound effect on local colony size and overall population size (Sendor and Simon 2003; Papadatou et al. 2011).

Given the magnitude and spatial scale of the effects on bat activity and diversity observed by Berthinussen and Altringham (2012a), it is likely that barrier and edge effects, together with increased roadkill are having a strong negative effect on the demographics and distribution of local bat populations in proximity to major roads. Similar effects have been found in other vertebrates. Reijnen and Foppen (1994) showed that a decreased density of willow warblers up to 200 m from a major highway was due to the negative influence of the road on population sizes, with reduced breeding success and increased emigration of territorial males. Studies on breeding grassland birds revealed a decrease in density of seven out of 12 species, with disturbance distances up to 3500 m from the busiest roads (50,000 vehicles per day), with collision mortality being a major contributor (Reijnen et al. 1996). A meta-analysis of 49 studies that between them investigated 234 bird and mammal species, found that bird population densities declined up to 1 km, and mammal population densities declined up to 5 km from roads (Benítez-López et al. 2010).

3.2.8 Secondary Effects—Infill and Increased Urban and Industrial Development

Bypasses are frequently built in the countryside to divert traffic around rather than through population centres, to reduce congestion and improve the environment for people in the town or village. In addition to the direct effects of the road itself, there are frequently other consequences. The typically narrow strip of land between the settlement and the new road may be too small to support viable bat populations. This land is also frequently taken over by residential and industrial/commercial development and indeed this development is often part of the initial plan. This leads to further loss and degradation of habitat and a direct increase in traffic. Many of the secondary effects of roads are more severe in the tropics (Laurance et al. 2009), where roads allow people easy access to the remaining undisturbed habitats, which as a consequence suffer further degradation and an increase in the hunting pressure for bush meat, including bats.

3.3 Can Roads Benefit Bats?

Although the balance of the impact of roads on bats is clearly strongly negative, there are potential benefits.

Roosts Some of the ancillary structures built with roads, in particular bridges (e.g. Keeley and Tuttle 1999), can provide roosts for bats. Road bridges over water or wooded valleys are the most likely to be used, those over busy roads much less so. Old stone road bridges over water are widely used by bats, most notably by Daubenton's bat in Europe, but also other *Myotis* species and by *Nyctalus* species (e.g. Senior et al. 2005; Celuch and Sevcik 2008; Angell et al. 2013). In North America bridges are widely used by Brazilian free-tailed bats, *Tadarida brasiliensis* (e.g. Allen et al. 2011) and some other species (e.g. Bennett et al. 2008). Effective mitigation and compensation for the loss of roosting and foraging sites will make the environment close to a road more attractive to bats, but may do so at the expense of greater risk of collision with traffic.

Light Artificial light, particularly short-wavelength light such as mercury-vapour (not most LED lights) attract insects that are common prey to bats. Insect swarms around lights are exploited by open-air foraging bats such as *Pipistrellus* and *Nyctalus* (Rydell 1992; Blake et al. 1994; Stone et al. 2009, 2012). One consequence of this is that bats feeding around lights on busy roads may be at significantly greater risk of mortality from collision with traffic. The balance between the positive and negative effects will be dependent on species, topography, the position of lights, etc. and further study would be useful. A very thorough discussion of the positive and negative effects of artificial light can be found in the chapter by Rowse et al.

Flight corridors In rural environments roads are often bounded by hedgerows or treelines. The wide verges often associated with hedges in landscapes managed for wildlife can be among the most species-rich habitats in some agricultural areas. Minor roads in particular can therefore be both foraging sites and commuting routes, but even major roads are used by some species (e.g. *Nyctalus leisleri*, Waters et al. 1999) where they are bounded by suitable habitat such as a woodland edge. Depending upon structure, this habitat could be used by a wide range of species. However, Bellamy et al. (2013) found that even low road densities had a negative effect on most species of bats, most noticeably the woodland-adapted species *Myotis* and *Plecotus*. Only the distributions of common pipistrelles and noctules had a positive association with roads at low to moderate densities and only when in close proximity (<100 m) to woodland. A similar result was found for railway verges (Vandevelde et al. 2014). As road density increased above moderate levels, the probability of presence of all species declined. The effects of roads of different classes have yet to be investigated in depth—the roads in this study were predominantly minor and rural.

3.4 Conservation in Principle: Avoidance, Mitigation, Compensation and Enhancement

In many countries, legislation has been passed stating that infrastructural development should be carried out in such a way as to minimise the impact of development on the environment, and on protected species such as bats in particular. In principle, there should be no net loss to the environment. In the European Union this is formalised in the Habitats Directive (Council Directive 92/43/EEC). In practice, the system is usually flawed, sometimes severely, due to a lack of knowledge, resources and commercial and political will. Poor goal-setting, planning and execution contribute to either failure, or the absence of any evidence for success, for all wildlife (Tischew et al. 2010) and bats in particular (Altringham 2008; Berthinussen and Altringham 2012b; Stone et al. 2013). As in many other areas of conservation a more scientifically robust, evidence-based approach is urgently needed. European policy and practice also involve a hierarchal approach, starting with avoidance of environmental damage, moving to mitigation when damage is deemed to be unavoidable, then compensation when mitigation is not possible or only partial. Finally, there is an increasing expectation that replacing like with like is not enough, particularly given the uncertainty of success in mitigation and the continued loss of biodiversity. When habitat is lost or degraded, some level of habitat enhancement must accompany development so that in principle, the habitat is better than it was before development. The reality is less than perfect.

The first step in a conservation strategy to minimise the impact of a new road should be to select a route that avoids important bat habitat. To be effective this requires an understanding of the behaviour and ecology of the affected species and detailed knowledge of their distribution. Our knowledge in both areas is growing but far from complete. One approach that can deliver detailed, site-specific information relatively quickly is GIS-based HSM, which can be based on existing data sets, such as those held by museums and record centres (e.g. Jaberg and Guisan 2001; Bellamy and Altringham 2015) or data collected specifically for the purpose, for example by acoustic survey (e.g. Bellamy et al. 2013). This approach yields fine scale distribution maps of probability of occurrence for each species with an estimate of reliability, providing a useful practical tool. However, the route that best avoids bats may not meet human social and economic criteria, particularly if conservation is undervalued. The next step is therefore to build the road in such a way as to mitigate against its effects—that is remove or minimise the many detrimental effects described above. In principle, mitigation under European legislation (Habitats Directive, Council Directive 92/43/EEC) reduces ‘damage’ to a minimum that is consistent with maintaining bat populations in favourable conservation status.

Where significant loss cannot be avoided, it is expected that compensation will provide alternative roosting and foraging habitat to at least make good the loss. The expectation now is that there is in fact habitat enhancement, to allow for uncertainties in mitigation and to promote long-term habitat improvement.

In practice, avoidance and mitigation are compromised by competing operational and financial constraints. Furthermore, for practical and economic reasons, habitat restoration and creation are long-term processes and it may be many years before these sites are useful to bats, by which time a disturbed bat colony may have been lost. As we will show in the following section, the absence of adequate and well-planned survey and monitoring means that the consequences of road-building and the effectiveness of current avoidance, mitigation, compensation and enhancement practices are all largely unknown (Altringham 2008; O'Connor et al. 2011). In some cases, they have even been shown to be ineffective (Berthinussen and Altringham 2012b).

3.5 Conservation in Practice

We are not aware of any cases in which proposed roads have been rerouted to avoid key bat habitat. Almost all work in this area concerns attempts to remove or minimise the damaging effects of roads. This has usually involved building structures that aim to guide bats safely under or over roads to reduce both the barrier effect and roadkill. The structures built may be multifunctional, for example underpasses for people and wildlife, and use by bats has often been an incidental and unanticipated use of structures built for other purposes, such a drainage culverts. Additional features include tree and hedge planting to guide bats towards crossing points, modified lighting schemes to achieve the same ends or deter bats from crossing at dangerous locations and a wide range of more general 'enhancements' to improve roosting or foraging opportunities.

3.5.1 Over-the-Road Methods: Gantries, Green Bridges, Hop-Overs and Adapted Road/Foot Bridges

Bat bridges or 'bat gantries' have been built on many UK and continental European roads in recent years. However, the most widely used design (Fig. 3.5) in the UK does not help bats to cross the road safely, even when on the line of pre-construction flyways and after up to nine years in situ as shown in Fig. 3.6 (Berthinussen and Altringham 2012b). Other designs have yet to be tested effectively. Berthinussen and Altringham (2012b) found that only a very small proportion of bats that approached gantries 'used' them (i.e. flew in close proximity to them) and for those that did, their flight paths were not raised above the traffic collision zone (Fig. 3.6). This failure of a widespread design highlights the need for effective monitoring and assessment to be an integral part of mitigation practice.

Overpasses built to carry minor roads or footpaths appear to be largely ineffective (Bach et al. 2004; Abbott et al. 2012a) and certainly less effective than underpasses as crossing points (Bach et al. 2004; Abbott et al. 2012a). Most of the structures evaluated have been no more than footbridges and road bridges, with no adaptations to encourage bats, such as tree or shrub planting or careful design of lighting. To date studies have assessed only use, not effectiveness, in that the criterion for success in most studies has been use by an unspecified proportion of bats. A more useful approach would be to assess what proportion of bats crossing a road do so with the aid of crossing structure (Berthinussen and Altringham 2012b).

Fig. 3.5 The most common bat gantry design in the UK—steel wires with plastic spheres at intervals that are intended to be acoustic guides for bats

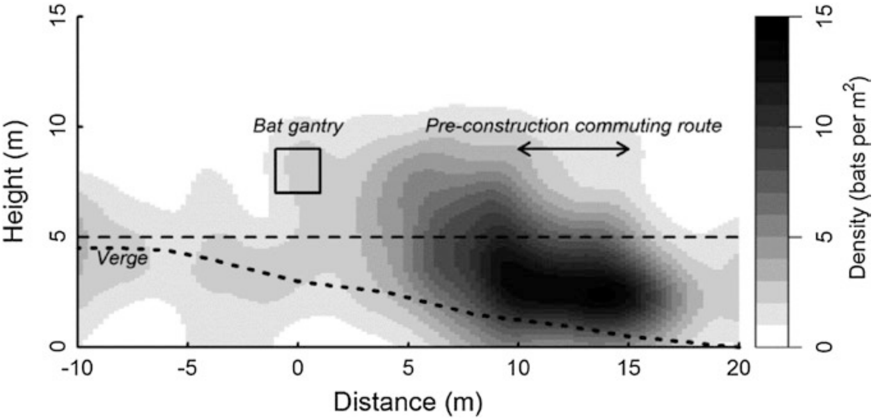

Fig. 3.6 Bat crossing activity at a ‘bat gantry’ that had been in place for nine years. Gaussian kernel and bandwidth of 1 m used ($n = 1078$). The gantry is located at distance 0 m on the x-axis, with distance from the gantry increasing to the *left* and *right*. The height of the gantry is marked by the *square* at 0 m, and the pre-construction commuting route is 10–15 m to the *right*. ‘Unsafe’ crossing heights are located below the *dashed line*, which is the maximum vehicle height in Europe. The *dotted line* marked verge shows the decrease in verge height above the road from *left* to *right*. From Berthinussen and Altringham (2012b)

Land or green bridges have been designed and built specifically for other wildlife, and if planted with tall vegetation and linked to existing bat flyways, they have obvious potential as bat crossing structures. As yet, few have been assessed, but bats have been shown to use one land bridge in Germany. Stephan and Bettendorf (2011) found that only a small proportion of woodland-adapted bats crossed a busy motorway using a new land bridge: most crossed the road itself at other locations. It will be interesting to see if bats adapt to it over time. Specific features of the design and connectivity to surrounding habitat of green bridges are probably critical factors for bat use—as they will be for other structures. Further research is required before conclusions can be drawn, but several features are likely to be positively related to use: their strategic location on known flightlines, connectivity to treelines, mature vegetation on the bridge, and bridge width.

'Hop-overs' (Limpens et al. 2005) have been put forward as a relatively low cost and unobtrusive way to encourage bats to cross roads at safe heights. These consist of close planting of trees up to the road edge on both sides of the road, with tall vegetation in the central reservation of wide roads. Branches should overhang the carriageway, ideally giving continuous canopy cover over the road. Safety concerns arising from overhanging branches may have led to reluctance to adopt hop-overs and even to remove trees from road margins. However, many roads have overhanging trees along their margins, so this is an illogical or at least inconsistent objection. The effectiveness of hop-overs has yet to be assessed. Russell et al. (2009) observed that bat flights across a 20 m road gap were at greater heights where bats approached the road along flight routes with taller roadside vegetation and Berthinussen and Altringham (2012b) found a positive correlation between road-crossing height and the height of the roadside embankment.

3.5.2 Under-the-Road Methods: Underpasses, Culverts and Other 'Tunnels'

Many studies show that a wide range of bat species use underpasses to fly beneath roads (e.g. Bach et al. 2004; Kerth and Melber 2009; Boonman 2011; Abbott et al. 2012a; Berthinussen and Altringham 2012b). However, most of these studies report only that a small number of bats of particular species were seen to fly through an underpass. In some cases not reported here underpasses were monitored using automated bat detectors with no guarantee that detected bats actually flew through the underpass. For an underpass (or indeed any other mitigation structure) to be effective it must help to maintain bats in favourable conservation status. That is, it must protect the population, not a few individuals, by making a road permeable and safe to cross. Assessing abundance, let alone changes in abundance, is very difficult without considerable survey effort. It is also difficult to measure changes in the permeability of a road to bats without monitoring a very large proportion of the bats in the vicinity of a newly built or upgraded road. Ideally, we would need data before the construction of the road and compare them with data after the road had been built. However, it is possible to determine whether the majority of bats at a location use an underpass (or bridge, gantry, etc.) to cross a road safely. Despite the existence of three underpasses within a 5 km stretch of motorway bisecting a forest, resident Bechstein's bats rarely used them and lost access to important roosting and feeding habitat (Kerth and Melber 2009). Lesser horseshoe bats made frequent use of three underpasses along a 1 km stretch of motorway, but 30 % still crossed directly over the road at traffic height

(Abbott et al. 2012b). Some bats have been recorded making extensive detours to avoid crossing roads (e.g. Kerth and Melber 2009 and references cited in Bach et al. 2004), but we do not know how prevalent this behaviour is: many bat species appear reluctant to deviate from their original flight paths after road severance (Kerth and Melber 2009; Abbott 2012; Berthinussen and Altringham 2012b). Where a road cuts through a dense network of flight routes it may not be straightforward providing a population with an adequate number of safe crossing points. Efforts to re-route bat flight paths, for example by planting new hedgerows linking old routes with new underpasses, should be undertaken well in advance of road clearance, and ideally tested for effectiveness before road opening. Bats were not diverted effectively to underpasses studied by Berthinussen and Altringham (2012b): the great majority of bats flew over the road, near to the original commuting routes. In the same study, one underpass on a known flightline was used by 96 % of the bats on the commuting route.

Underpasses are more likely to be used if they are well connected to the landscape by treelines, hedges or watercourses (Boonman 2011; Abbott 2012), but there is scope for further study in this area. Where possible, they should be located on pre-construction flight routes and tall enough to allow bats to pass without changing flight height or direction (Berthinussen and Altringham 2012b). Even with these precautions, a high proportion of bats may ignore the underpass and fly over the road above it, particularly if the underpass is too small. Underpass height, more than width, was the critical dimension determining the number of bats flying through underpasses in studies in Ireland (Abbott 2012; Abbott et al. 2012a, b). Required heights of underpasses will generally be lower for woodland-adapted species (~3 m) compared to generalist edge-adapted species (~6 m), and open-air species are more likely to fly high above roads. For small gleaning bat species, such as some *Myotis* species, which generally have small home ranges, it may be beneficial to build a higher number of small underpasses (Fig. 3.7) along a road instead of a few large underpasses, which then would by located outside of the home range of most individuals. Mitigation practice would benefit greatly from objective testing and reporting to determine if underpasses are actually providing safe passage for a high enough proportion of bats to protect a local population.

Bats can potentially make use of underpasses that are used by people during the day but have little use at night, such as pedestrian underpasses, minor roads, railways and forestry or agricultural tracks. Use could be maximised by restricting lighting in and around these underpasses, placing them on tree and hedge lines, and making smaller wildlife underpasses or drainage culverts larger to accommodate woodland-adapted bat species. Provision of well-placed, numerous and spacious underpasses should be integral to the overall design of road mitigation, particularly near major roosts. Roads built on embankments are likely to be particularly dangerous to bats, particularly when they sever treelines, since bats appear to maintain flight height on leaving the treeline, bringing them into collision risk over raised road sections. These sites are ideal candidates for underpasses, since they can be built relatively cheaply.

Fig. 3.7 A bat of the genus *Myotis* using a small underpass (about 2 m in diameter) to cross a motorway in Germany. Above the underpass, a wall was built to prevent bats from flying directly into the traffic. Similar walling/fencing has been used in the UK but has not yet been shown to be effective (e.g. Billington 2001–2006)

3.5.3 Light Avoidance

To reduce the potential for disturbance of roosts, flight routes and feeding sites lighting is often directed down toward the road surface, and light spill into the surroundings is minimised. However, since the most vulnerable bats, such as *Rhinolophus* species, fly close to the ground, downward pointing lighting may still have a significant impact on their behaviour. Restricting lighting in crossing structures such as pedestrian underpasses could increase their use by bats. In addition to choosing the intensity, wavelength and direction of lighting, it could also be controlled be timers and motion sensors. Lighting at river and stream crossings should always be avoided, as these are particularly important foraging areas and commuting routes for bats.

Conversely, light may be used to purposely deflect bats away from a dangerous flight route toward a safe crossing point. This has been done, but has not yet been tested for effectiveness and may exacerbate any barrier effect. This assessment is important not only to protect bats, but other wildlife too, since many species avoid light.

3.5.4 The Importance of Connectivity and the Maintenance of Existing Flightlines

An important consideration that is frequently referred to is the need to maintain existing flightlines. There is evidence to support this and it is clearly a sensible precaution. As discussed above, Berthinussen and Altringham (2012b) found that an underpass on a pre-existing flightline was used by 96 % of the bats crossing the road, but attempts to deflect bats to two other underpasses displaced from known routes were not successful.

An extension of this is the general recommendation to maintain and enhance a ‘connected’ landscape, i.e. a landscape with a broad range and high density of interconnecting linear features such as hedgerows and treelines. This would not only increase the value of the landscape for foraging and commuting, but may give bats more flexibility in how they adapt to a changing landscape and in particular the appearance of barriers in the form of roads. This makes intuitive sense, given the known behaviour of many bat species, and there is a growing body of evidence based on spatial analysis to support it (e.g. Boughey et al. 2012; Bellamy et al. 2013; Frey-Ehrenbold et al. 2013; Bellamy and Altringham 2015). These studies highlight, using different approaches, the importance of these features to bats, and also reveal species differences: woodland-adapted species (e.g. *Myotis*, *Plecotus, Rhinolophus*) and small generalists (e.g. *Pipistrellus*) make more use of (and are more dependent upon) these features than larger open-air species (e.g. *Nyctalus*, *Eptesicus*).

3.5.5 Habitat Improvement and Effective Landscape-Scale Planning

Some general forms of mitigation not specifically related to roads are also relevant, such as the planting of trees and the creation of ponds to replace lost habitat or enhance existing habitat as compensation for damage done by roads. Berthinussen and Altringham (2012a) have shown that the effects of major roads are less easily detected in high quality habitat. This is not a reason to build roads in high quality habitat, since a greater number of bats will still be affected than alongside a road through poor habitat, and the species affected may be more vulnerable. However, it is a reason to attempt to mitigate and compensate using habitat improvement, when a road is built in good habitat. Improvements must not increase roadkill or the costs may outweigh the benefits, so habitat design will be an interesting challenge.

Habitat improvement methods have not been tested effectively, so the scale of the benefits is generally unknown. Habitat improvement and creation obviously have the potential to be beneficial if done on an appropriate scale, but are unlikely to be effective in the short or even medium term, since new woodland and wetland take many years to become established. Over the time taken for habitat to mature, bat colonies may be lost, so long-term planning is needed. Considerable financial incentives may be needed to persuade landowners to undertake habitat improvement. Woodland and wetland creation are more likely to be used for compensation and enhancement than direct mitigation.

As discussed earlier, the Habitats Directive stipulates that in preparing development plans, the avoidance of damage is the preferred option. Mitigation and compensation should only be considered when alternative sites, routes or methods are unavailable and the avoidance of damage is not possible. There must also be over-riding social, economic or safety reasons for development. The planning of new road and rail routes now makes extensive use of GIS-based techniques to assist in the evaluation of the many factors involved. However, the environmental components of these analyses often rely on limited and biased data and do not take full advantage of the developing GIS and modelling techniques described earlier. GIS-based HSM is becoming widely used in ecology. HSM uses the detailed relationships between bat presence and habitat variables to build detailed and accurate distribution maps from relatively small datasets. Bellamy et al. (2013) and Bellamy and Altringham (2015) have used HSM to produce high resolution, accurate predictive maps of the distribution of eight bat species in the Lake District National Park. Similar maps have been, and are being, prepared for other protected areas. These techniques determine the associations between bats and their habitat over multiple spatial scales to give greater accuracy and ecological insight. As our knowledge of bat distributions improves, we will be in a better position to identify those routes that will have minimum impact on bats, and better able to devise appropriate mitigation strategies.

3.5.6 Rail

The effects of rail systems on both bats and other wildlife are even less well understood than those of roads. However, intuitively they have characteristics that may reduce their impact on wildlife. Rail systems are often (but not always) narrower than roads, giving them a smaller footprint and potentially creating a less-effective barrier to animal movement. Trains pass a given point on a network much less frequently than vehicles on roads, which are often continuous. On the busy East Coast line in northern England train noise was detectable for only 8 min/h and this noise decreased to background levels over very much shorter distances than road noise (Altringham 2012). It is nevertheless important that the effects of railways are assessed objectively, particularly in view of the proposed new HS2 line in England, on which trains will travel faster and more frequently. In a study on bat activity of railway verges, Vandevelde et al. (2014) found that bat of the genus *Myotis* seem to avoid the vicinity of railways whereas species foraging in more open space such as pipistrelle and noctule bats use railway verges as foraging habitat.

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Chapter 4
Responses of Tropical Bats to Habitat Fragmentation, Logging, and Deforestation

Christoph F.J. Meyer, Matthew J. Struebig and Michael R. Willig

Abstract Land-use change is a key driver of the global biodiversity crisis and a particularly serious threat to tropical biodiversity. Throughout the tropics, the staggering pace of deforestation, logging, and conversion of forested habitat to other land uses has created highly fragmented landscapes that are increasingly dominated by human-modified habitats and degraded forests. In this chapter, we review the responses of tropical bats to a range of land-use change scenarios, focusing on the effects of habitat fragmentation, logging, and conversion of tropical forest to various forms of agricultural production. Recent landscape-scale studies have considerably advanced our understanding of how tropical bats respond to habitat fragmentation and disturbance at the population, ensemble, and assemblage level. This research emphasizes that responses of bats are often species and ensemble specific, sensitive to spatial scale, and strongly molded by the characteristics of the prevailing landscape matrix. Nonetheless, substantial knowledge gaps exist concerning other types of response by bats. Few studies have assessed responses at the genetic, behavioral, or physiological level, with regard to disease prevalence, or

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the extent to which human disturbance erodes the capacity of tropical bats to provide key ecosystem services. A strong geographic bias, with Asia and, most notably, Africa, being strongly understudied, precludes a comprehensive understanding of the effects of fragmentation and disturbance on tropical bats. We strongly encourage increased research in the Paleotropics and emphasize the need for long-term studies, approaches designed to integrate multiple scales, and answering questions that are key to conserving tropical bats in an era of environmental change and dominance of modified habitats (i.e., the Anthropocene).

4.1 Habitat Conversion: A Key Aspect of Global Change

Bats are valuable indicators of biodiversity and ecosystem health, and respond to a range of stressors related to environmental change (Jones et al. 2009). Alteration in land use is one of the principal aspects of global environmental change and a key driver of biodiversity loss in terrestrial ecosystems. Indeed, biodiversity impacts of land-use change are generally considered to be more immediate than those from climate change (Sala et al. 2000; Jetz et al. 2007; Pereira et al. 2010). However, the effects of land-use change on tropical species could exacerbate those of changing climate, leading to challenges for long-term conservation efforts (Struebig et al. 2015), including those for bats. Over the last decades, human transformation of much of the Earth's natural ecosystems has greatly accelerated, and the twenty-first century will herald profound changes in land use, particularly in developing tropical countries (Lee and Jetz 2008). The most recent quantification of global forest change revealed an overall increasing trend in annual forest loss across the tropics between 2000 and 2012 (Hansen et al. 2013), highlighting the continued prevalence of tropical deforestation.

Drivers of tropical deforestation have shifted from being promoted mostly by government policies for rural development toward urban population growth and industrial-scale, export-oriented agricultural production (DeFries et al. 2010). Fueled by unabated human population growth, global food demand is escalating, and the current trajectory of agricultural expansion will have serious negative long-term consequences for the preservation of the planet's biodiversity (Tilman et al. 2011; Laurance et al. 2014). In tropical countries, conversion of natural habitats to agricultural and pastoral land is one of the greatest threats to biodiversity (Phalan et al. 2013), as cropland expansion in recent decades has largely come at the expense of intact old-growth forest (Gibbs et al. 2010). Rampant commercial logging is also a major force of tropical forest destruction and degradation, with around 20 % of such forests subjected to some level of timber harvesting (Asner et al. 2009).

Loss of habitat as a result of extensive land conversion and associated fragmentation are ubiquitous throughout the tropics. Resulting landscapes typically comprise a mosaic of human-modified habitats that include agroforests, agricultural land, and tree plantations, as well as remnants of old-growth, logged forest, and secondary forests regenerating from clearance or burning (Gardner et al. 2009; Chazdon 2014).

Indeed, except for large areas of tropical forest in Papua New Guinea and in the Amazon and Congo basins, such a description accurately characterizes most tropical landscapes (Melo et al. 2013). Anthropogenic activities in many tropical countries have resulted in the creation of fragmented landscapes that are dominated by small (often < 50 ha), isolated, and irregularly shaped forest patches. These patches are highly prone to edge effects (Broadbent et al. 2008; Ribeiro et al. 2009), defined as systematic changes in abiotic and biotic variables at the boundary between adjacent land-use types. Although deforestation and degradation of old-growth forests are the dominant forms of land-use alteration, forest regeneration and the expansion of secondary forests are the second most important type of land-use change occurring across the tropics (Asner et al. 2009; Dent and Wright 2009). These recovering forest habitats could potentially mitigate, or even reverse, current trends of forest loss and degradation as well as concomitant biodiversity loss (Wright and Muller-Landau 2006; Dent and Wright 2009; Chazdon 2014). A pan-tropical meta-analysis of land-use change studies points to the irreplaceable value of old-growth forests, but also highlights the high species diversity found in regenerating logged forests compared to secondary forests (Gibson et al. 2011). Although the long-term conservation value of regenerating forests has been questioned (Melo et al. 2013), biodiversity representation clearly varies among logged and secondary habitats, and so not all recovering forests should be treated equally.

4.2 Tropical Bats in a Changing World

Bats exhibit the general mammalian pattern of greatest diversity in the tropics, from both a taxonomic and a functional perspective (Willig et al. 2003). Bats also provide ecosystem services that are critically important in tropical ecosystems—as pollinators and seed dispersers for hundreds of plant species and as agents of suppression of arthropod herbivores and insect pest species (Muscarella and Fleming 2007; Kalka et al. 2008; Williams-Guillén et al. 2008; Kunz et al. 2011; Maas et al. 2013). Nonetheless, many tropical bat species face an uncertain future and show declining population trends due to many of the threats outlined previously (e.g., Kingston 2013).

How do tropical bats fare in the Anthropocene, in which they are exposed to increasing levels of land-use change, potentially exacerbated by climate change (Struebig et al. 2015), and the synergistic effects of both processes? Simple pan-tropical meta-analyses suggest that the impacts of land-use change on mammal diversity, particularly on bats, are somewhat less severe than for other animal groups (Gibson et al. 2011). Nevertheless, such studies can potentially miss subtle, yet important, responses in assemblage structure. In this chapter, we summarize the accumulated knowledge on the responses of tropical bats to human-induced habitat fragmentation and forest disturbance. By providing a synthetic overview of the topic, we hope to shed light on the conservation value of anthropogenically modified habitats for bats across the major tropical regions and identify future research priorities.

4.3 Review Methodology

We followed a systematic review methodology (Pullin and Stewart 2006) to synthesize information about tropical bat responses to habitat fragmentation, logging, and deforestation. Studies were identified through a comprehensive search in the ISI Web of Science online database (accessed in September 2013), performing a topic search using the string "bat? AND *tropic* AND (fragment* OR logg* OR deforest* OR disturb*)," without restriction on publication year. The use of this combination of key words allowed for the identification of an inclusive set of studies on the effects of fragmentation, logging, and disturbance on tropical bats. The search identified 248 publications that were subsequently screened for suitability for the review based on the article's title, abstract, and, when necessary, text. We excluded review articles and studies that were conducted in urban landscapes (see Chap. 2). As our purpose here was to review evidence for the effects of *anthropogenic* habitat modification on tropical bats, we also excluded studies that were conducted in naturally fragmented landscapes (e.g., forest islands embedded in savannah, oceanic islands). Our review thus focuses on a range of human-modified matrix types of varying structural complexity and contrast—from relatively low-contrast secondary forests, agroforests, and plantation forests, to high-contrast agricultural fields and water matrices resulting from dam construction.

From the 248 studies, 93 met our criteria. In addition, we extended our search using the same key word combinations in Google Scholar through which we identified an additional eight relevant studies within the first 100 records. Sixteen additional publications were found based on a search of our own literature databases, thus bringing the total number of studies considered in our synthesis to 117. Each article was characterized according to geographic region, taxonomic focus, response type, and disturbance type. Response types included (a) population- and assemblage-level responses, (b) genetic effects, (c) behavioral responses, (d) physiological responses, parasite and disease prevalence, and (e) effects on the provisioning of ecosystem services. Disturbance type included the following broad categories: (a) habitat fragmentation, (b) logging, (c) secondary forests and succession, (d) agroforestry systems, (e) tree plantations, and (f) agriculture.

4.4 Biases in Our Understanding of Responses of Tropical Bats to Habitat Alteration

The collated literature revealed substantial geographic and taxonomic biases in the current understanding of tropical bat responses to anthropogenic disturbance. Studies covered 34 distinct study landscapes in 21 countries. Despite a general increase in the number of studies over the last 20 years (Fig. 4.1), most research has been undertaken in the New World tropics (96 studies), with research in Southeast Asia and Australasia lagging far behind (19 studies) and studies in

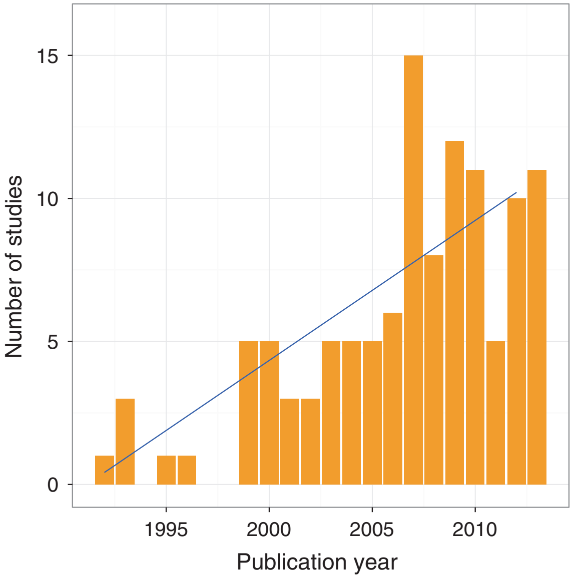


Fig. 4.1 Number of publications on the effects of fragmentation, logging, or disturbance on tropical bats based on a systematic search of the literature. There is a general increase in publications over the last 20 years (linear model fit, $R^2_{\text{adj}} = 0.55$, $p < 0.001$). Data for 2013 represent an underestimate as the literature search did not include the entire year, and therefore, they were not considered in the model fit

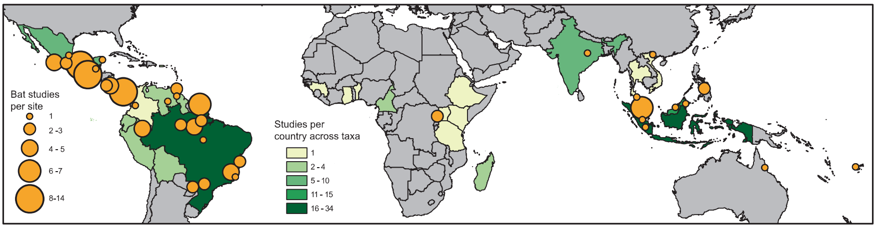


Fig. 4.2 Map illustrating the geographic distribution of research effort based on 117 studies of bats in anthropogenically modified landscapes. Sizes of *orange circles* represent the number of studies per site, where a site is defined as a particular study landscape. Colors of tropical countries represent the number of studies based on the pan-tropical analysis of the impact of disturbance and land conversion on birds, mammals, arthropods, and plants by Gibson et al. (2011)

Africa being rare (2 studies; Fig. 4.2). Geographic variation in this research effort (Fig. 4.2) broadly parallels the pattern reported for multiple taxa across the tropics (Gibson et al. 2011). A few notable differences include a disproportionately high number of bat studies in Mexico and low number of studies in Indonesia compared to other taxa. A large taxonomic bias therefore characterizes our understanding of disturbance effects on tropical bats as a consequence of the prevalence of studies in the Neotropics. With a few exceptions (Estrada et al. 2004; Estrada Villegas

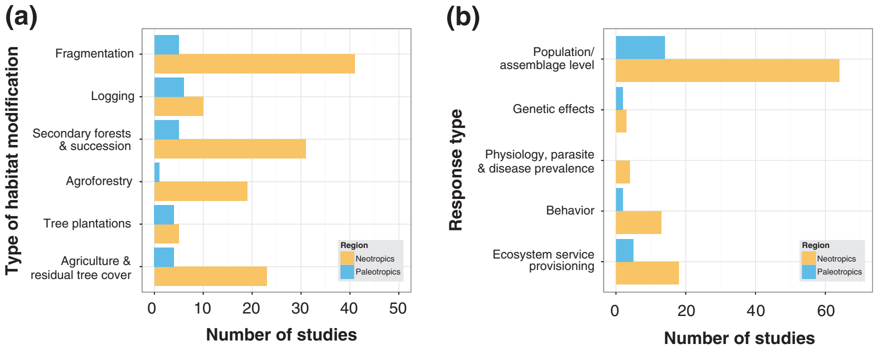


Fig. 4.3 Number of studies by region (Neotropics [$n = 96$ studies] vs. Paleotropics [$n = 21$ studies]) based on **a** type of disturbance or habitat modification and **b** type of response. Studies in many cases, especially for (**a**), matched more than one of the broad categories and were counted multiple times

et al. 2010; Williams-Guillén and Perfecto 2011), New World studies focused on the species-rich Phyllostomidae, in turn largely reflecting the use of mist nets to capture bats. Phyllostomids are easily sampled with mist nets and dominate studies. In contrast, non-phyllostomids are underrepresented in samples based on mist netting. Although acoustic methods hold much promise for sampling non-phyllostomid and non-pteropodid bats, considerable difficulties remain in the wider implementation of these techniques in tropical countries, including the lack of call libraries, taxonomic uncertainty, and practical challenges of tropical climates (Harrison et al. 2012). As a result, acoustic sampling has not yet been employed intensively in landscape-scale studies of tropical bats (see also Cunto and Bernard 2012). Finally, a considerable bias exists with respect to studied aspects of fragmentation and disturbance. Comparatively few studies have targeted bat responses to logging or agroforestry (Fig. 4.3a). The vast majority of studies evaluated responses at the population or assemblage level. Far fewer have examined the consequences of anthropogenic disturbance for the provision of ecosystem services by bats. Genetic, physiological, and behavioral effects remain poorly explored, as do effects on disease dynamics associated with bat hosts (Fig. 4.3b).

4.5 Responses at the Population and Assemblage Level

4.5.1 Habitat Fragmentation

Habitat fragmentation has become a major research theme in conservation biology, as reflected in the burgeoning literature on the subject (Fahrig 2003; Ewers and Didham 2006a; Lindenmayer and Fischer 2006; Fischer and Lindenmayer 2007; Collinge 2009). Although the exact definition of “habitat fragmentation” is contentious (Fahrig 2003; Ewers and Didham 2007; Fischer and Lindenmayer 2007), we follow a widely used definition—the landscape-scale process by which habitat loss results in the subdivision of continuous habitat into smaller patches that are isolated from each other by a matrix of modified habitat (Didham 2010).

4.5.1.1 General Patterns

Despite numerous and increasing attempts to detect consistent responses of tropical bats to habitat fragmentation, studies to date suggest relatively few generalizations. At the population level, many studies have documented that abundance responses to fragmentation are highly species and ensemble specific. For instance, in the Neotropics, abundances of gleaning animalivorous bats (Pons and Cosson 2002; Meyer et al. 2008; Meyer and Kalko 2008a) and certain forest-dependent aerial insectivores (Estrada Villegas et al. 2010) decline in response to fragmentation, whereas frugivorous and nectarivorous bats often increase (Sampaio et al. 2003; Delaval and Charles-Dominique 2006; Meyer and Kalko 2008a). In the Paleotropics, insectivorous bat species that roost in tree cavities or foliage are more vulnerable to fragmentation than are cave-roosting species (Struebig et al. 2008, 2009). At the assemblage level, studies that have compared fragmented and continuous forest in terms of species richness, diversity, and composition demonstrate inconsistent responses (Cosson et al. 1999; Schulze et al. 2000; Estrada and Coates-Estrada 2002; Faria 2006). Differences among sites with regard to fragmentation history and structural contrast between fragments and the surrounding matrix complicate the detection of general patterns. This may be a more important issue for the study of tropical bats compared to other taxonomic groups because of the wide range of dispersal abilities exhibited by chiropteran species.

4.5.1.2 Area and Isolation Effects

Early fragmentation studies generally emphasized the effects of area and isolation, reflecting the pervasive influence of island biogeographic theory (IBT, MacArthur and Wilson 1967) in ecology, while ignoring influences of the surrounding landscape matrix. This same pattern is also apparent within the fragmentation literature on tropical bats. Studies have found evidence for effects of both fragment area (Cosson et al. 1999; Struebig et al. 2008, 2011) and isolation (Estrada et al. 1993a; Meyer and Kalko 2008a, b) on population- and assemblage-level responses, whereas effects were weak or absent in others (Faria 2006; Pardini et al. 2009). Moreover, bat ensembles and species often respond differentially to fragment area or isolation, with responses of some taxa being particularly strong (Struebig et al. 2008; Estrada Villegas et al. 2010).

The relative importance of isolation versus area in shaping bat responses to fragmentation is governed by three main factors: the range of fragment sizes relative to isolation in the landscape, the history of landscape change (time since isolation, rate of change), and, probably most importantly, the type and quality of matrix habitats in which fragments are embedded. For instance, the high explanatory power of area relative to isolation reported by Struebig et al. (2008) likely reflects the low structural contrast between fragments and matrix (mostly rubber and oil palm plantations), limited range of isolation distances compared to area in the study system, and a possible time lag in the realization of isolation effects due to landscape change being fairly recent. In contrast, isolation rather than island area best predicted bat species richness and composition on Neotropical land-bridge islands (Meyer and Kalko 2008a) where fragments were surrounded by water.

The simplified dichotomous view of landscapes underlying IBT, albeit applicable in special cases (e.g., land-bridge islands), often fails to capture the influence that other land-cover types in the surrounding matrix can have and so may not be broadly applicable to most anthropogenically modified landscapes (Kupfer et al. 2006; Laurance 2008). After more than 40 years of research beyond the origins of IBT, it is now clear that for most animal taxa, including tropical bats, the majority of terrestrial habitat fragments are not islands in a homogeneous sea of inhospitable habitat. Indeed, island ecosystems support tropical bat biodiversity in fundamentally different ways compared to complex agricultural mosaic landscapes, the former adhering to IBT predictions of species loss, while countryside ecosystems are capable of maintaining high levels of species richness, evenness, and compositionally novel assemblages in human-made habitats (Mendenhall et al. 2014).

4.5.1.3 Responses to Landscape Structure

Fragmentation studies have increasingly shifted their focus from being largely patch-centered toward taking a broader landscape-scale approach, thus acknowledging the overriding importance of the matrix and the existence of gradients of habitat conditions and quality as crucial determinants of species responses (Kupfer et al. 2006; Driscoll et al. 2013; Cisneros et al. 2015). Such gradients are provided, for example, by mosaics of old-growth forest, successional habitat, and different forms of agriculture.

This paradigm shift is to some degree reflected within the more recent bat literature, as a growing number of studies have adopted matrix-inclusive approaches to studying fragmentation, although overall the number of studies is still small. In the broader literature, empirical evidence suggests widespread negative effects of habitat loss on many taxa (i.e., reduced abundance or density), whereas the effects of fragmentation per se are generally much weaker and may vary strongly in magnitude and direction of response (Fahrig 2003). In agreement with this, forest cover is a better predictor of bat assemblage characteristics (species richness or composition) than are measures of landscape configuration in Neotropical land-bridge island systems (Meyer and Kalko 2008a; Henry et al. 2010). On the other hand, consistent responses to landscape composition or configuration at the assemblage level were harder to identify in studies conducted in fragmented Neotropical rain forest landscapes in which the matrix was a mix of anthropogenic land uses (Gorresen and Willig 2004; Klingbeil and Willig 2009, 2010; Cisneros et al. 2015). A difficulty facing bat fragmentation studies is that responses tend to be highly species specific, which is often overlooked by diversity metrics applied at the assemblage level (Klingbeil and Willig 2009). This might be more important in low-contrast systems, in which the quality of matrix habitats likely mitigates some of the negative effects of fragmentation on biological communities.

At the population level, available evidence suggests that tropical bats respond in complex ways to landscape composition (i.e., the amount of suitable habitat available across the patch types represented in the landscape) and configuration (Gorresen and Willig 2004; Henry et al. 2007b; Klingbeil and Willig 2009, 2010). For instance, Klingbeil and Willig (2009, 2010) found that, apart from being scale dependent (see Sect. 4.5.1.4), abundance responses by phyllostomid bats to landscape structure in the Amazon were highly species and ensemble specific, and differed between seasons. In the dry season, abundances of frugivores responded primarily to changes in forest cover (i.e., landscape composition), whereas configurational metrics elicited the strongest response in the wet season. Gleaning animalivores showed the opposite pattern, responding to landscape configuration in the dry season and to landscape composition in the wet season. Such divergent responses suggest an important role of spatiotemporal variation in the abundance and diversity of food resources (Klingbeil and Willig 2010; Cisneros et al. 2015). Together with seasonal differences in time and energy budgets linked to reproduction, these will affect species' foraging and movement behavior, and could lead to seasonal shifts in diet composition (Durant et al. 2013; Cisneros et al. 2015). Such links remain little explored, yet future research in this regard may prove highly informative.

4.5.1.4 Spatial and Temporal Scale Dependence in Responses to Fragmentation

The scale at which bat species perceive their environment in fragmented landscapes is likely influenced by spatiotemporal variation in the distribution of resources, as well as by species-specific differences in ecological traits such as diet, wing morphology, and movement behavior. For example, in a low-contrast fragmented system in Malaysia, the provision of large cave systems in the landscape provided clear population subsidies for cave-roosting bats, but also potentially masked the impact of forest fragmentation on this ensemble (Struebig et al. 2009). Consequently, single-scale assessments may be inadequate for capturing the complex interactions between species' ecology and landscape patterns (Gorresen and Willig 2004). While there is accumulating evidence of the diverse ways by which tropical bats respond to landscape structure, equally important is the increased recognition that the detection of such responses is also sensitive to the spatial scale at which the system is examined (Gorresen et al. 2005).

Recent studies provide evidence for widespread scale dependence in associations between landscape metrics and bat responses at the assemblage, population, ensemble, and species levels (Gorresen and Willig 2004; Meyer and Kalko 2008a; Pinto and Keitt 2008; Klingbeil and Willig 2009, 2010; Henry et al. 2010; Cisneros et al. 2015). Pinto and Keitt (2008) quantified forest cover at a range of scales (buffers with radii from 50 to 2000 m) and found positive associations with bat abundance, whereby the scale that elicited the strongest response was species specific. Differential species responses to forest cover in this case were best explained by interspecific variation in diet, body size, and home range size. Similarly, multiple species- and ensemble-specific abundance responses of phyllostomid bats to landscape characteristics at multiple focal scales (buffers with 1, 3, and 5 km radii) have been reported from moderately fragmented, lowland Amazonian forest (Klingbeil and Willig 2009) and highly fragmented Atlantic forest in Paraguay (Gorresen and Willig 2004). In both studies, species were demonstrated to interact with their environment simultaneously at a range of spatial scales. In the Amazon, a change in the focal scale of response occurred between dry and wet seasons, a finding which is likely linked to seasonal differences in food abundance and diversity as well as energetic constraints associated with reproduction (Klingbeil and Willig 2010; Cisneros et al. 2015). Scale dependence in response patterns has also been observed in landscapes with an aquatic matrix (Meyer and Kalko 2008a; Henry et al. 2010), suggesting that scale effects are ubiquitous and operate in fragmented landscapes across a broad range of matrix types.

Overall, such findings emphasize that multiscale approaches to determining the effects of landscape structure on tropical bats are essential. In agreement with recent findings for tropical birds (Banks-Leite et al. 2013), the available evidence suggests, however, that the extremely idiosyncratic responses of tropical bats to landscape structure make it difficult to identify any particular landscape predictor or spatial scale that performs best at predicting responses at the assemblage level.

Despite the general importance of a landscape-level perspective in the study of habitat fragmentation, patch characteristics remain important for patch-dependent species (Driscoll et al. 2013). However, fragmentation studies on tropical bats that have jointly assessed the relative contribution of patch- and landscape-scale variables for explaining response patterns are scarce. Meyer and Kalko (2008a) found that the relative importance of local- versus landscape-scale characteristics in explaining species richness and compositional patterns of phyllostomids on Panamanian land-bridge islands varied with spatial scale. At the patch scale, isolation distance from the mainland was the strongest predictor, whereas the proportion of forest cover in the surrounding landscape was the most prominent descriptor explaining variation in assemblage attributes at larger scales.

Although the importance of spatial scale and spatial variation in matrix quality have received some attention in the bat fragmentation literature, we know little about how species responses to fragmentation vary over time or how they are mediated by changes to the matrix. Across many human-modified landscapes in the tropics, secondary forest regrowth may reclaim once deforested land, for instance in response to the abandonment of agriculturally unproductive areas (Bobrowiec and Gribel 2010; Chazdon 2014). Matrix recovery following disturbance can alter responses of fragment biota that may be driven by temporal changes in resource availability and of permeability of the matrix to dispersal (Bissonette and Storch 2007; Driscoll et al. 2013). In this context, research at the Biological Dynamics of Forest Fragments Project in the Brazilian Amazon indicates strong divergence in phyllostomid bat assemblage structure, high levels of species turnover, and marked reorganization in the rank order of the most abundant species in response to changes in matrix quality and composition over 15 years (Meyer et al., unpublished data).

Time lags in the manifestation of species responses to fragmentation are ubiquitous and constitute an important temporal aspect to consider when studying fragmentation impacts (Ewers and Didham 2006a; Bissonette and Storch 2007), but so far have been rarely investigated in tropical bat studies. Notable exceptions are a series of studies conducted in the St. Eugène land-bridge island system in French Guiana, in which fragmentation effects prior to, and for several years after, fragmentation provided clear evidence for time lags in species loss (Cosson et al. 1999; Pons and Cosson 2002; Henry et al. 2010). These time lags occurred gradually over the course of ca. 10 years.

Future assessments of tropical bat responses to fragmentation (and other types of anthropogenic disturbance) should therefore address not only the spatial but also the temporal dimension of human impacts. This is particularly notable as long-term studies in intact habitats reveal tropical bat assemblages to be highly dynamic in space and time (Pech-Canche et al. 2011; Kingston 2013).

4.5.1.5 Edge Effects

Recent reviews concur that edge effects critically affect biodiversity in habitat fragments (Ewers and Didham 2006a; Fischer and Lindenmayer 2007; Laurance et al. 2011). However, responses of tropical bats to habitat edges remain understudied, particularly in the Paleotropics. Current evidence from the Neotropics suggests that responses vary according to matrix contrast and land-use history, and are ensemble and species specific.

Several studies have modeled bat responses in relation to the amount and complexity of edge habitat, revealing that some tropical bats are sensitive to habitat edges (Gorresen and Willig 2004; Meyer and Kalko 2008a; Klingbeil and Willig 2009, 2010; Henry et al. 2010). While significant associations between species richness or composition with edge density have been found in fragmented systems with a water matrix (Meyer and Kalko 2008a), studies conducted in a low-contrast landscape did not detect significant edge-related responses at the assemblage level (Gorresen and Willig 2004; Klingbeil and Willig 2009, 2010). This again underlines the importance of matrix contrast in affecting species' edge sensitivity and also shows that, at least in landscapes with low-contrast edges, composite community measures such as species richness may fail to capture edge responses that may otherwise be evident at the species or ensemble level (Klingbeil and Willig 2009). At the population level, abundances of six frugivorous and gleaning animalivorous phyllostomid bat species in the Peruvian Amazon were positively related to edge density, whereby responses varied depending on spatial scale (Klingbeil and Willig 2009) and season (Klingbeil and Willig 2010). In contrast, in fragmented Atlantic forest, two frugivorous species exhibited negative responses to edge density (Gorresen and Willig 2004). The discrepancy in the direction of response may be explained by differences in the prevailing patterns of land conversion (small- vs. large-scale deforestation). A strong negative response of gleaning animalivores to edge cover was also found by Henry et al. (2010) in a land-bridge island system in French Guiana.

These studies indicate the sensitivity of phyllostomid bats to edges driven by changes in landscape configuration. However, quantifying the strength of edge effects requires explicit consideration of two distinct aspects: edge extent and edge magnitude. Edge extent is the distance over which a change in the response variable can be detected, and edge magnitude is the amplitude of the effect (Harper et al. 2005; Ewers and Didham 2006b). The few studies that have examined the magnitude of edge effects on tropical bats by comparing interior sites of large, mature forest stands and forest edges reported declines in phyllostomid richness, in landscape matrices of high (water; Meyer and Kalko 2008a) and low structural contrast (secondary forest and shade cacao plantations; Faria 2006). The pattern of reduced species richness at edges in the low-contrast system was mainly attributable to the decline of gleaning animalivorous species (Faria 2006; Pardini et al. 2009). Even though species composition did not significantly change between forest edge and interior, Meyer and Kalko (2008a) found that gleaning animalivorous bats exhibited a strong negative numerical response toward edges. In fact, edge sensitivity was identified as the species trait that best explained species vulnerability to fragmentation (Meyer et al. 2008). Similar to phyllostomids, aerial insectivorous bats in the same land-bridge island system had significantly lower species richness at edges compared to interiors. The two functional groups of narrow-space foragers and open-space bats responded differently to forest edges. Open-space foragers had higher abundance counts at edges, whereas those of forest species were not significantly altered (Estrada Villegas et al. 2010). Comparing general bat activity, Estrada et al. (2004) did not detect significant differences between continuous forest interiors and forest–pasture edges.

Only one study to date has tried to quantify the distance of edge influence for tropical bats. Delaval and Charles-Dominique (2006) captured phyllostomid bats along 3-km transects perpendicular to the edges of a road traversing primary forest in French Guiana. Capture rates along the transects were more than seven times higher than those at a control site, 150 km inside the primary forest block. Moreover, along the transects abundances decreased with increasing distance from the road edge, a pattern attributable to the proliferation of opportunistic frugivores such as *Carollia perspicillata* and *Artibeus jamaicensis* that exploit abundant food resources provided by young regrowth along road margins. Species richness decreased significantly with distance from the road edge, probably related to an influx of species from the open habitat into the edges. Species richness at edges was, however, not significantly greater than that in the control site that harbored seven species not present at road edges or along transects. Differences in rank abundance patterns between transects and control site provided further evidence that even narrow road clearings can alter bat assemblage structure over distances of at least 3 km into forest interiors.

Key research needs:

- Studies that try to disentangle the relative importance of habitat amount and habitat configuration in shaping species responses, in particular studies that identify portions of the gradient in habitat amount within which the effects of spatial arrangement become important, i.e., explicit tests of the "habitat threshold hypothesis" (Fahrig 2003).
- Research that addresses the relative tolerance of different species to changes in habitat configuration (see Villard and Metzger 2014).
- Studies that jointly assess the relative contribution of patch- and landscape-scale variables to explaining response patterns.
- Long-term investigations that address the effects of matrix transformation on bat species responses over time.
- More studies that quantify edge effects in terms of both magnitude and extent.
- Further research investigating how consistently species respond to habitat edges across a broad range of edge types to identify ecological traits correlated with and potentially driving edge sensitivity (Ries and Sisk 2010).
- Studies that try to disentangle edge and area effects (Fletcher et al. 2007; Banks-Leite et al. 2010).

4.5.2 Logging

Rain forests are selectively logged at 20 times the rate at which they are cleared (Asner et al. 2009), and large expanses (403 million ha) are officially designated for timber extraction (Blaser et al. 2011). Selective logging exposes vast areas to potentially detrimental edge effects (Broadbent et al. 2008) and may often be the precursor to complete deforestation (Asner et al. 2006). Yet, the impacts of selective logging on biodiversity depend critically on the harvest intensity (Asner et al. 2013; Burivalova et al. 2014) as well as the extraction techniques (Bicknell et al. 2014). Selective harvesting methods range from large-scale conventional extraction that can cause substantial loss in canopy cover and associated mortality of non-harvested trees, to reduced-impact logging (RIL), in which collateral damage is reduced as a result of improved planning and control of harvesting activities (Putz et al. 2008; Asner et al. 2013).

Recent meta-analyses indicate that selectively logged forests can retain a large proportion of the diversity of old-growth forest for a variety of taxa (Gibson et al. 2011; Putz et al. 2012) and the available evidence, though scant due to the low number of studies (Fig. 4.3a), largely supports this notion for tropical bats (Bicknell et al. 2014). At the assemblage level, selective logging appears to have little or no effect on bat species richness in the Neotropics (Ochoa 2000; Clarke et al. 2005a, b; Castro-Arellano et al. 2007). In contrast, compositional or structural differences between bat assemblages in logged and unlogged sites are more common, which suggests that if forests are unable to recover from logging disturbance, species losses may be detected in the long term (i.e., similar to time lags for fragmentation effects, see Sect. 4.5.1). Structural differences between bat assemblages in unlogged and logged forests are evident from changes in the proportional abundance of species within ensembles (Clarke et al. 2005a, b; Peters et al. 2006) and shifts in species rank distributions and dominance (Castro-Arellano et al. 2007). A consistent pattern emerging from Neotropical studies is that, similar to habitat fragmentation (see Sect. 4.5.1), selective logging appears to adversely affect the abundance of gleaning animalivorous phyllostomids, whereas frugivorous and nectarivorous species tend to increase in abundance (Ochoa 2000; Clarke et al. 2005a, b; Peters et al. 2006; Presley et al. 2008).

In a study in Trinidad, Clarke et al. (2005a) found that the magnitude of change in species composition is linked to the intensity of timber harvesting. Comparing a continuous logging system with few harvest controls (open range [OR] system) to a polycyclic, selective system that incorporated stricter controls on felling (periodic block [PB] system), the study demonstrated that PB-managed sites resembled undisturbed primary forest much more closely in bat species composition and abundance than did OR forest. Despite structural changes associated with PB management, bat assemblages in such well-managed forest stands had great potential for recovery to near predisturbance levels (Clarke et al. 2005b). The number of years post-logging was positively correlated with the number and abundance of species of gleaning animalivores but not frugivores, whereas the proportional abundance of the dominant frugivore decreased with forest recovery. Together, these findings suggest that PB or similar low-intensity selective management systems may be compatible with the conservation of bat diversity. Unfortunately, similar studies that evaluate responses of tropical bats to different management systems or across a series of logged sites of different ages within the same general study landscape are lacking.

Short-term population-level responses of phyllostomid bats to RIL in Amazonia were idiosyncratic (Castro-Arellano et al. 2007) and RIL sites had reduced species richness, linked to the local absence of rare species from logged forest, whereas the populations of common species remained unaffected (Presley et al. 2008). As argued by Presley et al. (2008), landscape context may be important in mediating the effects of RIL on bats, and for this harvesting practice to be sustainable, it may be essential that RIL blocks be located in close proximity to undisturbed forest to facilitate rescue effects that can mitigate the negative impacts of RIL on rare species. Furthermore, due to the short post-harvest interval (<42 months) in both studies, the observed responses may be short term (Castro-Arellano et al. 2007; Presley et al. 2008), stressing the necessity for longer-term evaluations of logging impacts.

In the only logging effect study on African bats, Monadjem et al. (2010), using acoustic sampling, found no significant differences in activity levels between primary and logged forests in Uganda for the insectivorous *Neoromicia nana*. Elsewhere in the Paleotropics, early studies reported higher species richness, diversity, and abundance in unlogged compared to selectively logged forest in Malaysia (Zubaid 1993) and profound changes in species composition due to logging in Sumatra (Danielsen and Heegaard 1995). However, in addition to having small sample sizes, these studies employed only mist nets, which are ineffective at capturing the numerous insectivorous species that dominate Paleotropical bat assemblages (Kingston 2013). Conclusions based on these studies alone should therefore be interpreted with caution. More recent studies in Southeast Asia have employed larger sampling effort and harp traps, which are adequate for sampling forest interior insectivores. In peninsular Malaysia, a comparison of forest reserves and adjacent logged-over forests >30 years post-extraction showed little overall difference in assemblage composition (Christine et al. 2013). In nearly all site comparisons, species richness and abundances were higher in logged forest. However, certain tree- or foliage-roosting species were only captured inside forest reserves, suggesting that forest reserves embedded in a matrix of production forest could play an important role as reservoirs to restock logged forest and to maintain populations of disturbance-sensitive species (Christine et al. 2013).

Logging effects may multiply spatially and temporally as a result of multiple harvesting cycles (Lindenmayer and Laurance 2012). However, only recently have researchers examined the impacts of multiple rounds of extraction. One such study examined bat assemblages on Borneo across a disturbance gradient ranging from old-growth to twice-logged to repeatedly logged forest (Struebig et al. 2013). Logging had little effect on bat species richness, even in heavily degraded forest that had been logged multiple times, corroborating research on other taxa in the region (Edwards et al. 2011). Changes in insectivorous bat assemblage structure and abundance between old-growth and repeatedly logged forest were nonetheless evident and degraded sites that were characterized by a low, open canopy harbored a depauperate bat fauna. Canopy height was an important determinant of assemblage change across the disturbance gradient, as was the availability of tree cavities for forest-roosting taxa. By quantifying microhabitat over the gradient, the study revealed that post-logging recovery of assemblages could be enhanced via restoration investments in canopy cover and tree cavity availability. Moreover, cave-dwelling hipposiderid and rhinolophid bats were less abundant in repeatedly logged sites, in line with findings from a study in Vietnamese karst forests in which these taxa were also less abundant in logged than in primary forest (Furey et al. 2010).

A key theme emerging from the recent logging effect literature is the potential confounding issue of spatial pseudoreplication in study design, a problem whereby study sites in continuous forest stands are inappropriately treated as independent replicates (Ramage et al. 2013). The most effective way to overcome these problems is to sample the same forest sites before and after logging. The only bat-logging study to have implemented such a robust Before–After–Control–Impact

(BACI) design to date was undertaken in RIL forests in Guyana (Bicknell et al. 2015). Differences in bat assemblage structure before and after logging were relatively weak and varied substantially across study sites. Although three species were classified as indicators of disturbed or undisturbed forest, there were no clear changes in bat assemblages at control sites, indicating that overall responses could not be reliably attributed to logging.

In conclusion, given the paucity of studies available, it remains difficult to ascertain definitive responses of tropical bats to logging. The short-term effects appear to be relatively benign, especially in low-intensity extraction systems. Reported effects vary, largely owing to differences among studies with regard to the type of forest management system, and spatial and temporal variability in disturbance attributes, including time post-harvest.

Key research needs:

- Studies comparing bat responses between different forest management systems and across a range of spatial and temporal scales.
- More studies implementing BACI designs, as exemplified by Bicknell et al. (2015).
- Integration of logging disturbance into studies of forest fragmentation in order to distinguish true fragmentation responses from those of forest degradation.

4.5.3 Secondary Forests and Succession

The future of tropical biodiversity will critically depend on our ability to manage the large expanses of regenerating secondary forests (Chazdon et al. 2009; Chazdon 2014) that account for approximately half of the remaining area of tropical moist forests (Asner et al. 2009). Studies that have examined the conservation value of secondary forests for tropical bats are largely in line with assessments with regard to other tropical taxa (Barlow et al. 2007; Gardner et al. 2010) by suggesting that regenerating forests act as important repositories of bat biodiversity. Secondary forests are effective at conserving a subset of primary forest bat species richness (Louzada et al. 2010), but usually host assemblages that differ in structure and composition from those in mature forest (Faria 2006; Barlow et al. 2007).

Secondary successional vegetation in Neotropical humid forests represents important habitat for many frugivorous and nectarivorous phyllostomids (e.g., *Carollia* spp., *Sturnira* spp., *Glossophaga* spp.). These taxa become numerically dominant in secondary forests representing early to intermediate stages (Brosset et al. 1996; Castro-Luna et al. 2007a, b; Willig et al. 2007; de la Peña-Cuéllar et al. 2012; Vleut et al. 2013). This pattern is likely attributable to an increase in the abundance, diversity, or quality of fruit and flower resources associated with early successional vegetation and emphasizes the fundamental importance of phyllostomid bats in the regeneration of tropical forests (Muscarella and Fleming 2007). In contrast, the abundance of frugivores was not elevated in earlier successional stages of tropical dry forest in Mexico (Avila-Cabadilla et al. 2009). This likely reflects distinct differences in the composition of early successional vegetation, and consequently resource scarcity, in tropical dry compared to wet forests. Pinto and Keitt (2008) found that the abundances of *Sturnira* spp. were positively associated with secondary forest cover, reflecting the species' preference for early successional vegetation. Conversely, *Carollia* spp. responded to forest cover that included both primary and secondary forests, implying that habitat connectivity may be more important than successional stage for populations in this genus. As with logged forests, these findings suggest species-specific responses to secondary vegetation linked to interspecific differences in diet, home range size, and body size. Contrary to the flexible responses observed for many frugivores and nectarivores, a large body of empirical evidence indicates that gleaning animalivorous phyllostomines are sensitive to forest degradation, as they are absent or occur at low abundance in secondary regrowth (Fenton et al. 1992; Brosset et al. 1996; Medellín et al. 2000; Faria 2006; Castro-Luna et al. 2007a, b; Mancina et al. 2007; Willig et al. 2007; Pardini et al. 2009; Bobrowiec and Gribel 2010; de la Peña-Cuéllar et al. 2012; Vleut et al. 2012, 2013).

Some studies have detected a clear pattern of species richness increasing across successional gradients (Avila-Cabadilla et al. 2009; de la Peña-Cuéllar et al. 2012), but this pattern has not been evident in others (Castro-Luna et al. 2007a; Mancina et al. 2007). Nonetheless, for Neotropical wet and dry forests, floristically more diverse and structurally more complex habitats harbor greater taxonomic and functional richness than do early or intermediate stages of succession. Here, vegetation complexity appears to be an important factor shaping assemblage composition (Medellín et al. 2000; Avila-Cabadilla et al. 2009; Bobrowiec and Gribel 2010; Avila-Cabadilla et al. 2012; de la Peña-Cuéllar et al. 2012). Late successional forest stands often host many bat species not found in earlier stages, in particular rare taxa, and through succession, the number of species and ensembles increases for frugivorous, nectarivorous, and gleaning animalivorous taxa (Avila-Cabadilla et al. 2009, 2012; de la Peña-Cuéllar et al. 2012). In tropical wet forest in Mexico, abundances of the most common bat species were associated positively or negatively with variation in canopy cover across successional stages, rather than with landscape attributes (Castro-Luna et al. 2007a). In contrast, a study in Mexican tropical dry forest found evidence for an important role of local (vegetation complexity) and landscape attributes (area and cover of different vegetation types) as determinants of variation in abundance, which were ensemble specific and scale dependent (Avila-Cabadilla et al. 2012). In Central Amazonia, gleaning animalivorous phyllostomid bats exhibited greater abundance and richness in *Cecropia*-dominated regrowth, whereas stenodermatine frugivores were more abundant in abandoned pastures and *Vismia*-dominated regrowth, demonstrating that different successional trajectories result from differences in land-use history (cutting versus cutting and burning) that lead to distinct differences in bat assemblage composition (Bobrowiec and Gribel 2010).

Despite the recovery potential of Neotropical bat assemblages during succession, the conservation value of secondary forests for bats critically hinges on landscape context and is maximized in mosaic landscapes in which patches of forest at different successional stages are located close to old-growth forest (Bobrowiec and Gribel 2010; Vleut et al. 2012).

Key research needs:

- Comprehensive assessments of the conservation value of secondary forests for bats in the Paleotropics, which are essentially lacking (but see Fukuda et al. 2009).
- Studies addressing the recovery potential of Paleotropical bat assemblages during secondary succession.

4.5.4 Agroforestry Systems

As agriculture and associated biodiversity losses continue to rise across the tropics, agroforestry systems have been advocated as biodiversity-friendly alternatives, capable of conserving biodiversity while enhancing rural livelihoods (Perfecto and Vandermeer 2008; Clough et al. 2011). Coffee (*Coffea arabica*, *Coffea canephora*) and cacao (*Theobroma cacao*) are the principal cash crops of many tropical countries (Donald 2004; Tscharntke et al. 2011) and are the primary examples in the bat literature (but see bat inventories of Sumatran rubber agroforests in Prasetyo et al. 2011). In traditional coffee and cacao agroforestry, these crops are commonly grown under a stratified canopy layer of a more or less diverse range of native shade tree species. Much of their potential for conservation derives from the fact that such traditional agroforestry systems resemble natural forest habitat in many structural aspects (Perfecto and Vandermeer 2008).

Empirical studies that have assessed the value of agroforests for tropical bats to date come almost exclusively from the Neotropics (Fig. 4.3a). Pineda et al. (2005) compared the bat fauna of Mexican cloud forest fragments and shade coffee plantations and found that both habitats had very similar species richness and composition, although there were changes in the species' rank order between habitats. Large frugivorous phyllostomids (*Artibeus* spp.) reached higher abundance in shade coffee than in the natural habitat, possibly as a result of increased food availability due to the cultivation of important fruit tree species alongside coffee, a management strategy that also favored the abundance and richness of fruit- and nectar-eating bats in coffee plantations elsewhere in Mexico (Castro-Luna and Galindo-González 2012a). Contrasting abundance responses for large *Artibeus* were found in another study in Mexico (Saldaña-Vázquez et al. 2010). Here, shade coffee plantations and disturbed cloud forest fragments did not differ in abundance levels and also had similar availability of food plants. On the other hand, abundances of *Sturnira* spp. were higher in forest fragments, probably linked to a decline in food resources for these small frugivores in the coffee plantations. This reduction in resources resulted from the pruning of understory vegetation and was reinforced by the effects of a resource-poor pasture matrix surrounding the forest fragments.

Williams-Guillén and Perfecto (2010, 2011) investigated how bat diversity patterns in coffee agroforestry change with increasing management intensity. Phyllostomid bats maintained similar richness across management regimes, but showed significant declines in abundance across the intensification gradient, from forest fragments through low-management shade polyculture and commercial polyculture to high-management coffee monocultures (Williams-Guillén and Perfecto 2010). Compositional similarity differed significantly between fragments and coffee plantations of all management intensities, and between high-shade polycultures and low-shade monocultures. The proportions of large frugivores increased with management intensity, in line with Pineda et al.'s (2005) findings. Conversely, those of nectarivorous and gleaning animalivorous bats decreased, the latter being absent from intensively managed coffee monocultures. Both forest fragments and the diverse and structurally complex shade polyculture systems may provide adequate roosting and food resources to sustain high levels of phyllostomid diversity. This contrasts strongly with the situation in low-shade monocultures, which offer reduced feeding and roosting opportunities, and may consequently serve more as commuting than foraging habitat. This was also suggested in a study on non-phyllostomid aerial insectivorous bats in the same landscape, which reported reduced foraging activity in the most intensively managed monocultures (Williams-Guillén and Perfecto 2011). Both of the functional groups of aerial insectivores, forest and open-space foragers, had similar species richness across habitat types. The two groups, however, showed opposite responses with respect to activity levels and compositional similarity. Forest-adapted species differed in ensemble composition across the management gradient and responded negatively to agricultural intensification in terms of activity. For open-space foragers, reductions in shade tree diversity and cover did not manifest in compositional changes, but were associated with increased levels of overall activity, albeit not feeding activity.

Collectively, these studies demonstrate the high conservation value of structurally diverse shade coffee for bats, but less so of intensively managed systems. The former constitutes a permeable high-quality matrix, while intensive coffee monocultures represent poor matrix habitat (Numa et al. 2005). Landscape context, in particular the dominant matrix type, is an important modulator of how bat assemblages respond to agroforest management intensity. Forest fragments harbored significantly greater phyllostomid richness than did management systems when the landscape matrix was dominated by sun coffee, whereas richness was similar among habitats in a shade coffee matrix (Numa et al. 2005).

For cacao, studies show results similar to those for coffee, supporting the notion that traditional, structurally complex shade cacao plantations sustain high levels of bat diversity. Insights come from a series of studies conducted in the Atlantic forest region of Una, Brazil. Cacao agroforests in this region provide foraging and roosting habitat for members of all feeding ensembles, including forest-dependent gleaning animalivorous species (Pardini et al. 2009), primarily because of the structural complexity retained compared to intact forest (Faria et al. 2006). In fact, bat assemblages in shade cacao showed greater richness, diversity, and abundance than did those in nearby mature or secondary forest (Faria 2006; Faria and Baumgarten 2007; Pardini et al. 2009). However, shade cacao plantations per se may not provide adequate habitat conditions for forest-dwelling bats, as the proximity of shade cacao to forest remnants was a key determinant of species persistence. Bat assemblages in plantations isolated by more than 1 km from forest were characterized by low richness and diversity, with clear shifts in species dominance, suggesting a crucial role of native forest remnants as population sources (Faria and Baumgarten 2007). Isolating distance to forest was also an important factor influencing species richness and abundance in Mexican shade plantations (Estrada et al. 1993a). These plantations maintained diverse and structurally similar bat assemblages to those in remnants of native forest (Medellín et al. 2000; Estrada and Coates-Estrada 2001b). As for coffee (Numa et al. 2005), landscapes dominated by cacao agroforests and comprising reduced native forest cover may harbor impoverished bat assemblages (Faria et al. 2006; 2007), highlighting that landscape context generally plays a crucial role in determining bat species responses in tropical agroforestry landscapes, as it does for fragmented forest systems.

In conclusion, both coffee and cacao, when grown under a traditional shade regime, comprise a high-quality matrix that offers suitable conditions for maintaining diverse phyllostomid assemblages. These agroecosystems, in turn, benefit from pest control services provided by bats as has been shown for agroforests in the Neotropics (Williams-Guillén et al. 2008) and Southeast Asia (Maas et al. 2013) (see Chap. 6). Studies in cacao agroforestry at least in some cases entailed comparison between large tracts of mature forest and the agricultural system (Medellín et al. 2000; Faria 2006), but these important baseline data are lacking for studies in coffee agroforests.

Key research needs:

- Studies that assess response patterns for non-phyllostomid bats.
- Assessments of bat responses to cacao agroforestry intensification, especially in view of globally increasing levels of conversion of shade cacao systems into unshaded monocultures (Tscharntke et al. 2011).
- Linkages between levels of bat biodiversity and crop yields.

4.5.5 Tree Plantations

Given the extent to which forested land is being converted to tree plantations across much of the tropics (Gibbs et al. 2010), there have been surprisingly few studies investigating the value of these habitats for bats. Three systems dominate tree plantation mosaics in the tropics: fast-growing timbers for the paper/pulp industry (e.g., *Acacia*, *Eucalyptus*), rubber (*Hevea brasiliensis*), and, increasingly, oil palm (*Elaeis guineensis*).

In a multitaxon assessment in Brazil, Barlow et al. (2007) found similar numbers of bat species in *Eucalyptus* plantations and secondary forests recovering from burning, but both habitats supported much lower richness than did unlogged forests. Bat assemblages in plantations were nested subsets of those in forests; approximately 11 % of all species were shared between plantations and primary forest, 4 % were shared with secondary forest, and 39 % found in all habitats (Louzada et al. 2010). Nevertheless, three species (ca. 6 % of total) were captured exclusively in *Eucalyptus* plantations.

A study in Brazilian Cerrado found lower species richness, diversity, and evenness of bat assemblages in *Eucalyptus* monocultures than in fragments of native Cerrado vegetation (Pina et al. 2013). Gleaning animalivorous phyllostomid bats were not captured in plantation forests. An earlier comparative study in Sumatra documented a distinct shift in bat assemblage structure in rubber and oil palm plantations, which supported only 13–25 % of the bat species richness found in forest (Danielsen and Heegaard 1995). However, more recent surveys have revealed additional species utilizing rubber plantations, especially those grown as agroforests or close to forest areas (Prasetyo et al. 2011). These studies point to an adverse response by bats to plantation development in both the New and Old World tropics. However, the extent to which these findings reflect true bat declines versus sampling bias (i.e., difficulties in capturing bats in open plantation habitats) is open to question. Tree plantations present a much more open habitat compared to forests, but can provide canopy structure similar to that in forest. This may present difficulties for capturing bats in these habitats, particularly in the Paleotropics, where much of the insectivorous bat fauna can only be captured in harp traps. Bat surveys in Sumatra and Borneo have resulted in extremely low capture rates for insectivorous species in oil palm plantations using mist nets and harp traps (Fukuda et al. 2009; Syamsi 2013), a finding that could reflect differential capture success in closed versus open habitats as well as true differences between habitats. Acoustic surveys could potentially contribute additional information concerning bat activity and the structure of bat assemblages in these habitats. The first insights from the Old World come from southern Thailand, where Phommexay et al. (2011) sampled bats in forest and neighboring rubber plantations using bat detectors, mist nets, and harp traps. Although diversity and overall bat activity were much lower in plantations than in forests, differences between the two habitat types were not as severe as indicated by capture-based surveys. Acoustic sampling in plantations detected less than half the number of bat species found in forest and fewer bat passes. Although bat activity was clearly reduced in plantations, a substantial number of feeding buzzes were detected, suggesting that bats were still foraging in this modified habitat.

Key research needs:

- Further studies, particularly those using acoustic methods, to accurately assess the conservation value of tree plantations for tropical bats.

4.5.6 Agriculture and Residual Tree Cover

Agricultural encroachment and cropland expansion are key threats to biodiversity in tropical countries (Phalan et al. 2013). The dominant crop will determine the permeability of the agricultural matrix, the likelihood of species persistence, and ultimately whether sustainable configurations in human-modified landscapes emerge in which biodiversity conservation and food production can be reconciled (Melo et al. 2013).

Apart from several studies in agroforestry systems (see Sect. 4.5.4) and oil palm plantations (see Sect. 4.5.5), little research has examined responses of tropical bats to forest conversion into other agricultural land uses, or the value of residual vegetation in agricultural matrices (Fig. 4.3a). By far, most of the available evidence comes from studies in Mexico and Central American tropical wet and dry forests. These studies generally suggest that human-modified landscapes comprising a heterogeneous mosaic of different land- and tree-cover types can preserve species-rich bat assemblages (Estrada et al. 1993a, b, 2004; Medellín et al. 2000; Moreno and Halffter 2001; Estrada and Coates-Estrada 2002; Harvey et al. 2006; Medina et al. 2007; Barragan et al. 2010; Mendenhall et al. 2014). For instance, in a comparison of bat diversity in forest fragments, agricultural habitats, and live fences in Mexico, agricultural habitats contained 77 % of the species recorded, whereby species richness declined with increasing distance from forest fragments (Estrada et al. 1993a). Certain frugivorous species (e.g., *Carollia* spp., *Sturnira* spp.) may become dominant in agricultural areas, whereas phyllostomine species are adversely affected by agriculture (Medellín et al. 2000). A similar pattern was found by Willig et al. (2007) in lowland Amazonian rain forest in Peru. Here, half of the frugivorous and nectarivorous species that responded consistently to habitat conversion reached highest abundances in agricultural areas, a response probably linked to the ample food resources provided by these habitats. Due to the presence of rare species not captured in forest, species richness in disturbed agricultural and early successional habitats was high compared to that in mature forest. However, the long-term persistence of most species likely still depends on the availability of forest (Willig et al. 2007). Moreover, these findings relate to small-scale habitat conversion and may not be generalizable to landscapes characterized by large-scale deforestation.

Knowledge of the conservation value of agricultural habitats for bats in the Old World is scant (see Chap. 6). In a study in Fiji (Luskin 2010), foraging densities of the Pacific flying fox, *Pteropus tonganus*, an important seed disperser were four times higher in agricultural habitats than in remnants of dry forest, illustrating a strong preference for foraging on abundant food resources in farmland. Resource subsidies provided by farmland were responsible for sustaining high abundances of the species despite severe deforestation across the region. Roosting sites, however, were restricted to native forest fragments, highlighting their importance for population persistence. Agricultural habitats provided important resources for some species of pteropodid bats in Borneo, as evidenced by high capture rates in orchards relative to forest habitats (Fukuda et al. 2009). Fukuda et al. (2009) suggest that some pteropodids in Southeast Asian dipterocarp forests, which are characterized by a supra-annual flowering and fruiting pattern, may augment food resources by feeding on cultivated plants during non-flowering periods when food supply in the forest is scarce. However, other fruit bat species were restricted to forest, suggesting that the value of agricultural land is species specific. Sedlock et al. (2008) reported that fewer species persist in mixed agricultural habitat than in tall secondary forest in the Philippines. Nevertheless, 19 of 26 species were present in agro-pastoral areas. Results from studies in the Paleotropics are thus largely congruent with those from the Neotropics in suggesting that agricultural habitats harbor considerable bat diversity and provide important foraging habitat for some fruit bat species.

Linear landscape elements (corridors of residual vegetation such as live fences or strips of riparian forest) and scattered trees, commonly found in Neotropical countryside landscapes, may enhance functional connectivity (Villard and Metzger 2014), and studies indicate that bats extensively use them (Estrada and Coates-Estrada 2001a; Galindo-González and Sosa 2003; Estrada et al. 2004; Harvey et al. 2006; Medina et al. 2007; Barragan et al. 2010). For instance, in agricultural landscapes in Nicaragua, riparian forests and live fences harbor greater bat species richness and abundance than do secondary forest and pastures with low tree cover (Harvey et al. 2006; Medina et al. 2007). Riparian forests constitute favorable habitats for foraging and roosting, particularly in tropical dry forest ecosystems, where they often have higher tree diversity and food availability compared to other types of cover (Estrada and Coates-Estrada 2001a; Harvey et al. 2006). Live fences and riparian corridors facilitate movement by bats across fragmented agricultural landscapes and may effectively reduce isolation between remnant forest patches, which, in turn, enhances species persistence at the landscape level. Similar to live fences, isolated pasture trees provide food and roosting opportunities for bats and act as important stepping stones for bat movement (Galindo-González and Sosa 2003), suggesting that they can render agro-pastoral landscapes more hospitable to bats and consequently deserve attention in conservation strategies. In contrast, studies concur that pastures are low-quality habitat for bats, likely as a consequence of resource scarcity (food, roosts) and elevated predation pressure (Estrada et al. 1993a, b, 2004; Harvey et al. 2006; Griscom et al. 2007; Medina et al. 2007).

Key research needs:

- In-depth studies in the Old World tropics that assess bat responses across a range of agricultural habitat types and landscape settings.
- Assessments of the value of residual tree cover in agricultural matrices for Paleotropical bats, particularly in Africa.
- Research addressing the effects of large-scale, commercial agriculture (e.g., cultivation of soybean, corn, sugarcane), which plays an increasingly significant role in driving deforestation in some tropical regions such as the Amazon.

4.6 Genetic Consequences

Tropical taxa are generally underrepresented in landscape genetic studies (Storfer et al. 2010). Bats are no exception, as only few studies have assessed how they are affected by anthropogenic habitat loss and fragmentation at the genetic level (Fig. 4.3b). Meyer et al. (2009) studied populations of two Neotropical bats in fragments that were isolated by a water matrix and detected significant population differentiation that matched the species' relative mobility. In contrast to the more mobile canopy frugivore, *Uroderma bilobatum*, population subdivision in the understory frugivore, *C. perspicillata*, showed a significant effect of fragmentation and isolation by distance, as well as reduced genetic diversity on islands relative to mainland populations. Also employing mitochondrial DNA sequence data, Ripperger et al. (2013) documented small-scale genetic differentiation for another small understory frugivore, *Dermanura watsoni*, in fragments embedded in a matrix dominated by agriculture. Landscape connectivity as measured by the amount of suitable habitat surrounding forest patches was most strongly correlated with genetic variation when quantified within small-scale (400 m) landscape buffers, likely reflecting the reduced mobility of this species. Importantly, empirical levels of genetic diversity in fragments were best explained by past rather than present habitat conditions. Because anthropogenic habitat fragmentation is recent on evolutionary timescales, populations may not show immediate genetic responses to fragmentation, highlighting the importance of considering time lags in these scenarios.

In a microsatellite study of three codistributed insectivorous bat species in forest fragments in peninsular Malaysia, Struebig et al. (2011) observed area-related declines in genetic diversity in *Kerivoula papillosa*, the species that was most sensitive to fragmentation based on ecological characteristics (low vagility, low population density, tree-cavity-roosting habit). Based on the genetic-area relationship observed for *K. papillosa*, the authors estimated that preserving the genetic diversity of this species at levels similar to those of intact forest would require extensive areas (>10,000 ha), several times larger than necessary to maintain comparable levels of species richness. In view of the fact that most forest patches in heavily fragmented production landscapes across Southeast Asia are much smaller, it is evident that maintaining genetic diversity of the dozens of forest specialist species that exhibit trait combinations similar to those of *K. papillosa* constitutes a substantial conservation challenge (Struebig et al. 2011). Roosting ecology and social organization may generally be important predictors of genetic structuring in insectivorous Old World bats. Rossiter et al. (2012) found that less vagile, tree-roosting species exhibit reduced gene flow, even across continuous intact rain forest, compared to more wide-ranging colonial cave-roosting species, indicating that the former should be disproportionately affected by landscape-scale habitat fragmentation.

Only weak genetic population subdivision was demonstrated for *Artibeus lituratus*, an abundant, highly mobile, and generalist frugivore, in a study in fragmented Atlantic forest (McCulloch et al. 2013). High levels of contemporary population connectivity in an abundant and widespread seed disperser like *A. lituratus* may buffer numerous plant species in Neotropical forests that rely on dispersal services of this bat species to counterbalance the negative impacts of deforestation.

In summary, the available evidence suggests, both in the New and in the Old World tropics, and irrespective of fragment–matrix contrast, that some bat species may be vulnerable to genetic erosion as a result of small-scale habitat fragmentation. Further, studies indicate that susceptibility in this context is linked to individual species traits such as mobility or roosting habit.

Key research needs:

- Increasing research on a broader range of species with different ecological and life-history traits, ideally using high-resolution genetic markers such as microsatellites or single-nucleotide polymorphisms (SNPs).
- Studies that quantify the extent to which frugivorous and nectarivorous bat species are capable of maintaining gene flow among plants in fragmented tropical landscapes.

4.7 Behavioral Responses

In addition to the direct effects on diversity and abundances, species' responses to anthropogenic habitat modification and disturbance can manifest as behavioral changes, which may include disruptions to species' dispersal, movement, activity patterns, and interspecific interactions (Fischer and Lindenmayer 2007). Few studies so far have addressed these issues for tropical bats (Fig. 3.3b).

Although a number of studies have reported movement distances and space use for a variety of tropical bat species (not reviewed here), few have explicitly addressed these phenomena in anthropogenically modified landscapes. Mark–recapture and radiotracking studies in the Neotropics suggest that in areas where landscape connectivity is relatively high, bats may regularly traverse open areas between forest fragments or between fragments and continuous forest. Evidence for interhabitat movements comes from landscapes with agricultural matrices (Estrada et al. 1993a; Estrada and Coates-Estrada 2002; Bianconi et al. 2006; Medina et al. 2007; Mendes et al. 2009; Trevelin et al. 2013) or from those with a more inhospitable aquatic matrix (Albrecht et al. 2007; Meyer and Kalko 2008a). Recapture data from a study in a fragmented landscape in Malaysia also indicate long-distance between-habitat movements for some cave-roosting species (Struebig et al. 2008). Whether a species is able to move over fragmented landscapes may be linked to the species' foraging ecology (Albrecht et al. 2007; Henry et al. 2007b). Overall, these studies were fundamental in determining the general capacity of tropical bats to move across human-modified habitats. However, they provide mostly circumstantial evidence and cannot establish whether anthropogenic disturbance elicits direct behavioral responses in bats that manifest as changes in movement distances or patterns of space use. Better insights into how habitat modification influences movement behavior can be gained through detailed radiotracking or long-term banding studies that compare movement patterns for species with different autecologies. Such studies, although difficult and costly to implement, would ideally compare continuous forest with fragments or other disturbed habitats.

Studies that have assessed behavioral changes to habitat modification in terms of effects on temporal activity patterns have followed such a rigorous approach. Disturbance-related changes in resource abundance, diversity, or predictability can be assumed to potentially alter temporal activity of species that exploit those resources (Presley et al. 2009b). Presley et al. (2009a) found no interspecific differences in activity patterns of eight abundant frugivorous bats in primary lowland Amazonian rain forest. However, for five species, activity patterns differed between primary or secondary forest and agricultural habitats, whereby bats in larger agricultural areas exhibited reduced crepuscular activity compared to those in undisturbed forest. Elsewhere in Amazonia, Castro-Arellano et al. (2009) detected no differences in activity levels for nectarivores and gleaning animalivores in response to RIL. Conversely, understory frugivores (*Carollia* spp.) decreased activity at dusk. Another study found reduced activity by some frugivores in small forest clearings created by tree removal, although the overall effects of RIL on activity patterns of frugivores were negligible (Presley et al. 2009b). In all cases, the curtailment of activity in open areas at twilight or during periods of high lunar illumination was best explained by increased predation risk (Saldaña-Vázquez and Munguía-Rosas 2013). Habitat modification and disturbance may consequently influence energy budgets of bats as they have less time available for foraging, with possible negative repercussions for their ability to meet daily energy requirements.

Human disturbance may also affect roosting behavior and roost site selection. In fragmented rain forest in Mexico, Evelyn and Stiles (2003) found that both sexes of cavity-roosting *Sturnira lilium* selected large-diameter trees in mature forest stands, as did females of the foliage-roosting *Artibeus intermedius*, whereas males of the latter species roosted in secondary forest. These findings underscore that preferences in terms of roosting and foraging habitat are not necessarily correlated and point to the importance of preserving mature forest patches in human-dominated landscapes for meeting the roosting requirements of tree-cavity-roosting species.

Key research needs:

- More studies, particularly in the Paleotropics, that assess the extent to which human-driven habitat change affects bat behavior in terms of roosting and foraging ecology.
- Research that addresses how such behavioral changes translate into fitness consequences (e.g., in terms of survival, reproductive success, physiology) that may affect long-term population persistence.

4.8 Effects on Selected Species Interactions

In recent years, bats have moved to the forefront of public attention, mostly as a result of accumulating evidence that they comprise important reservoir hosts for numerous zoonotic viruses (e.g., lyssaviruses, SARS, Ebola) that may pose a serious health risk to humans (Calisher et al. 2006; Hayman et al. 2013, Chap. 10). Recent studies have highlighted the urgency of gaining a better understanding of how habitat loss, land-use change and disturbance and an associated increase in bat–human interactions may, for instance, accelerate viral spillover (Peel et al. 2013). However, few studies to date have explored to what extent these stressors influence patterns of parasite and disease prevalence and transmission, as well as physiological stress responses in bats (Fig. 4.3b).

Cottontail et al. (2009) found that trypanosome prevalence in *A. jamaicensis* was significantly higher in fragmented sites than in continuous forest, linked to a loss of bat species richness and fragmentation-related changes in vegetation cover that may favor disease transmission. The negative relationship between trypanosome prevalence and bat species richness reflects the "dilution effect," i.e., a situation in which high host species richness reduces parasite transmission if vectors feed on multiple host species that vary in their ability to contract, amplify, or transmit the pathogen (Ostfeld and Keesing 2012). In contrast, prevalence of hemoparasitic nematodes (*Litomosoides* spp.) showed no significant difference among habitats, probably as a result of greater host specificity (Cottontail et al. 2009). In another study, fragmentation affected the physiological condition of *A. obscurus*, as evidenced by elevated hematocrit levels in forest fragments versus continuous forest, even though similar abundances in both habitats indicated a high degree of fragmentation tolerance. The opposite pattern was documented for *A. jamaicensis*, suggesting that abundance may in many instances be misleading as a metric of fragmentation sensitivity (Henry et al. 2007a). Pilosof et al. (2012) found a significant effect of anthropogenic disturbance on the abundance of ectoparasitic bat flies in three of four widespread Neotropical host bat species, whereby the direction of response differed among species. Species-specific roosting habits likely play a key role in mediating the effects of disturbance on parasite transmission. A study in Mexico found significantly lower prevalence of antirabic antibodies in non-hematophagous bats in disturbed agricultural areas (22.7 %) compared to relatively undisturbed dry forest sites (51.9 %), a pattern which may arise because of more frequent interspecies encounters in the undisturbed habitat (Salas-Rojas et al. 2004).

The important role of animalivorous, frugivorous, and nectarivorous bats in arthropod suppression, seed dispersal, and pollination in tropical ecosystems is widely acknowledged (Kunz et al. 2011). The degree to which such interactions are susceptible to habitat modification and disturbance is generally better understood for seed dispersal than for pollination or arthropod suppression. Mostly using fecal analysis or seed traps, numerous studies in various human-modified landscapes across the Neotropics have documented the quantity and diversity of seeds carried by bats (mostly *Carollia* spp., *Sturnira* spp., *Artibeus* spp.) into a diverse range of disturbed habitats including pastures, agricultural areas, coffee plantations, and secondary forests (Medellín and Gaona 1999; Galindo-González et al. 2000; García et al. 2000; Aguiar and Marinho-Filho 2007; Hanson et al. 2007; Wieland et al. 2011; Castro-Luna and Galindo-González 2012b; García-Estrada et al. 2012; García-Morales et al. 2012; Gorchov et al. 2013). Voigt et al. (2012) showed that bats of the genus *Carollia* were likely to carry seeds from mid-successional forest into adjacent primary forest, suggesting that directionality of seed transfer between disturbed areas and undisturbed forest may change with forest recovery. Isolated fig trees in abandoned pastures are attractive for many frugivores and may function as regeneration nuclei that effectively facilitate forest recovery (Guevara et al. 2004). Overall, these studies provide little evidence for major disruptions of seed dispersal mutualisms in response to habitat fragmentation and disturbance, although minor effects were detectable. For instance, small frugivorous bats disperse fewer large seeds in small, disturbed compared to large, undisturbed forest patches (Melo et al. 2009), suggesting a negative impact of disturbance on the dispersal of larger-seeded trees. Although Old World fruit bats in some areas may disperse seeds of early successional species (Hamann and Curio 1999), seed input into deforested or degraded areas tends to be low in human-modified landscapes in the Paleotropics (Duncan and Chapman 1999; Ingle 2003). Pteropodids generally play a much less significant role as dispersers of early successional plants compared to phyllostomids, but are important dispersers of late successional canopy trees (Muscarella and Fleming 2007). How habitat modification affects seed dispersal of large-seeded canopy trees by pteropodid fruit bats in Paleotropical forests requires further detailed study.

Research in fragmented Central American dry forest ecosystems found a decline in flower visitation rates, number of pollen grains deposited, and fruit set of certain bombacaceous tree species, suggesting that habitat disruption can impair the pollination services of nectarivorous phyllostomids, with negative consequences for plant reproductive success (Stoner et al. 2002; Quesada et al. 2003). However, effects were dependent on plant species (Quesada et al. 2004), making general predictions regarding the effects of habitat modification on the disruption of bat pollination difficult. Through its influence on bat foraging behavior, habitat disturbance may also limit pollen exchange between trees, leading to higher progeny relatedness in isolated trees relative to those in undisturbed forest (Quesada et al. 2013). In a fragmented landscape in tropical Australia, common blossom bats (*Syconycteris australis*) were high-quality pollinators of the rain forest tree *Syzygium cormiflorum*, as inferred based on pollen loads, visitation rates, and movement patterns (Law and Lean 1999). Nectarivorous bats often attain higher abundance in response to anthropogenic disturbance (see Sect. 4.5), suggesting that provisioning of pollination services may potentially be resistant and resilient to environmental perturbation.

Key research needs:

- Detailed studies that address the causal links between human-induced landscape change and bat physiological and immune responses, as well as disease susceptibility.
- Studies, particularly in the Paleotropics, that document the full dispersal cycle—from seed deposition through germination, seedling establishment, and recruitment—and how it is affected by habitat alteration.
- Further studies across a range of pollinator and plant species, as well as fragmented landscapes with different degrees of connectivity, to directly relate behavior and movement of pollinators with reproductive success and gene flow of trees.
- Studies that address the extent to which arthropod suppression services are affected by more intensive forms of habitat alteration and disturbance such as those associated with secondary forests, tree plantations, or cropland (see Wanger et al. 2014).

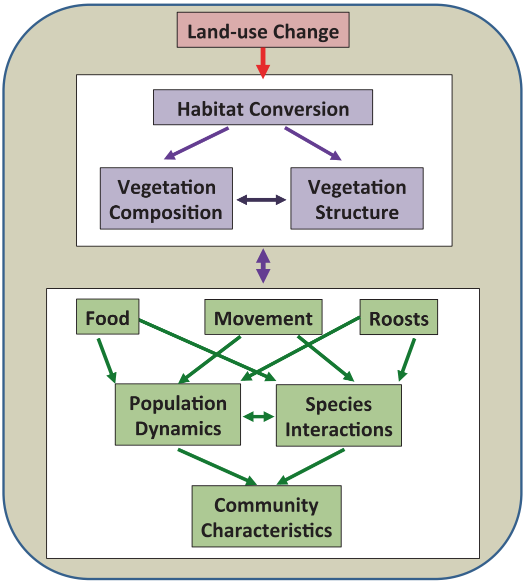
4.9 General Conclusions and Future Research Directions

As a consequence of a rapid increase in the annual number of publications over the past quarter century, ecological understanding has broadened and deepened concerning the influence of land conversion and habitat fragmentation on tropical bats at the level of populations, ensembles, and assemblages. Nonetheless, large geographic and taxonomic biases characterize current understanding.

Although many studies document that human-induced changes in land use alter bat species abundances and taxonomic dimension of biodiversity, surprisingly few studies have explored how these changes manifest with regard to genetic, behavioral, physiological, or disease-related phenomena. Similarly, little is known about the way in which land-use change affects functional or phylogenetic dimensions of biodiversity (but see Cisneros et al. 2015). Studies generally are not conducted in a spatially explicit manner (Fig. 4.4a), so multiscale (e.g., alpha, beta, and gamma diversities) or cross-scale interactions cannot be explored fully, and conclusions must be tempered in the absence of a more integrated understanding of the role of unmodified habitat in rescuing local populations from extinction. Key insights from landscape-scale studies comprise the species- and ensemble-specific nature of responses, as well as their dependence on spatial scale. The most fundamental developments include the recognition that habitat fragmentation is a complex process involving the nature of patches (i.e., landscape composition and configuration), as well as the nature of the matrix that arises as a consequence of direct, human modifications of the landscape (Fig. 4.4b). Finally, the consequences of changes in the bat fauna from habitat conversion and fragmentation have not been

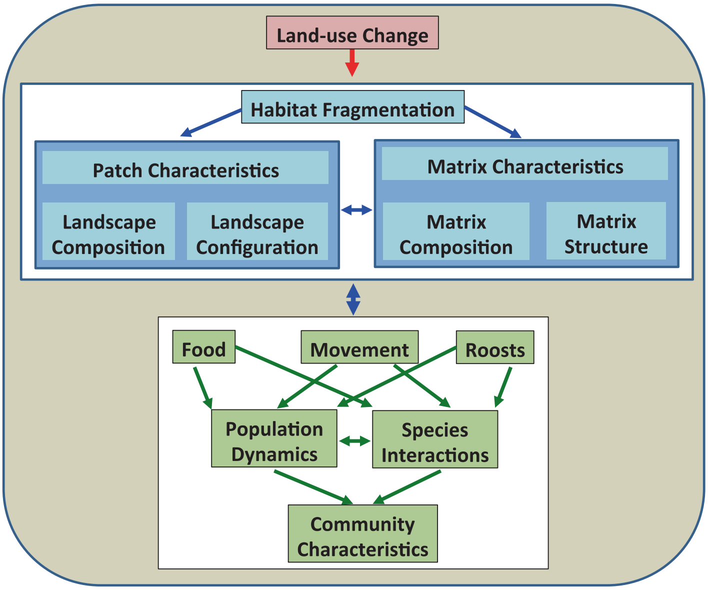
(a) APPROACHES THAT ARE NOT SPATIOTEMPORALLY EXPLICIT

Not Sensitive to Cross-Scale Interactions



(b) APPROACHES THAT ARE SPATIOTEMPORALLY EXPLICIT

Sensitive to Cross-Scale Interactions



◀ **Fig. 4.4** Two conceptual models that indicate the pathways whereby land-use changes affect bats in ways that **a** are not spatiotemporally explicit or **b** are spatiotemporally explicit. In both scenarios, effects of land-use change are mediated by alterations in the vegetation, but the underlying mechanisms differ (contrast the *purple boxes* with the *blue boxes*). Nonetheless, populations and assemblages of bats respond via similar mechanisms associated with feeding, roosting, and movement opportunities (*green boxes*). Generally, studies that explore the effects of habitat conversion (e.g., effects of logging or agriculture) on bats are not spatially explicit. Land-use change is reflected in habitat conversion that directly alters the composition and structure of the vegetation, with effects on the abundance and distribution of food resources or roosts, and the existence of "flyways" whereby bats navigate through the forest. In concert, these three characteristics affect the population dynamics of different bat species and the interaction likelihoods among species (e.g., bat species, other animal species, and disease-causing microorganisms). As a consequence, changes in bat species abundance distributions (e.g., richness, evenness, dominance, diversity, rarity) emerge with cascading effects on the vegetation as a consequence of altered seed dispersal, pollination, or regulation of insect herbivores. Generally, studies of habitat fragmentation are spatially explicit and explore how land-use change affects a focal habitat type (e.g., forest) by creating a network of patches embedded in a matrix of human-modified habitats. Such studies have the potential to explore how patch characteristics (e.g., landscape composition and configuration of forest patches) as well as matrix characteristics (e.g., structural or compositional attributes of the converted land) interact to affect the bat fauna. See text for additional details

quantified with regard to the maintenance of vital ecosystem processes or services. Clearly, we are still far from a comprehensive understanding of how tropical bats respond to habitat modification.

To advance ecological understanding, we have highlighted a number of more specific research needs across all themes in this chapter. We further stress the following key research directions as particularly worthy of pursuit, many of which have been summarized in different context for mammals in general (e.g., Willig 2001).

1. Geographic and taxonomic biases toward the Neotropics and a focus on just one bat family, Phyllostomidae, need to be overcome. Although research efforts in Southeast Asia are gaining momentum (Kingston 2013), Africa deserves greatly intensified research activities. As technological advances now make acoustic sampling of aerial insectivorous bats increasingly time- and cost-efficient, this ensemble should regularly be targeted in ecological research, including environmental impact assessments.
2. Research should be broadened to encompass the full spectrum of possible responses at the level of populations, ensembles, assemblages, and metacommunities. Novel mechanistic insights could be gained by studies that assess behavioral responses to particular types of habitat conversion or habitat fragmentation. Similarly, studies are needed to investigate physiological and immune responses, as well as disease susceptibility across a broad range of host and vector species. A better understanding of the genetic effects on bats from habitat modification requires integrated research on a suite of different species that explore the link between patterns of genetic variation and species' ecological and life-history traits. In general, the way in which species traits and

environmental factors interact to shape species responses to landscape change is unclear, as trait-based approaches have been rare (but see Farneda et al. 2015). Understanding how functional and phylogenetic biodiversity changes during habitat conversion and secondary succession is investigated rarely and remains poorly understood. Much also remains to be learned about how habitat disruption and modification affect the provisioning of critical ecosystem services, especially flower pollination and arthropod suppression.

3. Multiscale studies provide a more comprehensive understanding of pattern–process relationships in heterogeneous human-modified landscapes than do single-scale assessments. Future research should address bat responses to landscape change with respect to both spatial and temporal dimensions. Considerable progress in the field could be made by directing greater research effort and resources toward long-term studies that are capable of unveiling novel insights, which are hard or impossible to obtain from short-term, cross-sectional studies (cf. Lindenmayer et al. 2011). Studies currently underway at the Biological Dynamics of Forest Fragments Project (BDFFP) in Brazil (Meyer et al, unpublished data) or at the Stability of Altered Forest Ecosystems (SAFE) Project in Borneo (e.g., Struebig et al. 2013) provide examples of first efforts in this direction. The need for broader geographic coverage notwithstanding, directing more research to well-studied systems or long-term study sites, allows the responses of bats to land-use change to be compared to those of other taxa (e.g., Barlow et al. 2007; Bicknell et al. 2015; Ewers et al. 2015).
4. We stress the importance of robust study designs for assessing faunal responses to habitat alteration. Studies should have adequate replication (cf. Ramage et al. 2013) and involve controls or reference sites. Lack of controls is an important shortcoming of many of the reviewed studies, which often focused on comparisons of different types of disturbed habitats. This clearly limits their ability to ascribe observed effects to disturbance. We echo Kingston's (2013) call for studies to collect predisturbance, baseline information whenever possible, given that tropical bat assemblages exhibit considerable spatiotemporal variability even in unmodified habitats. In this context, Before–After–Control–Impact designs (e.g., Bicknell et al. 2015), in which sites affected by human disturbance are compared with undisturbed reference sites, both before and after impact, enhance inferential strength (Smith 2013), and add scientific rigor to future assessments of the effects of habitat modification on tropical bats.

Finally, an improved ecological understanding of bat responses to land-use change will be of little use to society unless it can be translated into improved management practices that ensure their long-term conservation and provision of critical ecosystem services. Across all themes in this chapter, we urge bat researchers to apply more of their science to policy and management questions. Examples of such applications include the effectiveness of specific management practices (e.g., farming intensity, cutting cycles) and mitigation measures (e.g., riparian conservation set-asides, artificial roosts).

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Chapter 5
Insectivorous Bats and Silviculture: Balancing Timber Production and Bat Conservation

Bradley Law, Kirsty J. Park and Michael J. Lacki

Abstract Forests are one of the most important habitats for insectivorous bats as they offer the potential for both roosting and foraging. We reviewed silvicultural literature from North America, Australia, and Europe and found that diverse research approaches have revealed commonalities in bat responses to forest silviculture. Almost all silvicultural treatments evaluated were compatible with some use by forest bats, though different bat ensembles respond in different ways. Ensemble ecomorphology was a consistent predictor of how bats respond to vegetative clutter and its dynamic changes as forests regenerate and develop a dense structure following harvesting. Sustaining high levels of bat diversity in timber production forests requires a mix of silvicultural treatments and exclusion areas staggered across the landscape, regardless of forest type or geographic region. Use of edge habitats, exclusion areas/set-asides, and riparian corridors for roosting and foraging by bats were consistent themes in the literature reviewed, and these habitat elements need to be considered in forest planning. Densities of hollow or dead trees sufficient to support large populations of roosting bats are unknown and remain a major knowledge gap, but will likely be species contingent. New paradigm shifts in forest management away from the use of even-aged systems to multi-spatial scale retention of mature forest including trees with cavities should be beneficial to bats, which are influenced by landscape-scale management. Such

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an approach is already in use in some regions, though there is a limited guidance on what constitutes a reasonable landscape threshold for retention. The effectiveness of such an approach will require long-term monitoring and research, especially with population studies which are currently lacking.

5.1 Introduction

Forests are one of the most important habitats for bats as they offer the potential for both roosting and foraging, and most species are reliant on forests for at least some part of their life cycle. Humans are also heavily reliant on the resources produced by forests, in particular timber. Consequently, forests are highly managed and modified in many areas. Understanding the effect that human manipulation of forested landscapes has on the resources required by bats is therefore of great importance to their conservation.

The use of silvicultural techniques to manipulate tree stands for timber production or biodiversity conservation goals presents several challenges. Forest bats are mobile and, as with forest birds, can use a large three-dimensional space to meet their life requisites (Kroll et al. 2012). Therefore, stand-level considerations alone are insufficient in sustaining habitat conditions for many forest bats as landscape-level needs are of equal or greater concern (Duchamp et al. 2007). Secondly, forest bats require roosting sites, high-quality foraging habitats, drinking sites, and features that provide connectivity among landscape elements. Providing all of these habitat requirements for an entire assemblage of bats simultaneously on a managed forested landscape is a difficult challenge, necessitating hierarchical approaches that assess spatial juxtaposition of habitat elements on the landscape and that implement silvicultural systems using multiple treatments applied both within and among stands.

Silvicultural practices vary greatly around the world. For example, in the northern hemisphere, clear felling typically results in cleared areas of 40–180 ha surrounded by relatively even-aged forests (Thomas 1988; Grindal and Brigham 1999; Swystun et al. 2001). In parts of Europe and North America, however, patch sizes are considerably smaller and some countries have abandoned clear felling altogether, favouring a more selective logging approach. Similarly, in parts of Australia, where broad scale clear-fall techniques are not utilised, selective logging results in a multi-aged forest (Nicholson 1999).

A key feature of insectivorous bats is their sophisticated sensory system, which enables them to navigate and forage in the dark. The foraging efficiency of echolocating bats is constrained by variations in vegetation because the echoes returning from prey need to be distinguished from background echoes returning from vegetation. These ‘clutter’ echoes can mask the echoes of prey making foraging inefficient in situations where vegetation is dense (Schnitzler et al.

2003). Forest bat species differ in echolocation signal design and wing morphology and this influences their flight behaviour and their tolerance to clutter, allowing classification into three broad foraging ensembles: (1) closed-space species are slow flying and highly manoeuvrable bats that can forage close to vegetation; (2) edge-space species exploit edge habitat and other linear features; and (3) open-space foragers have lower manoeuvrability and fly faster above the forest canopy or within large gaps in the forest. Changes to forest structure that influence the degree of clutter can, therefore, alter the availability of foraging habitat for each ensemble.

Our aim in this chapter was to explore how insectivorous bats respond to different silvicultural approaches used in forests around the world, incorporating studies within natural, or semi-natural, forests to intensive management within plantation forestry. We focus on three broad areas: North America, Australasia (including New Zealand), and Europe and refer the reader to Meyer et al. (2016) (Chap. 3) for tropical forests. While the majority of studies included in this review are published in scientific journals, we also include information from the grey literature (e.g. reports, conference proceedings, and unpublished theses) and some unpublished data where appropriate.

We look to highlight both commonalities and differences in the various approaches to the issue in different regions. We suggest that ecomorphology is one of the keys to understanding how bats use their environment and we use ecomorphological traits as a framework for predicting how the three broad functional ensembles of bats respond to forest logging (Hanspach et al. 2012; Luck et al. 2013). Conceptual models have been proposed previously for the relationship between the abundance of bats and key ecological resources manipulated by forest management (Fig. 5.1; Hayes and Loeb 2007). These posit the influence of thresholds for certain variables such as water availability, where further increases do not result in increased bat abundance. We assess the extent to which these models fit current data and extend them to (1) consider the time since logging as a response variable and (2) include an ecomorphological framework for the response of bats. We emphasise the importance of a long-term perspective when assessing bat responses in forests given that forests are long-lived ecosystems that undergo dynamic changes after disturbance. Finally, we consider the merits of multi-spatial scale management for bats and recommend future areas of research to advance the effective management of this diverse and functionally important group. There is some specialised terminology within this chapter that may be unfamiliar to those new to silvicultural literature, so we have provided a glossary at the end of the chapter with definitions. While the term woodland is often used to describe vegetation communities comprising trees but with a more open and lower canopy cover than forests, this definition varies by country. Here, we use the term forest to encompass the various definitions of woodland.

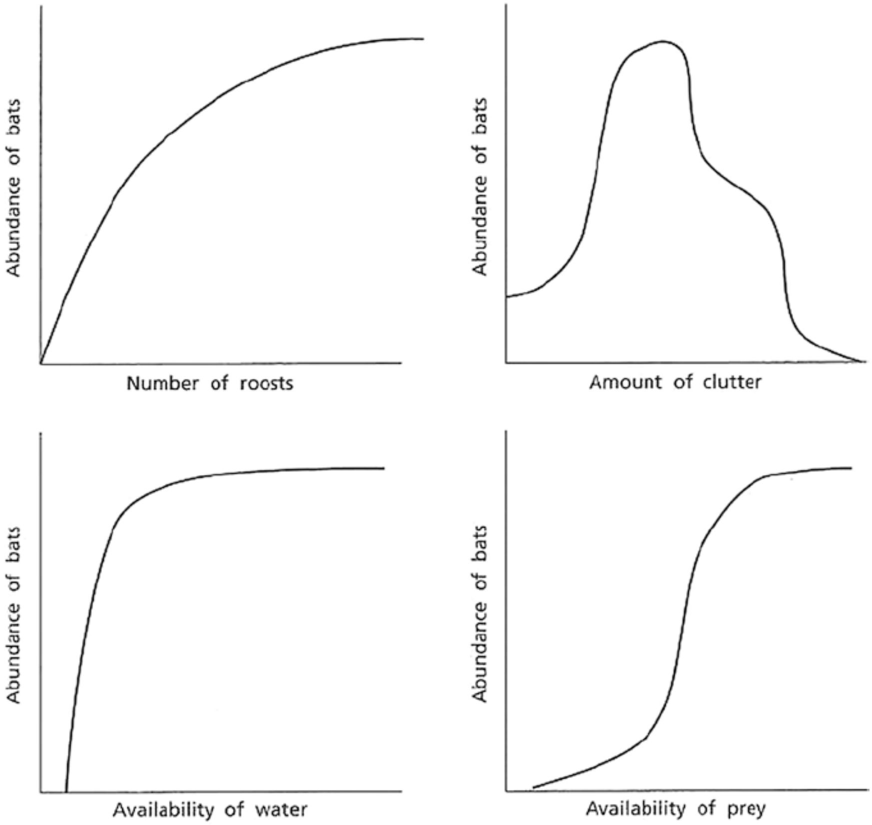

Fig. 5.1 Conceptual models illustrating hypothesised relationships among the abundance of bats and ecological resources within forests (Hayes and Loeb 2007)

5.2 Major Forest Areas

5.2.1 North America

Management of forests in North America is undergoing a renaissance, of sorts, as threats associated with habitat loss and fragmentation, climate change, increased fire frequency, and introduction of forest insect pests are leading to paradigm shifts in how forests should be managed to sustain biodiversity, increase carbon sequestration, and maintain the capacity for resource extraction (Boerner et al. 2008; Parks and Bernier 2010; Moore et al. 2012). Historically, even-aged management was practiced across the continent with clearcuts, shelterwood cuts, seed-tree cuts, and deferment cuts all used in management of forests regardless of region or forest type. These practices have reached their zenith in south-eastern pine plantations where production forestry has led to short rotation harvests of monotypic stands of loblolly pine, *Pinus taeda* (Wear and Greis 2013). More recently, silvicultural approaches have focused on mimicking natural disturbance events or ecologically based forestry (Mitchell et al. 2002; Long 2009), resulting in application of uneven-aged or multi-aged silvicultural systems (O'Hara 2002, 2009), and prescribed fires (Boerner et al. 2008), in both pine and hardwood forests. North America is >24 million km^2 in total land surface and lies entirely within the northern hemisphere. The continent supports a rich diversity of plant species across eight major forest types (Young and Geise 2003, Fig. 5.2) with each type encompassing from 1 to 8 subtypes (SAF 2010). Latitude plays a prominent role in the distribution of forest types across the continent, with a north-to-south pattern of northern coniferous, northern hardwood, central broad-leaved, oak–pine, bottomland hardwood, and tropical forests (Young and Geise 2003). Two other forest

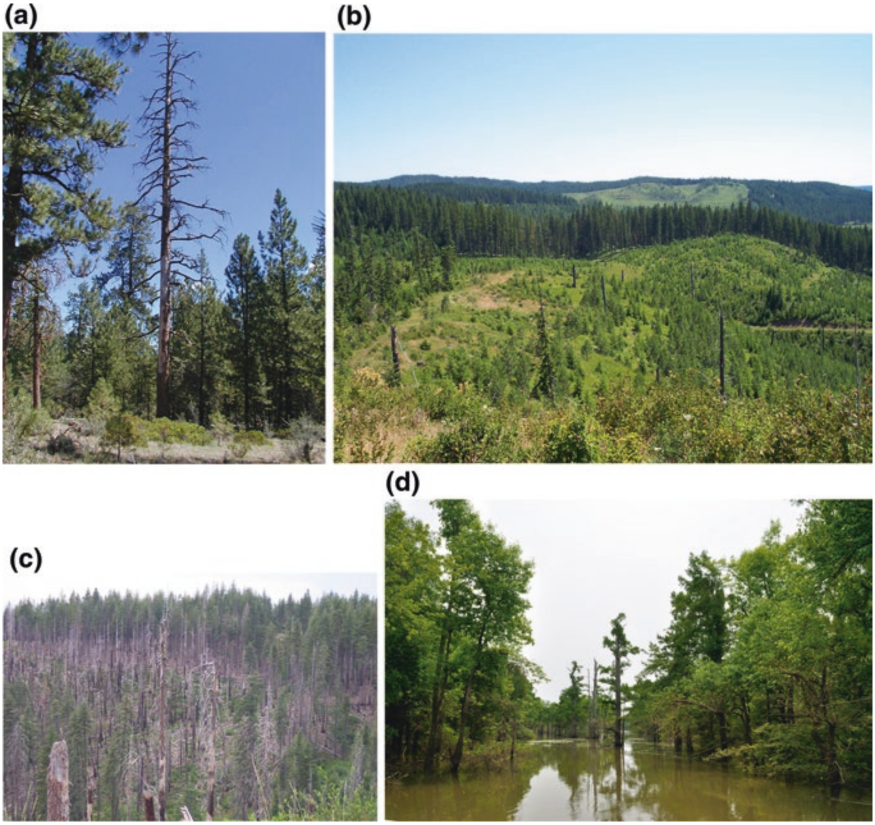

Fig. 5.2 **a** Standing dead ponderosa pine (*Pinus ponderosa*) used as a roost tree by long-legged myotis (*Myotis volans*) in Oregon, **b** forested landscape treated using clearcut logging in Idaho with natural regeneration present, **c** stand of dead trees in California typical of habitats used by bark- and cavity-roosting bats in western coniferous forests, and **d** bottomland hardwood forest in Western Kentucky, with hollow roost tree of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in the centre. *Photograph credits* M. Baker (**a**), M. Lacki (**b**, **c**), and J. Johnson (**d**)

types, Pacific coast and Rocky Mountain, are distributed largely in a north–south direction paralleling several mountain ranges and, thus, cross a greater expanse of latitudes. The northern coniferous and boreal forest, dominated by spruce, fir, and larch, covers the largest extent of North American land surface of any forest type, followed by Rocky Mountain and central broad-leaved forests. Rocky Mountain forests are dominated by pines across much of their range, with central broad-leaved forests supporting oaks, hickories, maple, and beech. Bottomland hardwoods, comprising gums, bald cypress, oaks, and willows, represent the smallest land area of any major forest type in North America (1.25 million ha remaining; Mississippi Museum of Natural Science 2005). Globally, North America has experienced some of the greatest forest losses with a 5.1 % decline in forest land cover from 2000 to 2005 (Hansen et al. 2010). Declines in forest cover have been greatest in the south-eastern USA, where 3.5 million ha have been lost from 1992 to 2001 (World Resources Institute 2014). Recent shifts in the region-wide approach to management of south-eastern bottomland hardwood forests, however, have brought about a reversal in the trend of loss of these forests (USDA Forest Service 2009; Miller et al. 2011).

5.2.2 Europe

Europe consists of 50 countries and is just over 10 million km^2 in land area. Forests cover approximately 45 % of the land area, most of which is found within the Russian Federation which comprises 40 % of the land area of Europe (FAO 2012). Europe’s native forest is very diverse with 13 broad categories encompassing 74 types (EEA 2006). Boreal forest consisting primarily of spruce or pine species dominates in northerly latitudes that comprise Scandinavia (Fig. 5.3). This is replaced by hemiboreal forest and nemoral coniferous and mixed broad-leaved/coniferous forest in southern Sweden and much of eastern central Europe, with alpine coniferous forest along the mountain ranges. Moving west, mesophytic deciduous and beech forest dominates, but there is increasing amounts of plantation forest. In the southern parts of Europe coniferous (pines, firs, junipers, cypress, cedar), broadleaved (oak, chestnut) and evergreen broadleaved forests are the main wooded habitats. Parts of Europe have undergone extensive deforestation and cover has been fragmented and depleted for several centuries. While 26 % of Europe’s forest area is classified as primary, this falls to <3 % excluding the Russian Federation, and approximately 52 % of all forests in Europe are now designated primarily for production (FAO 2012). In Europe, as in North America and Australia, there is growing interest in silvicultural practices that mimic natural forest ecosystem processes with the aim of developing mixed, structurally diverse stands (Lähde et al. 1999). This is a result of a move away from treating forests, particularly plantations, solely as a resource for timber, and an increased emphasis on sustainable management for multiple objectives including biodiversity conservation and recreation (Mason and Quine 1995). In practice, this has meant a

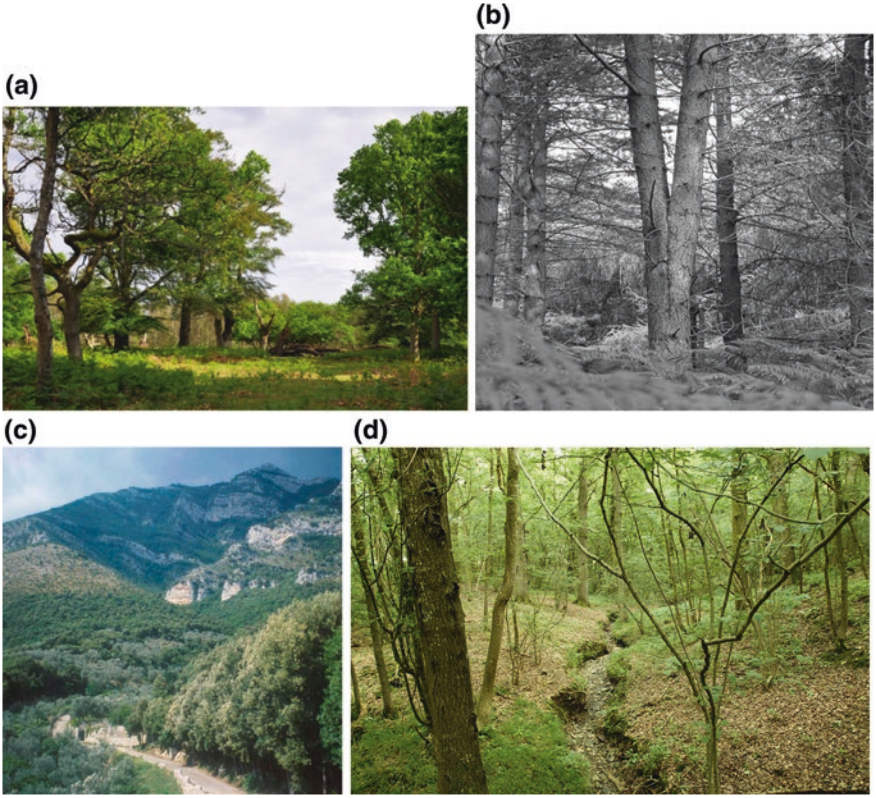

Fig. 5.3 **a** New Forest, United Kingdom: wood pasture, a historical European land management system providing shelter and forage for grazing animals as well as timber products, **b** double-leadered Corsican pines (*Pinus nigra* ssp. *laricio*) are used as roost sites by Natterer's bats (*M. nattereri*) in Tentsmuir forest in Scotland, UK; **c** wooded landscape, including olive groves, used extensively in southern Italy by *Rhinolophus euryale*; **d** typical Bechstein's bat (*Myotis bechsteinii*) foraging habitat in England, UK: a mixture of oak (*Quercus robur*) and hazel (*Corylus avellana*) woodland. *Photograph credits* J Sjolund, G Mortimer (**b**), D Russo (**c**), F Greenaway (**d**)

reduction in clear felling, although this varies greatly between countries. For example, it has been largely phased out in Switzerland and Slovenia, but is still the primary form of logging in the UK (Fries et al. 1997; Mason et al. 1999), but recent modifications include retaining stands with longer rotations where possible (Mason and Quine 1995), reducing the removal of deadwood (Humphrey and Bailey 2012), and techniques geared to mimic natural disturbance such as prescribed burning.

5.2.3 Australia

It is estimated that forests covered about a third of the Australian continent at the time of European settlement in 1788, but by the mid-2000s this had been reduced to about 19 % cover (Montreal Process Implementation Group for Australia 2008). Five million hectares of forest are classified as old growth (22 %) and over 70 % of these occur in conservation reserves. Timber harvesting on public land is now restricted to 9.4 million ha, or about 25 % of the areas potentially suitable for timber production, and much of this has been previously logged. Eucalypts dominate the forests of Australia, and they are highly diverse comprising 500–600 species (Fig. 5.4, Florence 1996). Eucalypt forests range from those with a high diversity of eucalypt species to those dominated by one or a few species, the latter most often occurring in the tall wet forests of temperate southern Australia, including Tasmania (Florence 1996). These different eucalypt species and forest communities grow on different soils, under varying climates and natural disturbance regimes that in turn influence the variety of silvicultural practices applied. Fire is

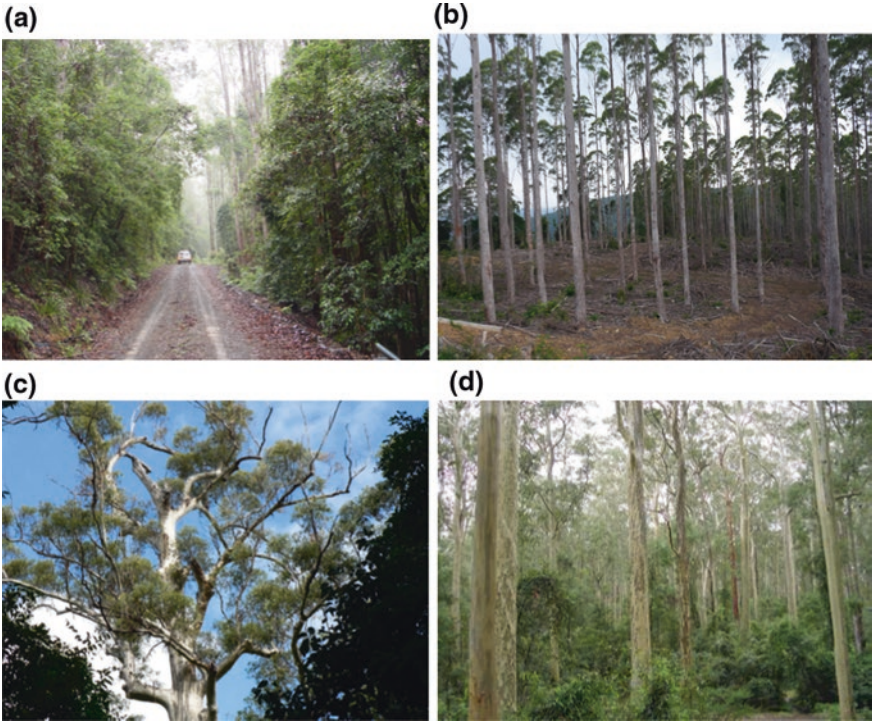

Fig. 5.4 Eucalypt forests of Australia: **a** narrow vehicle tracks through regrowth wet sclerophyll forest are used extensively by bats; **b** recently thinned regrowth forest potentially increases flight space and foraging opportunities for bats; **c** senescing crown of a Blackbutt *Eucalyptus pilularus* supports multiple hollow branches where bats, including maternity colonies, selectively roost; **d** an old-growth, spotted gum forest, *Corymbia maculata,* supports high densities of hollows and an open zone above a dense understorey/shrub layer, providing a variety of niches for foraging and roosting bats. *Photographs* B. Law

also a driving force behind the distribution and composition of eucalypt forests, and it occurs as massive wildfires that sweep across the landscape and less intensive prescribed burns that aim to reduce fuel loads and minimise damaging wildfires. To some extent, silvicultural practices aim to mimic these disturbance events and maximise regeneration after harvest.

Silviculture of Australian eucalypts is thus highly variable, although the techniques applied largely resemble those used elsewhere around the globe. For example, silviculture varies from clearcut practices in the tall wet eucalypt forests of temperate southern Australia (Tasmania and Victoria) to group selection and single tree selection in warm temperate and subtropical areas to the north. Clearcuts aim to mimic broadly the massive stand replacement events created by wildfires, which are an irregular feature of tall eucalypt forests in Australia. However, one important difference between clearcuts and wildfires is that wildfires leave legacies in the form of dead trees with hollows that can remain standing for decades. Regrowth after harvesting may take many decades to self-thin sufficiently for the forest to begin to resemble the openness of mature or unlogged forest (Florence 1996). Selective logging can occur at a range of intensities that are almost a continuum from very low levels of tree removal targeting specific size/species of trees with ~10 % of tree basal area removed to almost a seed-tree retention silviculture with >60 % of stand basal area removed. In selectively harvested forests, nominal ‘rotations’ are about 60–80 years though these develop from repeated logging visits to the same coupes every 10–30 years to produce a dynamic of multi-aged mosaics of even-aged regeneration cohorts (Curtin et al. 1991). Selective logging is most commonly applied to forests comprising mixed eucalypt species and uneven ages. Rainforest has a restricted occurrence in Australia, and logging of this forest type is no longer permitted.

5.3 Complexity of Bat Habitat Needs

5.3.1 Mature, Large Diameter Trees

Older age classes of trees, especially old-growth forests, have historically been viewed as important habitats for bats (Altringham 1996; Fisher and Wilkinson 2005; Hayes and Loeb 2007) and are likely to contain a greater diversity and abundance of insect prey (e.g. Fuentes-Montemayor et al. 2012; Lintott et al. 2014). Early studies demonstrated variation in bat activity across stands of different age classes, with the levels of bat activity higher in older, mature stands than young stands (Thomas 1988; Erickson and West 1996; Crampton and Barclay 1998; Law and Chidel 2002). Older forests possess canopies that are more fully developed than regenerating or early-seral forests, with complex crown architecture (Wunder and Carey 1996). Old-growth forests are also likely to contain a larger number of microhabitats which are associated with higher bat species richness and higher levels of activity in common and Nathusius pipistrelles, *Pipistrellus pipistrellus* and *P. nathusii*, in oak, *Quercus* spp., forests in southern France managed for coppice (Regnery et al. 2013a). In a parallel study, time since cutting was the best predictor of the number of tree microhabitats which were 13 times more abundant in stands >90 years post-cutting, than those <30 years in age (Regnery et al. 2013b).

Considerable research has been undertaken on roost selection since pioneering radio-tracking studies in Australia (Lunney et al. 1988; Taylor and Savva 1988). A consistent trend throughout the world is that most bats prefer to roost in larger diameter trees (>30 cm, Russo et al. 2004; ~80 cm, Baker and Lacki 2006; see also Kalcounis-Rüppell et al. 2005), often in older forest stands or mature forests (Lunney et al. 1988; Taylor and Savva 1988; Brigham et al. 1997; Betts 1998; Crampton and Barclay 1998; Sedgeley and O'Donnell 1999; Law and Anderson 2000; Lumsden et al. 2002; Mazurek and Zielinski 2004; Russo et al. 2004, 2010; Ruczyński et al. 2010). Such trees have a greater likelihood of supporting larger populations of roosting bats and persist for longer than smaller diameter dead trees (Lacki et al. 2012); thus, their identification and provision in residual patches during timber harvesting is important. Where mature forest is absent across large areas at least some species find roosts in scattered hollow trees in regrowth forest where habitat trees were not specifically retained, indicating that bats typically roost in the largest available trees. One Australian study found that the 4-g eastern forest bat, *Vespadelus pumilus*, which ranges over relatively small areas, maintains similar sizes of maternity colonies in the scarce roosts remaining within regrowth forest compared to maternity colonies in old-growth forest (Law and Anderson 2000). Russo et al. (2010) found evidence of roost selection flexibility in barbastelle bats, *Barbastella barbastellus*; dead and dying trees, a favoured roost site for this species, were six times more common in unmanaged than managed European beech, *Fagus sylvatica*, forests in central Italy. Bats, however, were able to roost within managed forest, albeit in smaller numbers by exploiting roost sites in live trees and rock crevices. Few studies have investigated roost selection in younger forest where roosts are scarce, so generalisations are difficult (although see section on Plantations below).

5.3.2 Deadwood Availability and Hollow Tree Density

Until the late twentieth century, in many parts of Europe and North America, deadwood in managed forests was removed due to concerns over forest health. While this is still common practice in some areas, the key role played by dead and decaying wood in the functioning and productivity of forest ecosystems, and its importance for biodiversity, has gained increasing recognition over the past 20 years (Humphrey 2005). In Australia, deadwood removal has been confined to plantations, though recognition of the importance of specifically retaining old trees with hollows in managed forests originated in the 1980s. A preference for roosts in dead and dying trees has been noted for *Barbastella* and *Nyctalus* species in Europe (Russo et al. 2004; Ruczyński and Bogdanowicz 2008; Hillen et al. 2010), and high densities of dead trees appear to be strongly correlated with the presence of roosts of bark and cavity-roosting bats in forested ecosystems across North America (Mattson et al. 1996; Sasse and Pekins 1996; Rabe et al. 1998; Waldien et al. 2000; Cryan et al. 2001; Bernardos et al. 2004; Broders and Forbes 2004; Miles et al. 2006; Perry and Thill 2007b; Arnett and Hayes 2009).

The importance of high roost density has also been reported in Australia. In dry Jarrah forest of Western Australia, both Gould's long-eared bat, *Nyctophilus gouldi*, and the southern forest bat, *Vespadelus regulus*, preferred roosting in older forest that contained a much higher density of trees with hollows (16–32 trees ha^{-1}) than shelterwood creation and gap release sites (8–12 trees ha^{-1}) (Webala et al. 2010). These mature forest hollow tree densities are comparable to average densities of live and dead hollow trees in roost areas used by Gould's wattled bat, *Chalinolobus gouldii*, (17 ha^{-1}) and the lesser long-eared bat, *N. geoffroyi*, (18 ha^{-1}) in a fragmented landscape in south-eastern Australia (Lumsden et al. 2002). Greater densities of hollow trees likely facilitate roost switching in bark and cavity-roosting bats or fission–fusion behaviours (Kerth and König 1999; Willis and Brigham 2004). These behaviours lead to complex patterns of use and movement among available roost trees by colonies of forest bats. The variation in numbers of roosts between core and peripheral areas of roost networks is further influenced by the density and spatial distribution of available roost trees, as demonstrated for Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, in south-eastern bottomland hardwood forests of North America (Johnson et al. 2012b). Roost networks of northern long-eared bat, *Myotis septentrionalis*, in actively managed forests were scale-free and connected to a single central-node roost tree (Johnson et al. 2012a). A similar pattern was observed for the open-space foraging white-striped free-tail bat, *Tadarida australis*, in south-east Queensland (Rhodes et al. 2006). Given these patterns, we postulate that implementation of silvicultural systems, which promote retention of higher densities of dead and old living trees across forested ecosystems, should benefit bark- and cavity-roosting bats and facilitate 'natural patterns' in colony behaviours, social interactions, and the use of roost networks.

5.3.3 Understory Vegetation

The extent and composition of understory vegetation in forests strongly influences insect prey availability, the ability of bats to access the forest interior, and the microclimates available and is also likely to affect risk of predation. The degree to which understory cover affects the use of forests by bats depends greatly on their wing morphology and foraging behaviour, with some bats benefitting from a more open forest with little in the way of cover, while other species rely heavily on a well-developed dense understory (e.g. Hill and Greenaway 2008; Müller et al. 2012). Vegetation structure revealed by LiDAR in Germany indicated that while high levels of understory cover were preferred by edge-space and gleaning species, open-space foragers were more associated with relatively open forest stands (Jung et al. 2012). Foraging intensity also varies with canopy height, with the activity of open-space foragers highest above the canopy (Kalcounis et al. 1999; Müller et al. 2013), although few studies have surveyed bats at those heights. Similarly, in forest fragments in Scotland (UK), high activity levels of edge-space species, e.g. *Pipistrellus* spp., are related to low tree densities and an open understory, while closed-space gleaning species, e.g. Natterer's bat, *Myotis nattereri*, showed the opposite trend. These studies are supported by numerous species-specific studies. For example, roosts of Bechstein's bat, *Myotis bechsteinii*, and the barbastelle bat, *B. barbastellus*, are strongly associated with areas of thick understory (Greenaway and Hill 2004), and core foraging areas for brown long-eared bat, *Plecotus auritus*, a closed-space species, were associated with more cover and a well-developed understory layer more than peripheral areas (Murphy et al. 2012). An Australian study of vertical stratification (excluding above the canopy) in spotted gum forest also found the understorey to support the greatest insect abundance, although bat activity was up to 11 times greater in the canopy where there was less clutter and presumably insects were more accessible (Adams et al. 2009). There was no evidence that any one ensemble or ensemble species foraged exclusively at a particular height, although the open-space ensemble was most activity in the canopy.

5.3.4 Slope and Aspect

Slope and aspect influence roost selection in forest bats by creating variation in the amount and extent of solar heating at roosting sites due to differences in shading effects and the length of the day that roosts are in direct sunlight. Studies have demonstrated the importance of both slope position and reproductive stage in roost selection. For example, long-legged myotis, *Myotis volans*, in the northwestern USA switch between riparian bottoms and upper-slope positions during pregnancy, but select roosts in upper-slope positions during lactation, where they would be exposed to greater solar radiation (Baker and Lacki 2006). Studies of bats in south-eastern forests of North America have also observed preferences for roosting in upper-slope positions by foliage-roosting eastern red bat, *Lasiurus borealis*, and bark- and cavity-roosting bats (*Myotis* and *Eptesicus*) (Hutchinson and Lacki 2000; Lacki and Schwierjohann 2001; Perry et al. 2008), suggesting that higher slopes are important for roost selection in some forest bat species in both eastern and western parts of North America and should be accounted for in forest planning. Use of lower slope positions and riparian corridors for roosting is common in several bats in eastern and south-eastern forests, however, including bark- and cavity-roosting (Watrous et al. 2006; Perry and Thill 2008; Fleming et al. 2013) and foliage-roosting species (Perry et al. 2007a; Hein et al. 2008b; O'Keefe et al. 2009). Roosting on lower slopes was also found in a subtropical Australian forest, where lactating eastern forest bats, *V. pumilus*, roost in hollow trees in riparian zones during early summer, but shift up-slope during autumn when bats begin to mate (Law and Anderson 2000). Riparian zones may provide more buffered conditions for maternity roosts in warm, subtropical locations.

In the northern hemisphere, selection of south-eastern-facing (Willis and Brigham 2005), south-facing (Klug et al. 2012), and eastern-facing (Perry and Thill 2007a) sides of tree canopies by hoary bats, *Lasiurus cinereus*, is associated with positive energy savings and is hypothesised to facilitate rapid growth of young (Klug et al. 2012). Eastern red bat, *L. borealis*, another foliage-roosting species, was observed using the south aspect of tree canopies that were also located in south-facing slope positions (Mormann and Robbins 2007). Collectively, these behaviours suggest consideration be given to creating and maintaining edge habitats for foliage-roosting bats at the landscape scale, especially along south-facing slopes in the northern hemisphere in areas with sufficient topographic relief.

5.3.5 Forest Edge

Loss and fragmentation of forest habitat are accompanied by an increase in the ratio of forest edge to interior forest, and the response of bats to this can vary among species. Roosting ecology and edge-affinity have been identified as good predictors of the sensitivity of individual bat species to habitat fragmentation; 'forest interior' species (often tree-roosting bats) are negatively affected by fragmentation, as opposed to species which show affinity for forest edges (Meyer et al. 2008).

Edge habitats can influence roosting behaviour in bark- and cavity-roosting *Myotis* species differently. Indiana bat, *M. sodalis*, and northern long-eared bat, *M. septentrionalis*, two species with overlapping distributions in North America and similar preferences for roosting in dead trees (Foster and Kurta 1999; Lacki et al. 2009), choose roosts differently in the same forested landscapes. *M. sodalis* prefers roosts in edge habitats with low vegetative clutter and higher solar exposure of roost trees and *M. septentrionalis* selects roosts in shaded environments within intact forests (Carter and Feldhamer 2005). Russo et al. (2007) found that barbastelle bat, *B. barbastellus*, emerged later from tree roosts in more open forests, probably as a result of increased predation risks, and suggested that it was important to ensure canopy heterogeneity to provide a range of roosting conditions. Edge effects also influence foraging behaviour in forest bats although results from studies comparing bat activity at the edge compared to forest interior show contrasting results; all five species spanning the open/edge-space/closed-space spectra that were assessed in forests in Canada showed higher activity at the forest edge than in the interior (Jantzen and Fenton 2013). Bat activity was also high along coupe edges 5–8 years after clear fell in Tasmania (Law and Law 2011), partly because bats avoided the large harvested gaps in these coupes. In contrast, of three species surveyed within forest fragments on farmland in the UK, one edge-space species showed similar levels of activity at edge verses interior while the other two species (one edge-space and one closed-space) showed higher levels of activity within the forest interior (Fuentes-Montemayor et al. 2013). In Australia, harvested forests are often interspersed with old logging trails and fire trails, providing 'edge habitats' that facilitate the use of dense forest regenerating after harvest by bats that possess a range of traits (Crome and Richards 1988; Law and Chidel 2002; Webala et al. 2011). Activity on trails in regrowth forest is as high as it is in mature forest. Most importantly, foraging activity is typically much higher on forest trails than within the forest remote from trails or along narrow riparian zones (Law and Chidel 2002; Lloyd et al. 2006; Webala et al. 2011). Use of trails as linear edges in regenerating forest has also been reported in North America (Menzel et al. 2002). These observations highlight the importance of edge habitats to many bat species within each ensemble, in all the regions covered in this chapter.

5.4 Bat Responses to Silvicultural Treatments

Silviculture involves a diverse range of techniques to manipulate growth conditions, extract resources, and facilitate regeneration within forests. These influence the composition and density of tree species present, the extent and composition of the understorey vegetation and ultimately the resources available for bats. Here, we focus on the techniques for which there is at least some information on the response of bats to (1) different logging strategies, (2) thinning regimes, and (3) the use of harvest exclusion areas. We also examine the use of timber plantations by bats which, in some regions, is the focus of silvicultural activities. There is very little information on the effects of other techniques such as coppice and the use of chemical applications (e.g. herbicides to clear vegetation), and we highlight important knowledge gaps in the concluding section.

5.4.1 Logging

Historically, the strategy for logging in forest managed for timber extraction was to remove all trees within an area (clearcuts) as this is considered the most economically profitable method. In production State Forests in Australia, selective harvesting was most common before World War II, but it was subsequently recognised that this adversely affected the regeneration and growth of many of the fastest growing, commercial species, which subsequently led to increased intensity of harvests. Recent concern over the environmental (including biodiversity loss and soil erosion) and visual impacts, however, has led to increased use of more selective forms of logging including variable retention and group selection techniques, which are reviewed here.

A review of published data sets on response of forest bats to silvicultural logging indicates that there are major gaps in our understanding of relationships of bats with timber harvesting practices (Table 5.1). In particular, there is a notable

Table 5.1 Summary of bat response in activity and roost selection to silvicultural treatments referred to in this review for North America and Australasia

Treatment(s)	Treatment conditions	Forest type	Bat species	Bat response	Source
Bat activity					
Even-aged treatments					
North America					
Clearcut	30 ha	Pacific coast	*M. lucifugus*	None	Lunde and Harestad 1986
Clearcut	Not defined	Northern hardwood	*L. borealis*	Decrease	Hart et al. 1993
			L. cinereus	Increase	
			Myotis sp.	Decrease	
Clearcut	2–3 years old	Pacific coast	*E. fuscus*	Increase	Erickson and West 1996
			L. noctivagans	Increase	
			C. townsendii	Increase	
Clearcut	Not defined	Northern coniferous	Multiple	Mixed	Grindal 1996
Clearcut	Along streams	Pacific coast	*Myotis* sp.	Decrease	Hayes and Adam 1996
Clearcut	5–17 years old	Pacific coast	Multiple	Decrease	Parker et al. 1996
Clearcut and residual patches	Varied patch isolation	Northern coniferous	Multiple	Mixed	Swystun et al. 2001
Clearcut and residual patches	8–10 ha; 1.5 years old; 0.2–0.46 ha	Northern hardwood	*M. lucifugus*	Increase	Hogberg et al. 2002
			M. septentrionalis	Increase	
			L. noctivagans	None	
Clearcut	10 ha	Northern coniferous	*L. noctivagans*	Increase	Patriquin and Barclay 2003
			M. lucifugus	Increase	
			M. septentrionalis	Decrease	
Clearcut; deferment harvest	5 years old; 6–10 m^2/ha residual	Northern hardwood	*L. cinereus*	Increase	Owen et al. 2004
			L. noctivagans	Increase	
			Myotis sp.	None	
Shelterwood harvest	10 ha; 30–50 % decline in volume	Central broad-leaved	*L. borealis*	Increase	Titchenell et al. 2011
			L. noctivagans	Increase	
			E. fuscus	Increase	

(continued)

Table 5.1 (continued)

Treatment(s)	Treatment conditions	Forest type	Bat species	Bat response	Source
Seed-tree and shelterwood harvest	7.7 m^2/ha residual; 18 m^2/ha residual	Northern hardwood	Multiple	Increase	Dodd et al. 2012
Australasia					
Clearcut; post-wildfire	0–250 years old	Tall mountain ash eucalypt	Total activity	Increase with age	Brown et al. 1997
Clearcut and Variable retention	10–27 ha; 8 years old; 0.5–1 ha retention	Tall wet eucalypt forest	Multiple	Mixed	Law and Law 2011
Plantations	Non-commercial mixed; <10 and 20–25 years old	Eucalypts	Multiple	Positive, older plantations	Law and Chidel 2006
Plantations	Low rainfall monoculture; <11 years old	Eucalypts	Multiple	Neutral	Law et al. 2011
Uneven-aged treatments					
North America					
Group selection cuts	0.1–0.8 ha; ≤9 years old	Northern hardwood	Multiple	Increase	Krusic et al. 1996
Group selection cuts	60 % decline in volume	Northern coniferous	Multiple	Increase	Perdue and Steventon 1996
Small cutblocks	0.5–1.5 ha	Northern coniferous	Multiple	Increase	Grindal and Brigham 1998
Group selection cuts	0.02–0.5 ha gaps	Southern oak–pine	Multiple	Increase	Menzel et al. 2002
Canopy gaps	16–33.5 m wide	Northern hardwood	*E. fuscus*	Increase	Ford et al. 2005
			L. cinereus	Increase	
			Myotis sp.	Decrease	
Australasia					
Selective	18 % basal removal 1–6 years old	Tropical rainforest	Multiple	Mixed	Crome and Richards 1988
Selective	3 age classes	Wet sclerophyll eucalypt	Multiple	Mixed	de oliveira et al. 1999
Alternate coupe	15 ha coupes, 22 years old	Dry sclerophyll eucalypt	Multiple	Mixed	Law and Chidel 2001

(continued)

Table 5.1 (continued)

Treatment(s)	Treatment conditions	Forest type	Bat species	Bat response	Source
Group selection/plantation/old growth	13–97 ha catchments; 16 years old; tracks versus interior	Wet sclerophyll eucalypt	Multiple	Mixed	Law and Chidel 2002
Group selection cuts	3 age classes; riparian buffers 10–50 m	Wet and dry sclerophyll eucalypt	Multiple	Mixed	Lloyd et al. 2006
Group selection cuts	Old vs young regrowth; tracks vs interior; vertical stratification	Spotted gum eucalypt	Multiple	Mixed	Adams et al. 2009
Gaps and shelterwood	3 age classes; gaps <10 ha; tracks vs interior	Dry sclerophyll eucalypt	Multiple	Mixed	Webala et al. 2011
Variable retention	10–100 % retention; 100 ha blocks	Tableland eucalypt	Guilds	Mixed	Law unpubl. data
Intermediate treatments					
North America					
Thinning	10–13 years old	Pacific coast	Multiple	Increase	Erickson and West 1996
Thinning	≥10 ha; 55 % decline in density	Pacific coast	Multiple	Increase	Humes et al. 1999
Thinning	25 % decline in density;	Northern coniferous	Multiple	None	Patriquin and Barclay 2003
Thinning	45 % decline in density	Northern pine plantation	Multiple	None	Tibbels and Kurta 2003
Thinning	18 m^2/ha residual	Southern oak–pine	*E. fuscus*	Increase	Loeb and Waldrop 2008
			L. borealis	Increase	
			P. subflavus	None	
Salvage logging	Control, moderate, and heavily logged sites × 4 replicates (12–16 ha); 1 year post-fire	Douglas, white and ponderous fir	Multiple	Positive	Hayes 2009

(continued)

Table 5.1 (continued)

Treatment(s)	Treatment conditions	Forest type	Bat species	Bat response	Source
Australasia					
Thinning	4–9 years old	Spotted gum eucalypt	Multiple	None	Adams and Law (2011)
Europe					
Salvage logging	4 stand types varying by logging & structure × 8 replicates (5 + ha each)	Norway spruce, beech and silver fir	Multiple	Varied between foraging guilds	Mehr et al. 2012
Roost selection					
Even-aged treatments					
North America					
Clearcut	7–18 ha	Northern coniferous	*M. evotis*	Positive, tree stumps	Vonhof and Barclay 1997
Cutblocks with residual patches	Not defined	Northern coniferous	*Myotis* sp.	Positive, edges	Grindal 1999
Australasia					
Clearcut	11 years old	Dry sclerophyll eucalypt	Multiple	Positive, mature forest and diameter	Taylor and Savva 1988
Plantation/ regrowth versus old growth	30 years old	Wet sclerophyll forest	*V. pumilus*	Positive, gullies and diameter	Law and Anderson 2000
Plantation	Exotic; mosaic age classes	*Pinus radiata*	*C. tuberculatus*	Positive, old age classes and near water	Borkin and Parsons 2011b
Uneven-aged treatments					
North America					
Group selection and thinning	13.8 m^2/ha residual	Southern oak–pine	*M. septentrionalis*	Positive	Perry and Thill 2007b
Group selection and thinning	13.8 m^2/ha residual	Southern oak–pine	5 of 6 species	Positive	Perry et al. 2008
Australasia					
Alternate coupe	10–20 ha; 2–3 years old	Dry sclerophyll eucalypt	*N. gouldi*	Positive, gullies and diameter	Lunney et al. 1988

(continued)

Table 5.1 (continued)

Treatment(s)	Treatment conditions	Forest type	Bat species	Bat response	Source
Gaps and shelterwood	gaps <10 ha; buffers; 20–30 years old	Dry sclerophyll eucalypt	*V. regulus*	Positive, mature forest and diameter	Webala et al. 2011
			N. gouldi	Positive, retained trees & diameter	
Intermediate treatments					
North America					
Thinning	150–309 trees/ha	southern pine plantation	*L. borealis*	Positive	Elmore et al. 2004
Thinning	13.8 m^2/ha residual	Southern oak–pine	*L. borealis*	Positive	Perry et al. 2007a
			L. cinereus	Positive	

lack of long-term, longitudinal studies that track changes in bat assemblages and their forest habitat over time. Studies on bats in even-aged systems have largely focused on responses to clearcuts with limited exploration of two-age systems such as seed tree, shelterwood, or deferment harvests (Owen et al. 2004; Titchenell et al. 2011). Clearcut harvests have been used with less frequency, especially on public lands, for some time now (USDA and USDI 1994), though they still persist in cool temperate forests, such as those of Tasmania (Law 1996), and some European countries. Patterns in bat responses to clearcuts are still helpful, however, in understanding the potential effects on bats of future directions in forest management based on even-aged systems. Bat responses to uneven-aged systems, such as small cutblocks, patch cuts, or group selection harvests, have received greater attention and have been evaluated across multiple bat species and forest types, so inferences can be drawn on the efficacy of these silvicultural systems for bats. In North America, more studies have evaluated bat response to thinning than any other silvicultural treatment, with thinning often applied in combination with other treatments on the same landscape (Erickson and West 1996; Patriquin and Barclay 2003; Loeb and Waldrop 2008; Perry et al. 2008). Studies of treatment combinations are important as future directions in the management of forests in North America are emphasising multi-treatment prescriptions (Aubry et al. 2009; Harrod et al. 2009; Hessburg et al. 2010), to increase structural habitat complexity, both vertically and horizontally, while reducing the impact of insect infestations and the threats of wildfire and global climate change (Boerner et al. 2008; Parks and Bernier 2010; Duerr and Mistretta 2013). Some forest management strategies specifically target bats, though often bats are catered for under broad forest prescriptions that aim to accommodate the needs of a range of forest-dependent species in an area (Law 2004).

There is a surprising lack of European studies on the effects of any logging strategy on bats and the only study found for this review which directly related to this issue was one on the effects of salvage logging (see Sect. 4.1.4). This is especially concerning given the strict protection afforded to all bat species and particularly bat roosts under the EU Habitat Directive; this prohibits deliberate disturbance of all bats during any stage of their life cycle as well as the destruction of breeding sites or resting areas. As such, the timing of forest harvesting needs to consider whether bats may be roosting in targeted areas (e.g. Forestry Commission 2005). There are no such restrictions in Australia; though for New Zealand pine plantations, Borkin et al. (2011) recommends that harvests should be planned when bats are not heavily pregnant nor have non-volant dependents. In eastern North America, logging is currently restricted from 15 October through 31 March across the distribution of the endangered Indiana bat, *Myotis sodalis*, as this bat uses live and dead trees as maternity sites during the growing season (USFWS 2009). Restrictions are further constrained to a start date of 15 November within 16 km of known hibernacula of the species (USFWS 2009). The implications of white-nose syndrome and the extensive mortalities of cave-hibernating bats in North America (USFWS 2012) are likely to add species of forest bats to the threatened and endangered species list in the USA, leading to further restrictions on logging. Missing in all of the dialogue, however, is any direct link of impact, or mortality of bats, during logging operations and studies of these potential impacts are needed (but see Borkin et al. 2011).

5.4.1.1 Clearcut and Deferment Harvests

Response of forest bats to clearcut harvests has been mixed across forest types and species of bats (Table 5.1). For example, three studies each in different locations within the Pacific coast forest type found no response to clearcuts by little brown bats, *Myotis lucifugus*, in British Columbia (Lunde and Harestad 1986), a decrease in overall bat activity over clearcuts in south-eastern Alaskan rainforests (Parker et al. 1996), and an increase in activity of big brown bats, *Eptesicus fuscus*, silver-haired bats, *Lasionycteris noctivagans*, and Townsend's big-eared bats, *Corynorhinus townsendii*, in clearcuts in western Washington (Erickson and West 1996). Patterns in bat activity recorded in and around clearcut harvests are influenced by three factors: the number of years post-harvest when data were collected, the size and shape of cutblocks studied, and the assemblage of bat species present in the area. When reported, the age of clearcut stands in North America evaluated post-harvest ranged from 1.5 to 17 years. This range in age is wide and likely spans considerable variation in above-ground habitat structure due to differences in the amounts of regeneration present; thus, a varied response by bats across studies and geographic locations should be expected. In montane eucalypt forests of south-eastern Australia, bat activity peaked in 165-year-old wildfire regrowth rather than in younger regrowth from clear-felling operations (Brown et al. 1997). Unfortunately, the size and shape of clearcuts studied are rarely reported so an evaluation of the effects of cut size and shape on bat activity cannot be made.

Focusing on traits is likely to provide more insights into the response of bats to the large gaps created by clearcut harvests. In North America, two trends are evident. First, the creation of less obstructed flight space over clearcut stands generally leads to increased levels of activity of edge/open-space bats that possess moderate to high aspect ratios and often higher wing loadings (Lacki et al. 2007). This mix of bats includes the foliage-roosting *Lasiurus* species, along with others (*Lasionycteris* and *Eptesicus*) (Table 5.1). The length of years post-harvest at which this increase in bat activity is sustained is less clear and likely is affected by tree species composition and the speed at which regeneration proceeds in harvested stands at a particular geographic location. Second, the response to clearcut harvests between *Myotis* species varies both within and among species (Patriquin and Barclay 2003), with some increase in activity associated with linear edge habitats at the periphery of cuts but reduced activity in the centre of harvested stands, except where residual patches are left behind (Hogberg et al. 2002). As our ability to distinguish among *Myotis* species increases with technological advances in acoustic detectors and software packages (Britzke et al. 2011), resolution among the full suite of *Myotis* bats in North America should become possible allowing for a more in-depth and complete evaluation of bat response to edge effects in actively managed forests.

Data on bat responses to even-aged systems other than clearcuts are sorely lacking. A study of bat activity in deferment harvests found high levels of activity of silver-haired bats, *L. noctivagans*, in stands with 6–10 m^2/ha of basal area remaining (Owen et al. 2004), and the only study examining bat activity in shelterwood harvests (30 to 50 % reductions in basal area) observed higher levels of activity in three species of bats that have wing morphologies and echolocation call structures possessed by edge/open-space bats (Titchenell et al. 2011). Patterns of habitat use by radio-tagged northern long-eared bats, *M. septentrionalis*, a closed-space bat, showed this species spent limited time in deferment harvest stands, especially harvested sites with more open canopies and less cluttered foraging space (Owen et al. 2003).

For roosting bats, gap release and shelterwood systems retain tall and large diameter hollow-bearing trees within stands possessing less clutter than surrounding forest regenerating after harvest and these offer potential roosts for bats. However, in Western Australia, southern forest bat, *V. regulus*, avoided locating roosts in shelterwood treatments when older forest was available nearby (Webala et al. 2010). In general, remnant trees in these silvicultural treatments, including retained 'habitat trees', were not preferred as roost sites by *V. regulus*, though a second species (*N. gouldi*) frequently used such trees. One possible reason for avoiding using 'habitat trees' as roosts was the relatively low density of hollow roosts (see 3.2 Deadwood availability and hollow tree density).

5.4.1.2 Variable Retention Harvests

Variable retention has recently been proposed as an alternative to standard clearcuts, whereby old-growth elements are retained within the clearcut coupe

(Baker and Read 2011). Variable retention increases the availability of edges, for example, around retained patches (aggregates) of undisturbed forest within the clear-fell coupe and along coupe boundaries as well as increasing the area of open space. Open- and edge-space ensembles would be expected to benefit from this treatment. The 200-ha Silvicultural Systems Trial, in Tasmania, provides one of the main experimental sites in Australia for investigating responses to variable retentions. Bat activity was similar in control coupes of 45- to 60-m-tall old-growth Messmate Stringybark, *Eucalyptus obliqua*, forest, compared to variable retention coupes 5–8 years after logging (Law and Law 2011). Activity was lower above the dense young regeneration of clear-fell-burn-sow (no retention) coupes and marginally lower for dispersed tree retention coupes. This suggests that the retention of old-growth elements as aggregates or patches moderates the unsuitable young regrowth zone for total bat activity, while retention of dispersed individual trees is less effective. Surprisingly, bat activity was low at the retained aggregates themselves, both in their centre and along the edge, and it is not known to what extent bats roost in these locations. Overall the results are consistent with conceptual models (Fig. 5.1), whereby activity is predicted to be higher in areas of medium clutter levels and where hollow abundance is high. Individual bat taxa responded to treatments consistent with predictions from ecomorphology. Closed-space bats were less active in clearcuts than unharvested forest, large edge-space bats were more active in clearcuts (especially along edges), and smaller edge-space bats were less influenced by patch type and location within coupes; consistent with other studies of forest clearcuts from North America (Grindal and Brigham 1999; Menzel et al. 2002; Patriquin and Barclay 2003).

The age of regenerating forest is likely to be an important influence on how bats respond to variable retention. An unreplicated, operational scale (100-ha forest blocks) experiment established in 1984 in the temperate forests of southern New South Wales (Waratah Creek) (Kavanagh and Webb 1998) was sampled acoustically for bats after 18 years of regrowth. Treatments retained different amounts of tree canopy within four different forest blocks comprising 100 % (control), 50 % (0.5 ha patches in a chessboard pattern), 25, or 10 % tree canopy retention. Control sites supported 2–4 times more activity than logged sites, with 10 % retention supporting the lowest activity level with just 50 bat passes per night of sampling (Fig. 5.5; B. Law, unpubl. data). Thus, bat activity remained low even 18 years after logging and the amount of canopy retained within a block had little impact on activity, except for the block with the most intensive logging which supported the lowest activity level. As expected, the activity of closed-space bats was similar, though low, between the control and treatments, after 18 years. Activity of edge-space bats was three times lower in logged stands, suggesting a loss of edges and spaces between trees, especially in the treatment where logging was most intense. Logging treatments had little effect on open-space bats that forage above the canopy, except that activity was lower where logging intensity was greatest.

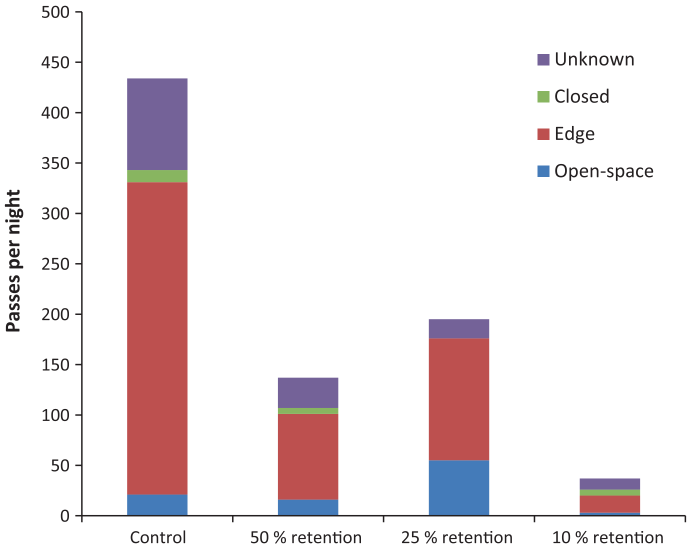

Fig. 5.5 Total bat activity (762 passes, 10 taxa) recorded 18 years after logging in an unreplicated, variable intensity logging experiment in New South Wales, Australia. Data are mean number of passes per night for two Anabat detectors deployed per forest block (~100 ha) over two entire nights of recording and exclude activity on trails (B. Law, unpubl. data). Different bat ensembles are open-space, edge-space, closed-space, and unknown

5.4.1.3 Group Selection Harvests

Changes in ensemble activity with group selection harvest are likely to depend on gap size, with an increase in edge-space activity if gaps are small and open-space activity if gaps are large. Immediately after harvest, closed-space bats are expected to decline, but we predict subsequent recovery if the retention of roost trees is catered for. All studies examining bat responses in North America to group selection harvests, canopy gaps, or small cutblocks consistently reported increases in activity of bats, primarily open/edge-space species, with the opening up of forest canopies, regardless of forest type or assemblage of bats present (Table 5.1). The one exception was a decline in activity of *Myotis* bats in canopy gaps in forests of the central Appalachian Mountains, with this drop off in use inversely correlated with increasing diameter of canopy gaps (Ford et al. 2005). In this study, the maximum gap diameter examined was 33.5 m in width, with the decline in activity with increasing gap size largely attributable to response of closed-space *Myotis* species. Studies in oak–pine forests in Arkansas have demonstrated the use of dead and live trees along gap edges for roosting by several bat species (Perry and Thill 2007b; Perry et al. 2008), demonstrating the importance of maintaining canopy gaps in managed forests. The almost universal response by bats of increased activity with canopy gap formation means this silvicultural treatment holds much promise for management of foraging habitat of bats in the short-term. Use of gaps by forest bats following a decade or more of successional change is likely to be different, however, with overall declines in activity plausible as open/edge-space species disappear or decline in abundance with increasing gap clutter. Such temporal changes need to be identified along with the optimal gap size(s) and the density of gaps required by different species of bats to permit commercially viable, sustained yield harvests while fostering high levels of bat activity and provision of roosting habitat in managed forests.

In contrast to many North American studies that have been undertaken in gaps soon after harvesting, in Australia, most bat research has focused on the use of older regrowth regenerating from group selection harvest, particularly characterising bat species by their traits in relation to the use of these dense stands. There is a general pattern of forest clutter increasing over time after group selection harvest so that old regrowth (>30 years) has significant higher clutter levels than young or older forest, which constrains use by bats to closed-space species with a low wing aspect ratio (Law and Chidel 2002; Webala et al. 2011). Less manoeuvrable edge-space species with a high wing aspect ratio tend to be scarce in regrowth forest (except on flyways provided by tracks and creeks), although their activity is greater in the subcanopy and canopy than understorey (Adams et al. 2009). Vegetation is more cluttered in regrowth at these upper heights (closer stems and less vertical space in the subcanopy), and this leads to less bat activity in such situations (Adams et al. 2009). It is not known whether open-space and low-frequency edge-space species are active above the canopy of these young forests, although this was confirmed by Müller et al. (2013) for mature forests in Europe.

5.4.1.4 Salvage Logging

Salvage logging involves the removal of dead wood after a natural disturbance (e.g. windthrow, forest fires, and insect outbreaks) and has been employed even in protected forests, provoking some controversy. To our knowledge, no research has examined the implications for roost availability of this practice, although removal of standing dead wood will inevitably reduce the abundance and diversity of roosts and would have a considerable impact when carried-out over large scales (Lindenmayer and Noss 2006). We found two studies which investigated changes in bat activity following salvage operations. In Germany, closed-space species reduced their activity in both types of forest clearing (bark beetle and logging), while the activity of open-space species slightly increased, and edge-adapted species showed a mixed response (Mehr et al. 2012). These results are similar to a study in Oregon where the highest bat activity was in the more intensely logged sites (Hayes 2009).

5.4.2 Recovery Times After Timber Harvest

Long-term studies are largely missing from assessments of the response of bats to silvicultural methods. A typical approach uses chrono-sequences or snapshots of comparisons between different silvicultural methods or logging histories and makes the assumption that the matching of treatments is equal and evenly distributed across the same environmental niche and landscape context. Most importantly, a one-year snapshot may not be representative of temporal variation and dynamism over a longer period (Recher et al. 1983; Maron et al. 2005); thus, conservation plans developed from snap-shots can have limitations. Long-term studies are ideal for tracking changes to vegetation structure as forests regenerate after harvesting and how different ensembles of bats respond to these dynamics.

One longitudinal study in Australian eucalypt forests, initiated in 1998, has been investigating alternate-coupe-integrated harvesting for woodchips and sawlogs, and although currently unpublished, a summary is presented here (B. Law and M. Chidel, unpubl. data). Alternate-coupe harvesting divides management units (e.g. 200-ha areas) into small (~15 ha) coupes that are alternately harvested in a chessboard fashion, every 20 years. In 1998, bat activity was recorded after 22 years of regrowth from the first cycle of logged coupes (Law and Chidel 2001). Bat activity in the cluttered regrowth was about half that of adjacent, more open unlogged coupes. This effect was most notable for less manoeuvrable, open- and edge-space vespertilionids that were more active in unlogged coupes.

The site was then sampled at intervals over 13 years following the second round of alternate-coupe logging (B. Law and M. Chidel, unpubl. data; Fig. 5.6). During this period, total bat activity remained low in old regrowth coupes (22 years old in 1998). Activity in unlogged controls remained similar to the initial samples taken prior to second round harvesting. Within the recently logged coupes, activity peaked soon after logging in the large gaps, but it quickly declined and remained at low levels (similar to that found in old regrowth coupes) once young regenerating eucalypts established within eight years of logging. In terms of clutter and total bat activity, these results are only partly consistent with the conceptual models of Hayes and Loeb (2007). The model predicts low bat activity when clutter is very low, yet this was not the case in this study, possibly because gaps were patchy within the 15-ha coupes due to the requirement for retention of 5 habitat trees per ha plus equivalent numbers of recruits, indicating that gap size or scale is likely to be an important issue influencing activity. High activity at intermediate clutter levels (unlogged coupes) and low activity at high clutter levels (old regrowth coupes) are consistent with the model. The response of individual species and ensembles are yet to be analysed for this study.

The lack of recovery after 36 years in old regrowth coupes is consistent with a number of other studies where low activity persisted for more than 30 years after disturbance (Brown et al. 1997; Adams et al. 2009; Webala et al. 2011), but differs from selective harvesting of wet sclerophyll forest in subtropical Queensland where recovery of bat activity was apparent in a site logged 33 years previously

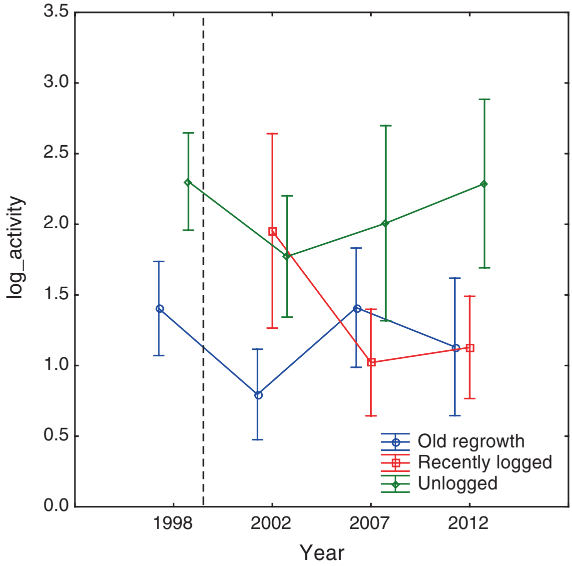

Fig. 5.6 Changes in total bat activity over 14 years in an alternate-coupe logging system in southern Australia (B. Law and M. Chidel, unpubl. data). The *dashed vertical line* indicates second round logging of the alternate unlogged coupes in 1999, which took place 23 years after the first round of logging of adjacent coupes in 1976. All but two unlogged coupes were harvested in 1999 and are thereafter referred to as recently logged coupes. Bat activity is a log transformation of the number of passes per night (±95 % confidence limits) after adjusting with mean nightly temperature as a covariate

(de Oliveira et al. 1999). It is important to note that none of these studies consider activity levels on tracks, riparian zones, or other areas of retention that potentially could ameliorate the effects of clutter from dense regrowth and loss of tree hollows.

5.4.3 Thinning Young Forests

The goal of thinning is to improve the quality and growth of the remaining trees (especially diameter) by reducing the density of trees in a stand. Reducing tree density will decrease canopy cover, at least initially, with increased light levels reaching the forest floor and thus influencing understory cover. Adams and Law (2011) reviewed the literature on thinning and bats and proposed hypotheses for testing that included: (1) activity of edge- and open-space species will increase from pretreatment levels where thinning reduces stem separation to 7 m (~200 stems per ha) but will remain at low levels where average stem separation is less than 3 m (~1100 stems per ha); (2) highly cluttered forests will have low bat activity away from flyways, regardless of the number of potential roosting sites and the abundance of insects, while bat activity in open forests will be highest where roost availability and insect abundance are high.

Consistent with the hypotheses, bat responses to silvicultural thinning have been examined across several forest types in North America with increases in bat activity associated with thinning in Pacific coast (Erickson and West 1996; Humes et al. 1999) and southern oak–pine (Loeb and Waldrop 2008) forests, but not in northern red pine, *Pinus resinosa*, plantations (Tibbels and Kurta 2003) or northern coniferous forests (Patriquin and Barclay 2003). An explanation for these differences is not readily clear, as the extent of thinning is not always reported in metrics that can be compared among study sites, and the suite of bat species present varies among locations. Further, data for bat activity within the *Myotis* genus could not be resolved to the species level with technologies used, preventing an evaluation of responses by ensemble. Patterns in roost selection of *Lasiurus* species in southern oak–pine forests indicate that thinned stands are frequently selected by these bats for roosting. Thus, as with clearcut harvests and larger-sized canopy gaps, stands thinned to basal areas <14 m^2/ha appear to be well suited to less manoeuvrable edge-space *Lasiurus* species by providing suitable roosting and foraging habitats (Perry and Thill 2007a; Perry et al. 2007a, 2008).

The response of bats to forest thinning has received little attention in Australia. A preliminary study found high variability in activity for all bats and ensembles between thinned and unthinned eucalypt stands and among vegetation layers within the forest (Adams and Law 2011). Unexpectedly, thinned regrowth had a higher percentage cover for the shrub layer, and the vertical gap between canopy and understory trees was halved, which represented an increase in clutter in the zone where bats frequently fly and this could have undermined any benefit of wider stem spacings. However, the variability in bat activity within the thinned/control treatments was too high to unequivocally state that thinning had no effect.

While thinning is a commonly employed silvicultural technique across Europe, there has been no study of its effects on bat activity, occurrence, or species richness. There are, however, a few studies which have looked at effects of tree density on bats, thereby providing indirect evidence on likely effects of thinning. For example, in one study, where tree density varied between 180 and 2500 stems per ha in mixed deciduous/coniferous fragments within agricultural landscapes in Scotland (UK), activity of the soprano pipistrelle, *Pipistrellus pygmaeus* (an edge-space forager), decreased with increased tree density. In contrast, the abundance and activity of *Myotis* spp., and the abundance of Diptera, both increased with tree density (Fuentes-Montemayor et al. 2013). This mirrors findings by Müller et al. (2012) where the activity of closed-space foragers and prey abundance increased at higher vegetation densities, while the activity of open-space foragers, and to a lesser extent, edge-space foragers declined.

5.4.4 Harvest Exclusion Areas

Given the low levels of bat activity observed in young regenerating forest after logging, mitigations are needed to ameliorate the effect of high clutter levels and lower numbers of tree hollows. Edge habitat, such as tracks and clearcut boundaries, is extensively used by a range of bat species (Sect. 3.5). In Australia, harvest exclusion areas that support naturally open, undisturbed forest constitute a much greater proportion of the forest landscape compared to forest tracks and are therefore expected to be more important at ameliorating logging impacts on bats given that they also provide roosts in the hollows of old trees. Provided attention is paid to the size and location of harvest exclusion areas these can play a vital role in landscape connectivity, acting as corridors across forested landscapes, permitting bats to reach otherwise isolated blocks of preferred habitat within landscapes where fragmentation has altered the matrix and created an abundance of suboptimal habitat blocks. As the extent of habitat fragmentation increases, so does the importance of corridors on the landscape (Duchamp et al. 2007). Indiana bats, *M. sodalis*, preferred to fly along wooded corridors and avoided open fields in Michigan, even though commuting distances increased by more than 50 % (Murray and Kurta 2004), with similar results for *Pipistrellus* spp. in the UK (Downs and Racey 2006). Activity of bats in heavily fragmented, pine plantations in South Carolina demonstrated more use by bats of edges along corridors than habitats within the corridor interior or nearby stands of timber (Hein et al. 2009a), with bat activity directly correlated with the height of the corridor overstorey.

Riparian corridors in timber production forests are often excluded from harvesting in order to ameliorate impacts of harvesting on water quality as well as providing unharvested productive habitat for biodiversity. Riparian corridors are important areas of bat foraging activity (Hayes and Adam 1996; Zimmerman and Glanz 2000; Brigham 2007), with male and female bats segregating themselves along corridor reaches in upland landscapes, with males more abundant at higher elevations (Grindal et al. 1999; Senior et al. 2005). Activity of bats along riparian corridors appears to be scale-dependent, with vegetation architecture, i.e. shrub and tree cover, influencing the use of foraging space by bats at the local, or finest spatial, scale more than landscape habitat measures or abundance of insect prey (Ober and Hayes 2008). Abundance of Lepidoptera was high in riparian corridors in Arkansas prompting the authors to hypothesise that Ozark big-eared bat, *Corynorhinus townsendii ingens*, a moth strategist (Dodd and Lacki 2007), feeds extensively in and around riparian corridors in the Ozark Mountains (Dodd et al. 2008). Use of best management practices along streamside management zones for sustaining healthy, riparian ecosystems is a well-established forest management practice in many regions of North America (Stringer and Perkins 2001; Lee et al. 2004). Regardless, data on how these practices influence habitat use by forest bats in riparian areas remain limited, with experimental studies sorely needed on the effects of habitat quality within corridors (stand age and composition) and corridor dimensions (size and width) on roosting and foraging ecology of bats. One study in Australia demonstrated that bat activity, foraging rates, and species richness in riparian corridors within selectively harvested eucalypt forest was maintained at levels similar to riparian areas in mature forest (Lloyd et al. 2006). Higher activity was recorded on larger rather than smaller order streams, a pattern also not affected by harvesting history. Such results highlight the benefits of buffers, with riparian areas effectively providing habitat for foraging and commuting bats in selectively logged forests where clutter levels are likely to be high.

Mitigating the loss of roosting habitat in hollow-bearing trees is arguably even more important than maintaining suitable foraging habitat. Forested corridors are critical habitat elements for North American foliage-roosting bats by providing both roosting and foraging opportunities. Male Seminole bats, *Lasiurus seminolus*, in south-eastern loblolly pine, *P. taeda*, plantations chose roost trees in forested corridors within harvest exclusion zones over 60 % of the time, even though corridors represented only 11 % of the landscape area (Hein et al. 2008a). Corridors were 100 to 200 m in width and comprised largely of older-aged forests in riparian and upland slope positions. Use of forested corridors for roosting has been observed in other foliage-roosting species in south-eastern forests, with tri-coloured bats, *Perimyotis subflavus*, selecting riparian corridors (O'Keefe et al. 2009), male evening bats, *Nycticeius humeralis*, choosing upland corridors of mature forest (Hein et al. 2009b), and eastern red bats, *L. borealis*, roosting in the vicinity of gated roads (O'Keefe et al. 2009). Greenbelts in riparian corridors, or unharvested inclusions of mature mixed-pine hardwoods ≥50 years in age, were important roosting habitats for these same species in southern oak–pine forests of Arkansas (Perry et al. 2007b; Perry and Thill 2008).

Harvest exclusion areas, especially those surrounding streams, are commonly used as roosting habitat by many tree hollow roosting Australian bats such as Gould's long-eared bat, *N. gouldi,* eastern forest bat, *V. pumilus*, and southern forest bat, *V. regulus* (Lunney et al. 1988; Law and Anderson 2000; Webala et al. 2010). A range of factors will influence the pattern of roosting close to creek-lines, but a large pool of older and mature trees in a variety of decay classes is likely to be important. Riparian areas often support a different vegetation type, with rainforest being particularly common in Australia. The specialist golden-tipped bat, *Kerivoula papuensis*, preferentially roosts in the suspended nests of small birds within riparian rainforest and such areas are excluded from harvesting (Schulz 2000; Law and Chidel 2004).

Jarrah forest in Western Australia offers one example of providing pools of mature trees using zoning. Since 2004, Fauna Habitat Zones (i.e. areas of mature forest >200 ha set 2–4 km apart within areas available for logging) have been retained for species, including bats, that rely on blocks of forest supporting mature forest attributes or characteristics (Webala et al. 2010). In some forest blocks, approximately 54 % of the total area (11,740 ha) is currently reserved from logging as conservation reserves, informal reserves (riparian buffers, diverse ecotype zones, road reserves), old-growth forest, and fauna habitat zones. Of these, about 39 % are permanently reserved, including riparian buffers, from logging in the future. Testing the effectiveness of this level of retention remains a priority for forest bat research. Collectively, these findings indicate that forested corridors are important habitat elements for roosting bats in forests across the globe.

5.4.5 Plantations

There is no internationally agreed definition of forest plantation and many very old forests we may think of as natural have been planted. However, for the purposes of this review, the term plantation is used to mean forests planted primarily for timber extraction using intensive management techniques. Timber plantations are perhaps the most extreme form of silviculture as they require replanting of typically exotic trees, with site and soil preparation required over large scales. Seedlings are planted at high densities to maximise growth and form of trees, and this has the consequence of producing high levels of clutter as the trees grow. All the silvicultural practices outlined in this section are also applicable to plantation forests. The response of bats has been documented in eucalypt plantations in Australia and pine plantations in New Zealand. As expected, bat activity in young plantations of eucalypts (<10 years) is typically low and considerably less than that found in nearby forest, and, somewhat surprisingly, activity is similar to levels over adjacent cleared farms (Law and Chidel 2006; Law et al. 2011). Bat activity is higher in older eucalypt plantations (~25 years), especially where drought and lack of maintenance leads to tree mortality and the creation of gaps (Law and Chidel 2006). Closed-space species (*Nyctophilus*) show some association with plantations as do open-space species (*Mormopterus ridei*), which presumably use the space above plantations together with adjacent open paddocks. Radio-tracked bats avoid roosting in young eucalypt plantations where tree hollows are absent, even though decorticating bark is present (Law et al. 2011).

Despite limitations in habitat quality, plantation forests provide large areas of additional habitat for threatened long-tailed bats, *Chalinolobus tuberculatus*, in New Zealand (Borkin and Parsons 2011a). Borkin and Parsons (2011b) found these bats roosting in crevices, fissures, and small hollows in the oldest stands of Monterey pine, *Pinus radiata*, plantations (25–30 years), with females choosing to roost within 150 m of waterways. In these plantations, bats selected home ranges with higher proportions of relatively old stands than available (Borkin and Parsons 2011a). Males selected edges with open unplanted areas within their home ranges, which females avoided, instead selecting older stands for foraging. Borkin et al. (2011) also documented the response to the clear-fell harvest of a pine plantation and found a pattern of declining numbers of roosts used, as well as smaller roosting areas and colony sizes. Over 3 years, 21 % of known roosts were lost with 15 % due to forestry operations and 6 % due to natural tree fall. To mitigate harvest operations, it was suggested that some suitable foraging and roosting areas should be retained within bat home ranges. Borkin et al. (2011) further suggested that priority management for this declining New Zealand bat should focus on plantation areas closest to water and harvests should be planned when bats are not heavily pregnant nor have non-volant dependents.

Pine plantations in the south-eastern USA are actively managed landscapes with extensive amounts of fragmentation and edge development. Nevertheless, these landscapes often support a diverse bat assemblage, in part due to enhanced foraging conditions along edge interfaces and to suitable foraging and roosting habitats along forested-riparian corridors (Miller 2003; Elmore et al. 2004; Hein et al. 2008b, 2009a). Experimental studies have demonstrated that activity of bats is affected by edge habitats, with highest levels of activity occurring along the edge interface regardless of echolocation call structure or wing morphology (Jantzen and Fenton 2013). Tree canopies also serve as edge interfaces in forested environments, with more manoeuvrable, high-frequency bats foraging along canopies and edges more often than less manoeuvrable, low-frequency bats (Pettit and Wilkins 2012). Relationships of age, formation, and structural characteristics of edge habitats with activity of foraging bats are complex, with newly formed, high-contrast edges supporting higher bat activity and stronger depth of edge influence, than older more developed, cantilevered edges which possess less contrast between adjacent habitats (Jantzen and Fenton 2013). Regardless, data indicate that managed forests with an abundance of edge habitat, typical of plantation forests in south-eastern North America, can support a diverse assemblage of forest bat species.

Spruce, pine, and fir species account for the largest share of the forest plantation area in Europe, with *Eucalyptus* species introduced from Australia common in the south. While eucalypt plantations appear to be avoided by some bats (Di Salvo et al. 2009), positive selection was found for the Mediterranean horseshoe bat, *Rhinolophus euryale*, in the Basque country (Aihartza et al. 2003). In Spain, *R. euryale* and Mehely's horseshoe bat, *R. mehelyi*, both closed-space foragers, were radio-tracked foraging in eucalypt plantations and dehesa (managed oak savanna) in proportion to, or greater than, their availability (Russo et al. 2005a, b). Numerous acoustic and radio-tracking studies have documented avoidance of bats from non-native coniferous plantations in Europe (e.g. Entwhistle et al. 1996; Walsh and Harris 1996). Perhaps as a consequence of this, the effects of plantation forestry practices on bat populations in Europe have been largely ignored, and surprisingly little is known about the use of timber plantations by bats. However, several long-running artificial 'bat box' schemes operated by the UK's Forestry Commission have indicated that some plantations contain large roosting bat populations (Park et al. 1998). Radio-tracking of Natterer's bat, *Myotis nattereri*, a species previously associated primarily with deciduous forests has uncovered the extensive use of areas used for commercial forestry, both for roosting and foraging (Mortimer 2006). This study conducted in a plantation in Scotland found that *M. nattereri* preferentially foraged within areas of Corsican pine, *Pinus nigra* var. *maritima*, and roosted in cavities formed from live double-leadered Corsican pine (Mortimer 2006). Given life-history parameters of the bats studied (survival, population densities) were similar or higher than those described within deciduous forests, and that double-leadered trees are usually targeted for removal by foresters as uneconomic, such findings illustrate the importance of studies in plantation forests.

A high percentage of open ground in some planted forests can benefit species that specialise on the predation of ground dwelling prey. Greater mouse-eared bat, *Myotis myotis*, for example, while often associated with deciduous forests, was found preferentially foraging in mature spruce monocultures with a high percentage of open ground in Germany, and intensively managed orchards and lowland forests with no undergrowth in Switzerland (Arlettaz 1999; Zahn et al. 2004). These studies collectively suggest that it is the forest structure that may be more important than tree species composition in many cases. Therefore, it seems clear that timber plantations have the potential to be of value to bats, but we lack an understanding of how populations of different species are affected by current silviculture practices.

5.4.6 *Prey*

The response of bat prey is also a critical issue when evaluating silvicultural treatments. Lepidoptera (moths–a fundamentally important prey group of bats) in temperate zone forests of North America differ little in species richness between stands regenerating after harvest and stands that remain unharvested (Burford et al. 1999; Summerville and Crist 2002; Dodd et al. 2008). Group selection logging of Australian eucalypt forests has found greater insect biomass in old regrowth Jarrah forest (>30 years since logging) than younger forest treatments (Webala et al. 2011) and a similar trend was found in spotted gum forests in eastern Australia (Adams et al. 2009). An additive effect of insect abundance and an index of vegetation openness in the spotted gum forests influenced bat activity, especially edge-space species with medium to high echolocation frequency. High values of insects and openness correlated with high levels of bat activity (Adams et al. 2009). Thus, dense clutter appears to constrain activity of some species even where insect abundance is high. This varies between bat ensembles, however, with closed-space foragers able to take advantage of the higher insect densities often associated with clutter, particularly Diptera, an important taxa for many bats (Müller et al. 2012; Fuentes-Montemayor et al. 2013; see also Sect. 4.3). While the prey base of bats can probably be sustained with application of many silvicultural systems, clearcut stands regenerating as monocultures support reduced levels of moth diversity, indicating that plant species richness is important for providing adequate populations of lepidopteran prey for insectivorous bats in managed forests (Summerville and Crist 2002; Dodd et al. 2012).

5.5 Multi-spatial Scale Forest Management

Integrating silvicultural systems into managed forested landscapes in ways that promote habitat for forest bats must account for the fact that bats are highly mobile and exhibit considerable variability in the use of habitats both spatially and temporally (Duchamp et al. 2007). Given that resource requirements differ among species and also sex, age, and reproductive classes within species (Perry et al. 2007a; Perry and Thill 2007b; Henderson et al. 2008), designing a forested-landscape matrix with a mosaic of resources that addresses the needs of all bat species in the region will likely require the application of a mix of silvicultural methods, each implemented with different objectives in mind (Guldin et al. 2007). These would include the retention of mature forest habitat at the landscape and stand scale in the form of large reserves, narrow and large strips, streamside reserves, aggregates, and clumps (Gustafsson et al. 2012). Lindenmayer and Franklin (2002) proposed a strategic landscape-scale approach with conservation measures applied at multiple spatial scales for forests. The four main strategies identified for conservation at multiple spatial scales include: (1) establishment of large ecological reserves, (2) application of landscape-level measures in off-reserve areas, (3) application of stand-level measures in off-reserve areas, and (4) monitoring and adaptive management.

There are limited data on bats for setting overall retention thresholds at the landscape scale. Gustafsson et al. (2012) suggested a strict minimum of 5–10 % retention of old-growth forest to achieve a positive ecological response for biodiversity. However, considerably higher levels are often recommended. For example, in Tasmania, 30 % is retained in some state forests (Gustafsson et al. 2012; see also Białowieża Forest in Europe ~20 %, Ruczyński et al. 2010). This retention should be spread across the landscape to facilitate dispersal. A key question is whether there are thresholds for the retention of mature forest that can optimise the trade-off between biodiversity conservation and production.

A recent study on Tasmanian bats, using both radio-tracking and acoustic detectors, assessed the response of bats to multi-spatial scale forest management (Cawthen et al. 2013). At broader scales, maternal bat colonies selected roosts in landscapes with the highest availability of hollow-bearing trees. At more fine-scales, however, maternal colonies did not exhibit strong selection for roost trees in patches with the highest availability of hollow-bearing trees. Instead, other attributes such as hollow type were important. For overall bat activity, the extent to which bats used different types of retained forest patches varied with the composition of the surrounding landscape. Large strips and small patches of wooded habitat were used by bats to a greater extent in landscapes with less mature forest in the surrounding area (<1 km radius). For small patches, this corresponded to landscapes with <22 % mature forest in the surrounding 1 km. No thresholds in bat activity were identified for large patches (370 ha) or small corridors (3 ha). Overall, these results indicate that in the landscapes sampled, activity is low in small retained patches where mature forest is readily available nearby, though these habitat elements do provide roosts and connectivity (and probably foraging habitat) where mature forest is rare or has been lost. Thus, the type, amount, and spatial arrangement of mature forest existing in the landscape need to be considered when retaining forest habitat at finer-spatial scales.

Clearly, the extent to which forest bats respond to changes at the landscape scale remains only partially understood. Studies of bat activity at stand and landscape scales in both north-western and north-eastern forests of North America demonstrated that patterns in habitat use of bats were largely determined by habitat characteristics at the local or stand level and not at landscape scales (Erickson and West 2003; Ford et al. 2006), suggesting that silvicultural systems that create a mosaic of treatments across forested landscapes with local differences in habitat structure will support a higher overall diversity of bat species (Wigley et al. 2007). This approach has been recommended in published studies (Loeb and Waldrop 2008; Perry et al. 2008); however, other sources report both stand and landscape metrics in North America and Europe to be important in selection of activity areas of bats (Loeb and O'Keefe 2006; Yates and Muzika 2006; Fuentes-Montemayor et al. 2013), with tri-coloured bats, *P. subflavus*, and eastern red bats, *L. borealis*, most affected by local stand structure, northern long-eared bats, *M. septentrionalis*, negatively affected by forest edge, and Indiana bats, *M. sodalis*, positively affected by dead tree density and non-forested land cover. Other studies corroborate that selection of roosting sites in both bark- and cavity-roosting and foliage-roosting bat species is strongly influenced by landscape-scale metrics in both eastern and western forests of North America (Limpert et al. 2007; Perry et al. 2008; Arnett and Hayes 2009; Lacki et al. 2010).

5.6 Summary and Future Possibilities

This review of the effects of silvicultural systems on forest bats demonstrated that almost all treatments evaluated were compatible with some use by forest bats, depending on the suite of species considered: closed-space species feed in intact forests, but respond to creation of small canopy gaps and less to reduced tree densities and open-edge interfaces; edge-space species exploit edge habitat along tracks, coupe edges, and other linear features such as creeks, but fare poorly within dense regrowth that often dominates soon after harvest; and, open-space foragers benefit *temporarily* from silvicultural treatments that significantly reduces cluttered air space and provides edge interfaces for roosting. These patterns were largely consistent across three different continents.

To sustain high levels of bat diversity in managed forests at the landscape scale, a balance of needs for these three groupings of bats is desirable and will likely require a mix of silvicultural treatments and exclusion areas staggered across the landscape, regardless of forest type or geographic region. Use of edge habitats, exclusion areas/set-asides, and riparian corridors for roosting and foraging by bats was a consistent theme in the literature reviewed, and these habitat elements need to be considered in forest planning. These landscape features accompany forest fragmentation, however, and it remains unclear to what extent increasing loss of the unharvested forest matrix will lead to declines in population numbers of forest bats. Unfortunately, data on densities of occupied roosts and, thus, potential for landscape-scale population estimates of bats are few (Clement and Castleberry 2013; Fleming et al. 2013). Regardless, population studies could integrate the potential benefits of multiple prescriptions at a scale over which bats themselves sample the landscape. Population studies are likely to provide the ultimate test of the effectiveness of a silvicultural regime, especially when such studies take a long-term perspective. Long-term studies on forest bats are notably lacking in the published literature.

Application of silvicultural treatments in regenerating forests to reduce tree densities and open gaps in the forest canopy shows promise for creating forested landscapes that support diverse and sustainable populations of bats. Forests with reduced tree density and vegetative clutter permit higher levels of light penetration, with this increased exposure hypothesised to enhance the suitability of live and dead trees for roosting by bark- and cavity-roosting bats in temperate climates (Boyles and Aubrey 2006). Further, LiDAR studies demonstrate that reduced clutter in the mid- and understory layers of forests is correlated with higher levels of activity by low-frequency (≤34 kHz) open-space bats (Britzke et al. 2011; Dodd et al. 2013). However, closed-space bat species that glean insects from vegetation and manoeuvre well within clutter benefit from a relatively dense understorey and higher tree densities, which can act as sources of insect prey (Fuentes-Montemayor et al. 2013). Therefore, management that encourages habitat heterogeneity to fulfil the requirements of different species is needed. Bat activity is also vertically stratified, but there is a paucity of information on the effects of high canopy forest structure on bat activity (Adams et al. 2009; Müller et al. 2013), and research to address this gap would be valuable.

The quality and density of old trees in exclusion areas must not be overlooked. Roost abundance stands out as a key variable in our conceptual model (Fig. 5.1). The posited relationship is for increasing bat populations with increasing numbers of roosts, though with a threshold at the upper end of roost abundance rather than at low roost abundance. Densities of hollow trees sufficient to support populations of roosting bats are unknown and remain a major knowledge gap (Law 1996), but will likely be species contingent and based on roost switching behaviours and social dynamics within colonies (Johnson et al. 2013) and the density of other hollow-dependent fauna. Even small colonies of bats can require a large number of roosts over the active season. For example, Russo et al. (2005a, b) estimated that over a period of a month a colony of 12 female barbastelle bats, *B. barbastellus*, would require approximately 18 different trees for roosting. Although the retention and sustained recruitment of large mature trees at various stages of decay is essential in harvested forests for the future long-term maintenance of bat roosts and other hollow-dependent fauna, this might best be achieved through regular harvest exclusion areas (unharvested buffers, old-growth forest, etc.) that can maintain high local densities of potential roosts. There remains little guidance on how much undisturbed forest should be retained at a landscape scale.

Paradigm shifts in forest management away from even-aged to retention systems (Puettmann et al. 2009) are already in place in Pacific coast forests of North America and Australian eucalypt forests and are being encouraged for use in management of forests globally (Gustafsson et al. 2012; Lindenmayer et al. 2012). These systems allow for maintenance in post-harvest forests of tree species compositions, canopy structures, and ecosystem functions typical of preharvest conditions. We conclude from our review that the use of multi-scale retention systems may be a compatible approach for sustaining habitats of bats in forests. These silvicultural systems are designed to provide spatial variation in retained tree densities and distribution of residual patches of uncut forest, both of which lead to habitat complexity within stands and across landscapes. These systems intentionally mimic natural disturbance regimes and have broad biodiversity benefits across multiple taxa (Long 2009). Retention of old forest patches is likely to be most important where harvest intensity is high, such as in clearcut or heavy selection practices, or where retention of critical habitat components is low. Stand-level (site-scale) retention should be greater where old-growth forest in the surrounding landscape is scarce and where logging practices are more intense. The effectiveness of this multi-scale approach will require testing through monitoring and research tailored for different environments, multiple taxa and silvicultural practices. Monitoring the effectiveness of these strategies is an essential part of adaptive management and a fundamental part of ecological sustainable forestry and the 'social license to operate' that is increasingly required by forest certification schemes (Lindenmayer and Franklin 2002).

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Glossary

Clearcut/Clear-fell Harvest Also referred to as uniform selection and heavy group selection, it removes all trees from a large management area and allows natural regeneration to take place, resulting in even-aged regrowth with high stem density. The aim is to mimic natural stand replacing events such as wildfire or large storms

Coupe/Cutblocks A defined area of forest, which may vary in size, in which harvesting takes place usually over one year

Deferment Harvests Sometimes also referred to as a shelterwood or clearcut with reserves. A deferment harvest retains a limited number of canopy trees (reserve trees) while allowing regeneration in the understory. These two tree levels are then allowed to develop together until the end of the next rotation, whereupon other trees are retained for canopy cover

Forest Zoning Where management for multiple objectives in a forest incorporates broad exclusion areas such that logging is excluded from patches of forest deemed to be environmentally sensitive or where patches of forest are specified to allow different silvicultural practices (Florence 1996)

Gap Release Creation of canopy gaps typically <0.1 ha to allow the growth of younger, often suppressed trees

Green Tree The retention of live trees on an otherwise harvested area as part of a variable retention harvest

Group Selection Harvest Removes all trees from small patches, with the aim of using disturbance to stimulate regeneration of new trees, but simultaneously maintaining a well-connected mosaic of patches of varying size, containing varying numbers of residual mature trees

LiDAR A remote sensing technology that measures distance by illuminating a target with a laser and analyses the reflected light

Patch Cuts An area of felling smaller than a clearcut but removing a larger number of trees than a group selection harvest

Prescriptions Targeted retention that aims to mitigate the effects of logging on environmental features. Hollow tree retention and riparian exclusion zones are two common prescriptions, but can also include exclusion zones surrounding significant bat roosts

SeedTree Harvest The retention of a few residual trees in a harvested area to provide seeds for the forest to regenerate

Self-thinning Density-dependent mortality within an even-aged stand of trees as they grow in size, leading to reduced tree density

Shelterwood Harvest See deferment harvest.

Shelterwood Systems Removal of canopy trees in a series of selective harvests leaving sufficient trees for regeneration and shelter. New seedlings are left to establish before mature trees are removed

Silviculture The art and science of manipulating a stand of trees by controlling the supplies of water, nutrients, and solar radiation by altering forest structure, towards a desired future condition (Guldin et al. 2007), typically for timber production but also for biodiversity conservation goals

Single Tree Selection Removes a scattering of high value individual trees from management areas, with repeat cuts taking place at regular intervals over time. However, intensity can vary. Cumulative effects can result in reduced hollow tree density unless there is a specific retention of old trees

Stand A group of forest trees sufficiently uniform in species composition or age to be considered a management unit

Thinning Felling to decrease tree stem density within young regrowth forests to reduce competition for resources among trees and promote the growth of the stand (Florence 1996)

Variable Retention Harvests Creation of multi-aged stands in clearcut zones by retaining clumps, patches, or aggregates of old trees within the clearcut

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Chapter 6

Bats in the Anthropogenic Matrix: Challenges and Opportunities for the Conservation of Chiroptera and Their Ecosystem Services in Agricultural Landscapes

Kimberly Williams-Guillén, Elissa Olimpi, Bea Maas, Peter J. Taylor and Raphaël Arlettaz

Abstract Intensification in land-use and farming practices has had largely negative effects on bats, leading to population declines and concomitant losses of ecosystem services. Current trends in land-use change suggest that agricultural areas will further expand, while production systems may either experience further intensification (particularly in developing nations) or become more environmentally friendly (especially in Europe). In this chapter, we review the existing literature

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on how agricultural management affects the bat assemblages and the behavior of individual bat species, as well as the literature on provision of ecosystem services by bats (pest insect suppression and pollination) in agricultural systems. Bats show highly variable responses to habitat conversion, with no significant change in species richness or measures of activity or abundance. In contrast, intensification within agricultural systems (i.e., increased agrochemical inputs, reduction of natural structuring elements such as hedges, woods, and marshes) had more consistently negative effects on abundance and species richness. Agroforestry systems appear to mitigate negative consequences of habitat conversion and intensification, often having higher abundances and activity levels than natural areas. Across biomes, bats play key roles in limiting populations of arthropods by consuming various agricultural pests. In tropical areas, bats are key pollinators of several commercial fruit species. However, these substantial benefits may go unrecognized by farmers, who sometimes associate bats with ecosystem disservices such as crop raiding. Given the importance of bats for global food production, future agricultural management should focus on “wildlife-friendly” farming practices that allow more bats to exploit and persist in the anthropogenic matrix so as to enhance provision of ecosystem services. Pressing research topics include (1) a better understanding of how local-level versus landscape-level management practices interact to structure bat assemblages, (2) the effects of new pesticide classes and GM crops on bat populations, and (3) how increased documentation and valuation of the ecosystem services provided by bats could improve attitudes of producers toward their conservation.

6.1 Introduction

Agricultural areas cover approximately 40 % of our planet’s terrestrial ecosystems (FAOSTAT 2011), with the 5 billion ha of land under farming and grazing now surpassing the extent of the world’s forested areas (Robertson and Swinton 2005; Power 2010). Agricultural areas are expected to continue to expand with increasing human population growth and resultant resource use: Low- and middle-income countries will experience a 100 % increase in demand for agricultural products by 2050 (Defries et al. 2010; FAO 2011). In the face of increasing pressure on natural resources, the conservation of remaining natural areas is critical for the survival of multitudes of species. However, the ubiquity of agriculture means that farmland cannot be ignored in the context of landscape-level approaches to biodiversity conservation (Vandermeer and Perfecto 2007; Loos et al. 2014).

A growing body of research demonstrates that not only do some agricultural systems harbor high levels of biodiversity and provide a variety of ecosystem services (Tilman 1999; Foley et al. 2005; Tscharntke et al. 2005), but also that characteristics of these agricultural systems may have profound effects upon remaining natural areas (Perfecto and Vandermeer 2010). Agricultural matrices can vary drastically in their quality and permeability, impacting dispersal rates, and hence, long-term population stability of organisms found in less disturbed areas (Ricketts 2001; Laurance 2008; Perfecto and Vandermeer 2010; Tscharntke et al. 2012). On a local scale, different agricultural management approaches often coexist. Some rely on varying chemical inputs (pesticides, fertilizer), or novel plant types (e.g., genetically modified crops incorporating genes for characteristics such as insecticide functions), resulting in environmental contamination, pollution, and dissemination of toxins that could negatively impact biodiversity across multiple spatial scales (Nelson et al. 2009; Power 2010). As a consequence, agricultural management has effects not only on biodiversity, but also on human health and economies.

In the tropics, the expansion of export-oriented agriculture results from population growth and shifts in consumption patterns of developing nations, and is carried out mostly to the detriment of old growth forests and extensively managed grasslands such as pastures (Defries et al. 2010; Lambin and Meyfroidt 2011). As a consequence, croplands are still expanding dramatically, and agricultural practices are likely to further intensify in the near future (more chemical and mechanical inputs, reliance on genetically modified plants with novel manufactured traits). Short-term increases in yield will come at the cost of reduced structural and taxonomic diversity within agricultural systems (Loos et al. 2014) and concomitant loss of crucial ecosystem services.

An additional factor affecting agriculture in the Anthropocene is climate change and the need to adapt cultures to novel environmental conditions: Many areas may become unsuitable for cultivation of their current dominant crops, while extreme weather events may result in reduced yields. Resulting declines in calorie availability, particularly in the developing world (Nelson et al. 2009), will increase the need for agricultural practices that meet both productivity and sustainability goals (Tilman et al. 2002; McShane et al. 2011; Tscharntke et al. 2012). These trends portend major shifts in land-use patterns (Lambin and Meyfroidt 2011) and hence biodiversity, with agricultural intensification, forest and tree roost loss anticipated to have particularly negative effects on bat species richness, abundance, and functional diversity (Fischer et al. 2009, 2010; Jones et al. 2009).

These emerging trends pose major threats to farmland bat assemblages and populations (Jones et al. 2009; Kunz et al. 2011) and could negatively impact human populations by altering the ecosystem services that bats provide. Thus, there is a critical need to assess how agricultural management affects bat populations, and how affected bat populations will in turn affect agricultural production. In this chapter, we review the effects of agricultural land use and management on bat assemblages and the behavior and ecology of individual bat species at field, farm, and landscape scales (Vickery and Arlettaz 2012). We also review the developing literature on ecosystem services—and disservices—provided by bats in agricultural areas. Finally, we synthesize this information to suggest key management recommendations necessary to maintain bat populations in agricultural landscapes and highlight critical knowledge gaps that must be resolved in order to conserve bat diversity and ecosystem functions in a planet increasingly dominated by food production.

6.2 Methods

We used the Web of Knowledge, Google Scholar, and PubMed search engines to locate publications with the keywords “bats” AND “agriculture,” “agroforestry,” “farm,” and “farmland.” Given the potential importance of bats in provisioning ecosystem services in agricultural areas, we also searched for “bats” AND “ecosystem services,” “pollination,” “pest consumption,” “pest control,” and “pest limitation.” The majority of sources stemmed from peer-reviewed publications, although we also included Master’s and Ph.D. theses and published reports if results from the study in question were not available as journal articles. We also inspected the bibliographies of relevant publications. Each co-author focused on a specific geographic area (RA, assisted by Olivier Roth: Europe; BM: Australia and tropical Asia; EO: temperate North America; PT: sub-Saharan Africa; KWG: tropical Americas). Our searches were limited to publications with English language text or summaries. We focused on agriculture and animal husbandry for the production of calories for human or animal consumption, excluding forestry systems dedicated to timber or fiber production (see Law et al., Chap. 4), studies in which fallows or abandoned fields were the only agricultural systems investigated, as well as investigations that focused on fragmentation without explicit consideration of the effect of agricultural matrix (see Meyer et al., Chap. 3).

We divided results from the literature search into two broad categories of investigations: (1) How agricultural practices affect bat assemblages, ecology, behavior, and/or physiology; and (2) how bats affect agriculture through the provision of ecosystem services such as pollination and pest suppression. Within the first category, most studies addressed effects of land conversion and agricultural management on bat assemblage structure, abundance, activity levels, and behavior. We further subdivided results to consider habitat conversion to agriculture and agricultural intensification. We define agricultural intensification as consisting of at least one of the following: decreased structural complexity of native vegetation (natural and seminatural elements structuring the landscapes such as woodland patches and hedges), increased application of agrochemicals (pesticides, fertilizer), increased crop plant density, increased mechanization, or increased reliance on GM plants. We reviewed results from searches to locate studies which contrasted aspects of bat assemblage structure, abundance, activity, ranging behavior, or diet in either natural and agricultural habitat, or different agricultural systems of contrasting management.

To better quantify the responses of bats to habitat conversion and agricultural intensification across multiple disparate studies, we conducted a meta-analysis. We emphasize that this meta-analysis is based on correlational studies, rather than from controlled experiments; because assignment of treatment locations is not randomized in the majority of these studies, confounding factors could result in spurious effect sizes (Egger et al. 1998). We thus view our meta-analysis as a tool for exploring trends across a diverse suite of studies, with limited conclusive power.

We reviewed studies for the inclusion of mean values for at least one response variable in both natural and agricultural areas, or two or more agricultural areas of differing intensification; 32 studies using mist netting, harp trapping, acoustic monitoring, or a combination of these methods included appropriate data. We classify the response variable metrics into two separate categories for analyses, measures of species richness and measures of relative activity or abundance (i.e., pass rates from acoustic monitoring or capture rates from mist netting). We also consider habitat conversion and intensification responses separately.

For each pairwise comparison (natural–agricultural, or agricultural–agricultural), we calculated the effect size as the log odds ratio of the mean value from the lower intensity system divided by the mean from the higher intensity system. Thus, a positive effect size indicates higher species richness or activity/abundance in natural versus agricultural areas or lower intensity versus higher intensity agriculture. We followed García-Morales et al. (2013) and considered mean effect sizes with 95 % confidence intervals that did not include 0 as indicative of a significant effect. In the case of studies comparing multiple natural or agricultural habitats or presenting means for multiple species or species groups (i.e., producing multiple pairwise comparisons for any given combination of metric and response type), we averaged the odds ratio to avoid pseudo replication. Due to the diverse nature of the studies and a lack of clarity about numbers of replicates in some studies, we did not weight studies by sample size or replicates. For our analysis, we thus considered each study as an equally weighted case for the final model. We conducted analyses in R Version 3.0.2 (R Development Core Team 2013) using the packages lme4 and lmerTest. This diverse set of studies includes different methods (e.g., acoustic monitoring versus mist netting) from different regions with ecologically and taxonomically characteristic bat assemblages. To account for some of this variation, we included study method and continent as random effects. Fixed factors included latitudinal zone (temperate, subtropical, and tropical) and whether or not the high-intensity system comprised an agroforestry system (including monocultural orchards).

We also located several studies on ecotoxicology and demography, focusing on the effects of pesticide and GMOs use on bats. A complete review of the effects of pesticides on bats is beyond the scope of this chapter, particularly since bats and contaminants have received recent reviews (O’Shea and Johnston 2009; Bayat et al. 2014). We therefore focus on studies that explicitly link bat agrochemical exposure to changes in bat populations. Similarly, although fertilizers comprise a large portion of the chemical inputs to agriculture, their impacts on bats are indirect.

In considering the benefits of bats for agricultural production (i.e., crop yield), we focus on the provision of two ecosystem services: agricultural pest limitation by insectivorous bats and pollination by tropical bats. We did not consider their role as seed dispersers since human management of farmland vegetation limits the effect and value of bat seed dispersal. Similarly, although bat pollination is key for the unmanaged reproduction of several economically important crops, such as

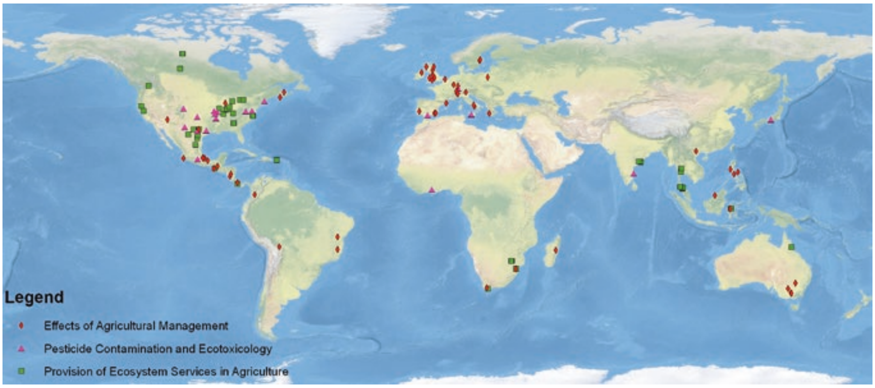

Fig. 6.1 Locations of studies on effects of habitat conversion or agricultural intensification (*red diamonds*) on bats, pesticide contamination (*pink triangles*) on bats, and ecosystem services (*green squares*) provided by bats in agriculture

bananas and agaves (Kunz et al. 2011), we did not consider these particular crops because they are mostly propagated vegetatively in such plantations. We instead focus on crops that are almost exclusively reliant on bat pollination under standard cultivation practices. Multiple investigations have characterized the diets of insectivorous bats at the order level, claiming potential consumption of pest insects. To more confidently assess consumption of insects damaging crops, we focused on studies in which known (species level identity) or probable (family level identity) agricultural pests were identified from feces of bats foraging in farms or areas dominated by agriculture. We exclude dietary studies that have sampled exclusively from natural habitats or do not describe the agricultural systems within which bats may have been foraging. We also briefly contrast these with ecosystem *disservices* of bats in agricultural areas. Bats are associated with costs to agriculturalists, particularly in the subtropics and tropics where frugivorous bats raid crops and sanguivorous bats attack domestic livestock. As with other sections, we focus on direct impacts on productive systems and do not consider the impacts of bat transmission of disease except where it directly impacts agriculture.

The majority of the nearly 140 investigations reviewed in this chapter have been conducted in temperate North America and Europe (Fig. 6.1). The bulk of studies documenting how habitat conversion or agricultural intensification affects bats has been conducted in Europe and the Neotropics (Fig. 6.1, Table 6.1). Within temperate zones, studies have focused mainly on annual cultivars and pasture, while research in tropical areas is dominated by studies on agroforestry systems, particularly coffee and cacao. Results on ecotoxicology of farmland bats come primarily from North America. Studies demonstrating the consumption of agricultural pests also derive primarily from North America, whereas studies of other ecosystem services provided by bats are limited to the tropics.

Table 6.1 Studies investigating the effects of agriculture on bat assemblage structure, ecology, or behavior across six continents

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
North America					
Braun de Torrez (2014)[a]	Temperate woodland savannah (mesquite-juniper)	Native and commercial pecan groves	General bat assemblage	≈ species richness, ↑ abundance, activity, habitat use	≈ species richness, abundance, activity, ↕ by species
Farrow and Broders (2011)	Boreal forest, temperate broadleaf forest	Mixed agricultural landscape	*Perimyotis subflavus*	↓ activity levels	
Gehrt and Chelsvig (2003)[a]	Temperate prairie, woodlands, and wetlands	“Intensive” agricultural landscape	General bat assemblage	↓ activity, habitat selection	
Henderson and Broders (2008)	Boreal forest, temperate broadleaf forest	Mixed agricultural landscape	*Myotis septentrionalis*	↓ mobility	
Rambaldini and Brigham (2011)[a]	Montane forest	Vineyards	*Antrozous pallidus*	↓ activity	
Tuttle et al. (2006)	Arid desert	Rangeland with troughs	*Myotis* spp., *Antrozous pallidus*		↓ drinking efficiency
Europe					
Arlettaz and Perrin (1995), Arlettaz (1996,1999), Arlettaz et al. (1997), 2001)	Temperate agricultural landscape within European Alps	Mixed farmland	*Myotis myotis, Myotis blythii*	↕ foraging habitat selection	↕ habitat use, ↓ dietary diversity
Bontadina et al. (2002)	Temperate agricultural landscape	Mixed farmland	*Rhinolophus hipposideros*	↓ foraging habitat selection	
Boughey et al. (2011)	Temperate agricultural landscape	Conventional farmland	*Pipistrellus* spp., *Nyctalus noctula*, *Eptesicus serotinus*		↕ activity
Davy et al. (2007)[a]	Mediterranean landscape	Olive groves	General bat assemblage	↓ activity	↓ activity

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Dietz et al. (2013)	Temperate agricultural landscape	Traditional farmlands (orchards, meadows, pastures)	*Rhinolophus ferrumequinum*, *Myotis emarginatus*	↑ habitat selection	↓ habitat selection
Downs and Racey (2006)	Temperate agricultural landscape	Mixed farmland with woodlands and hedges	*Pipistrellus* spp., *M. daubentonii*	↓ activity	↓ activity
Drescher (2004)	Temperate agricultural landscape	Apple orchards, vineyards, pastures	*Myotis myotis*	↑ foraging activity	↓ foraging activity
Ekman and de Jong (1996)[a]	Temperate agricultural landscape	Habitat islands within crop fields	*Myotis brandti*, *Eptesicus nilssoni*, *Plecotus auritus*, *Pipistrellus pipistrellus*	↓ activity, species occurrence	
Flaquer et al. (2008)	Mediterranean landscape	Olive groves, fruit orchards, rice	*Myotis emarginatus*	↑ foraging activity (olive groves)	↓ foraging activity (orchards, rice)
Frey-Ehrenbold et al. (2013)[a]	Temperate agricultural landscape	Seminatural to intensively managed farmland	General bat assemblage		↓ activity, species richness
Fuentes-Montemayor et al. (2011)	Temperate agricultural landscape	Conventional farmland and agri-environment scheme farmlands	*Pipistrellus* spp.		↑ activity
Fuller et al. (2005)[a]	Temperate agricultural/woodland landscape	Organic and non-organic cereals	General bat assemblage		↓ species density, activity
Jones and Morton (1992)	Temperate agricultural/woodland landscape	Hay/silage, grazing	*Rhinolophus ferrumequinum*		↓ activity
de Jong (1995)	Temperate agricultural landscape	Agriculture-dominated landscape	*Myotis* spp., *Pipistrellus pipistrellus*, *Plecotus auritus*	↓ activity	
Lesiński et al. (2013)	Temperate agricultural and woodlands	Annual crops (organic and conventional)	*Eptesicus serotinus*		↓ activity

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Lisón and Calvo (2011)[a]	Semiarid Mediterranean landscape	Rainfed olive/almond, irrigated peach/citrus	General bat assemblage	≈ activity	
Lisón and Calvo (2013)	Semiarid Mediterranean landscape	Rain fed crops/xerophytic vegetation	*Pipistrellus* spp.	↕ activity (varies by species)	
Lundy and Montgomery (2010)	Temperate agricultural landscape	Improved and unimproved pasture	General bat assemblage		↓ foraging activity
Obrist et al. (2011)[a]	Temperate agricultural landscape	Managed and abandoned chestnut orchards	General bat assemblage		↑ foraging activity
Pocock and Jennings (2007)[a]	Temperate agricultural landscape	Organic/conventional farmland; hay/silage fields	General bat assemblage		↓ activity (loss of linear features), ≈ activity (agrochemical use, silage)
Rainho (2007)	Semiarid Mediterranean landscape	Cereal crops and olive groves	General bat assemblage	↓ activity	↓ activity
Russ and Montgomery (2002)	Temperate agricultural landscape	Mixed farmland with woodlands, tree lines	General bat assemblage	↓ activity	↓ activity
Russo and Jones (2003)[a]	Mediterranean landscape	Traditional farmland habitats, chestnut woodland	General bat assemblage	≈ activity	
Russo et al. (2002)	Mediterranean landscape	Olive groves, traditional farmlands	*Rhinolophus euryale*	↑ home range composition, foraging time	
Stahlschmidt et al. (2012), Stahlschmidt and Brühl (2012)[a]	Temperate agricultural/ woodland landscape	Apple orchard	General bat assemblage	↓ activity (*Pipistrelle*, *Eptesicus*), ≈ activity (*Myotis*)	

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Verboom and Huitema (1997)	Temperate agricultural landscape	Linear features in traditional farmland landscapes	*Pipistrellus pipistrellus*, *Eptesicus serotinus*		↓ activity
Walsh and Harris (1996a, b)	Temperate agricultural landscape	Mixed farmland	General bat assemblage	↓ activity	↓ activity
Wickramasinghe et al. (2003, 2004)	Temperate agricultural landscape	Organic and conventional farmland	General bat assemblage		↓ activity
Australia					
Fischer et al. (2010)	Temperate woodland/ agricultural landscape	Low tree density livestock pasture	General bat assemblage		↓ activity
Hanspach et al. (2012)	Temperate woodland/ agricultural landscape	Pasture with varying levels of tree cover	General bat assemblage	↕ activity, species richness (peaks at intermediate tree cover)	↓ activity, species richness
Lentini et al. (2012)[a]	Temperate woodland/ agricultural landscape	Cereal, canola, and pasture-dominated landscape with and without linear features	Mollossidae; Vespertilionidae; Emballonuridae		↓ activity, ≈ species richness, feeding
Lumsden et al. (2002)	Temperate woodland/ agricultural landscape	Fragmented human-dominated landscape	*Nyctophilus geoffroyi*, *Chalinolobus gouldii*	↕ roost locations	↓ roost locations
Lumsden and Bennett (2005)[a]	Temperate woodland/ agricultural landscape	Pasture with varying densities of trees	General bat assemblage	↓ abundance, ↑ activity	↓ abundance, activity
Neotropics					
Avila-Cabadilla et al. (2009)	Tropical dry forest	Pasture	Phyllostomids	↓ abundance, species richness	
Castro-Luna and Galindo-González (2012)[a]	Tropical montane rainforest	Diverse and simplified shade coffee, pasture	Frugivorous phyllostomids		↓ abundance, species richness

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Estrada et al. (1993)	Lowland tropical rainforest	Shaded (coffee, cacao, mixed) and unshaded (citrus, allspice) plantations, pastures	Phyllostomids, non-phyllostomids sampled with mist nets	↓ species richness	↓ species richness
Estrada and Coates-Estrada (2001)	Lowland tropical rainforest	Shaded (coffee, cacao, mixed) and unshaded (citrus, allspice) plantation	General bat assemblage	↑ abundance, ↓ expected species richness	↓ abundance, expected species richness
Estrada and Coates-Estrada (2002)[a]	Lowland tropical rainforest	Coffee, cacao, citrus, banana, pasture	General bat assemblage	↑ abundance, ≈ species richness	
Estrada et al. (2004)[a]	Lowland tropical rainforest	Fencerows, citrus, pasture	Non-phyllostomids	≈ activity	↓ activity
Faria (2006)[a]	Brazilian Atlantic forest	Shade cacao in a forest dominant landscape	General bat assemblage	↑ abundance, species richness	
Faria et al. (2006)[a]	Brazilian Atlantic forest	Shade cacao in a cacao dominant matrix	General bat assemblage	≈ species richness	
Faria and Baumgarten (2007)[a]	Brazilian Atlantic forest	Shade cacao in two contrasting landscapes	General bat assemblage		↓ abundance, species richness
García Estrada et al. (2006, 2012)	Montane tropical rainforest	Shade coffee	Phyllostomids	≈ abundance, dietary diversity, ↓ species richness	≈ abundance, dietary diversity, species richness
Harvey et al. (2006)[a]	Tropical dry forest	High and low tree cover pasture	General bat assemblage	↓ abundance, species richness (frugivores, nectarivores)	↓ abundance, species richness (frugivores), ≈ abundance (nectarivores)
Harvey and González Villalobos (2007)[a]	Tropical humid forest, premontane wet forest	Cacao agroforest, banana agroforest, plantain monoculture	General bat assemblage	↕ abundance, species richness	↓ abundance, species richness

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Medellin et al. (2000)	Montane tropical rainforest	Cacao, oldfield, and corn	General bat assemblage	↑ abundance, ↓ species richness	↓ abundance, species richness
Medina et al. (2007)[a]	Tropical moist forest	High and low tree cover pasture	General bat assemblage	↓ abundance, species richness	↓ abundance, species richness
Numa et al. (2005)[a]	Tropical montane rainforest	Sun and shade coffee in contrasting landscapes	Phyllostomids	↑ abundance, ↓ estimated species richness	≈ estimated species richness (within landscape), ↓ estimated species richness (between landscapes)
Pineda et al. (2005)[a]	Tropical montane cloud forest	Shade coffee	General bat assemblage	↑ abundance, ≈ species richness	
Saldaña Vázquez et al. (2013)	Tropical montane rainforest	Shade coffee	*Sturnira ludovici*	↓ abundance, females	
Sosa et al. (2008)	Tropical montane rainforest	Shade coffee	General bat assemblage	≈ species richness	↓ abundance
Williams-Guillén and Perfecto (2010)[a]	Tropical montane rainforest	Shade coffee	Phyllostomids	↑ abundance, ≈ species richness	↓ abundance, ≈ species richness
Williams-Guillén and Perfecto (2011)[a]	Tropical montane rainforest	Shade coffee	Non-Phyllostomids	↓ activity (cluttered space foragers), ↑ abundance (open space foragers), ≈ species richness	↓ activity (cluttered space foragers), ↑ abundance (open space foragers), ≈ species richness
Vargas Espinoza et al. (2008)	Premontane tropical rainforest	Citrus orchards	General bat assemblage	≈ abundance, species richness	
Africa					
Noer et al. (2012)	Subtropical Savanna	Sugarcane	*Chaerephon pumilus*, *Mops condylurus*	↑ foraging time	

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Randrianandrianina et al. (2006)[a]	Tropical rainforest/ mixed use landscape	Smallholder gardens	General bat assemblage	↓ species richness, ↑ activity, foraging	
Sirami et al. (2013)[a]	Subtropical grassland, fynbos	Intensive wheat, vineyards, orchards	General bat assemblage	↓ abundance, ≈ species richness	↓ abundance, ≈ species richness
Taylor et al. (2013b)[a]	Subtropical Savanna	Macadamia	General bat assemblage	≈ activity (molossids), ↓ activity (vespertilionids)	
Asia					
Fukuda et al. (2009)[a]	Fragmented tropical rainforest	Orchards, palm oil	Hipposideridae, Vespertilionidae, Pteropodidae	↑ abundance, ↓ species richness	≈ abundance, ↓ species richness
Furey et al. (2010)[a]	Limestone karst, tropical rainforest	Landscapes dominated by rice paddies and degraded forest	Insectivorous bat assemblage		↓ abundance, ≈ species richness
Graf (2010)[a]	Montane tropical rainforest	Forest and shade cacao	General bat assemblage	↑ abundance, species richness	↓ species richness
Mildenstein et al. (2005)	Tropical moist forest	Fruit orchards and hardwood tree plantations	Pteropodidae bat assemblage	↓ habitat selection	
Sedlock et al. (2008)	Montane and premontane rainforest	Mosaic of pasture, root crops, orchards, and fallows	Insectivorous bat assemblage	↓ species accumulation	
Van Weerd and Snelder (2008)[a]	Tropical moist forest	Village homegarden polycultures, shrublands used for grazing	General bat assemblage	↑ abundance, species richness	↓ abundance, ≈ species richness

[a] Studies included in meta-analysis

“Conversion response” indicates effects of agriculture versus non-anthropogenic habitat; “intensification response” indicates effects of agricultural intensification (i.e., increased amount of agrochemicals, decreased structural complexity, infrastructure construction). “↓” indicates a negative effect on specified response variable; “↕” variable effects depending on species, ensemble, or habitat contrast; “≈” no marked effects observed; “↑” positive effect on response variable

6.3 Effects of Agricultural Intensity on Bat Assemblage Structure, Behavior, and Ecology

We found 70 studies addressing the effects of habitat conversion or management on the assemblage structure, behavior, or ecology of bats. Fifty-two studies assessed bats in both natural and agricultural areas. Twenty-two studies (42 %) demonstrated negative effects of habitat conversion, twelve (23 %) showed variable responses (e.g., only some species or ensembles declined, different agricultural systems were associated with different effects), twelve (23 %) showed increased richness, activity, or abundance in agricultural areas, and six (12 %) showed little or no difference between agricultural and natural areas. Forty-five studies addressed some aspect of agricultural intensification, with 38 of these (84 %) documenting a negative effect of intensification on bats, four showing variable or neutral (9 %) responses, while three studies (7 %) documented increases in bat richness, abundance, or activity in more intensive systems.

Response variables differ in response to habitat conversion and agricultural intensification (Fig. 6.2, Table 6.2), with measures of species richness showing no significant change between treatments. In contrast, measures of relative activity and abundance show stronger responses (Fig. 6.2). Agroforestry systems are more structurally similar to the original non-anthropogenic land uses, making them less intensive than annual crops dominated by one plant species or pasture systems lacking structural complexity. This relationship presumably explains why agricultural systems that incorporate trees and other large woody perennials on farms and throughout the agricultural landscape have little effect on bat activity and abundance (Fig. 6.2). Agroforestry systems appear to mitigate negative effects on bat assemblages in cases of both habitat conversion and agricultural intensification (Table 6.2).

Several studies have considered the effects of agricultural management at landscape scales versus focusing exclusively on farm-level management practices (Estrada et al. 1993; Ekman and de Jong 1996; Verboom and Huitema 1997; Numa et al. 2005; Faria et al. 2006, 2007; Faria and Baumgarten 2007; Fuentes-Montemayor et al. 2011; Boughey et al. 2011; Maas et al. 2013). Within agricultural areas, bat activity increases with proximity to natural areas (Estrada et al. 1993; Verboom and Huitema 1997; Boughey et al. 2011) and in less fragmented landscapes (Fuentes-Montemayor et al. 2011; Frey-Ehrenbold et al. 2013) or in landscapes with more natural elements such as hedgerows and woodlots (Verboom and Huitema 1997).

Agricultural areas also serve as matrix habitat connecting fragmented non-anthropogenic habitats. Although one study has suggested that landscapes dominated by crops and open fields have a stronger negative influence on bats than water (Ekman and de Jong 1996), a recent analysis of bat responses to isolation on islands versus in forest fragments embedded in agricultural matrix suggests that the anthropogenic matrix is more permeable than water matrix (Mendenhall et al.

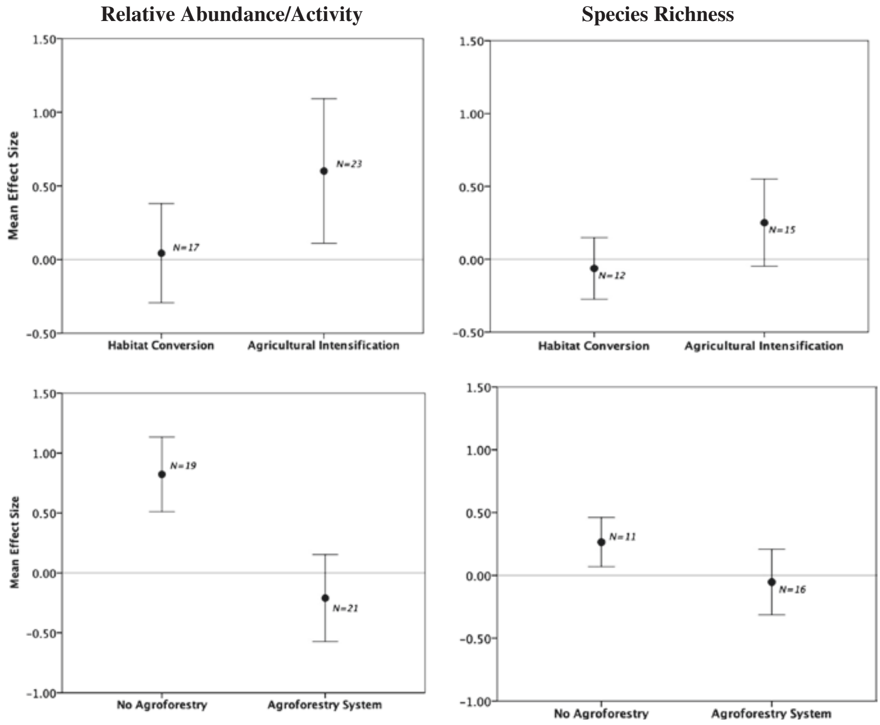

Fig. 6.2 Mean effect size (log odds ratio, circles) ±95 % CI of relative abundance and activity (*left*) and species richness (*right*) of habitat conversion versus agricultural intensification (*top row*), and of contrasts (both habitat conversion and agricultural intensification) with and without agroforestry systems (*bottom row*). Positive effect sizes indicate reductions in relative abundance and activity or species richness in response to habitat conversion and intensification

2014). Thus, agricultural intensification at the landscape level should make the matrix less permeable due to the reduction of natural resources and structural elements such as trees, affecting not only the persistence of bats in fragmented landscapes, but *also* the degree to which bat assemblages show a negative response to agriculture. A few investigations have confirmed such interactions between farm- and landscape-level intensification: Intensification in cacao matrices in Brazil (Faria et al. 2006, 2007; Faria and Baumgarten 2007) and coffee matrices in Colombia (Numa et al. 2005) resulted in reductions in the species richness and abundance of bats in diverse shade agroforests relative to forest fragments. In Europe, effects of landscape management on bat assemblage structure and ecology in temperate landscapes dedicated to the production of annual crops remain largely unexplored compared to the extensive information available at the field and farm scales.

Table 6.2 Effects of latitudinal zone and agroforestry systems on effect size (log odds ratio) for two response variable types under habitat conversion and agricultural intensification

Response variable	Land change type	Model	AIC	χ^2	*P*
Abundance/ activity	Habitat conversion	Effect size ~ (Method) + (Continent)	60.7		
		Effect size ~ Agroforestry + (Method) + (Continent)	**49.7**	**13.00**	**<0.001**
		Effect size ~ Latitude + (Method) + (Continent)	62.0	0.00	1.000
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	51.9	12.15	<0.001
	Intensification	Effect size ~ (Method) + (Continent)	52.4		
		Effect size ~ Agroforestry + (Method) + (Continent)	**49.2**	**5.22**	**0.022**
		Effect size ~ Latitude + (Method) + (Continent)	53.6	0.00	1.000
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	50.6	4.923	0.026
Species richness	Habitat conversion	**Effect size ~ (Method) + (Continent)**	**20.7**		
		Effect size ~ Agroforestry + (Method) + (Continent)	21.7	0.99	0.319
		Effect size ~ Latitude + (Method) + (Continent)	24.0	0.00	1.000
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	24.1	1.82	0.178
	Intensification	**Effect size ~ (Method) + (Continent)**	**22.9**		
		Effect size ~ Agroforestry + (Method) + (Continent)	24.4	0.54	0.460
		Effect size ~ Latitude + (Method) + (Continent)	26.3	0.06	0.806
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	27.0	1.34	0.248

Parentheses indicate random effects, and *bold text* indicates best fitting model based on AIC value

6.4 Pesticide Impacts on Bat Populations

Agricultural intensification may remove potential habitat for bats and their prey; the effects of increased agrochemical inputs, such as increased exposure and changes in prey availability, may put resident bats under further pressure.

Bats may directly consume pesticides by feeding on fruits, flowers, and arthropods exposed to chemical application. Even bats foraging outside of agricultural areas can be exposed to pesticides via biomagnification as residues are incorporated into the tissues of organisms at higher trophic levels (Bayat et al. 2014).

Investigations of exposure of bats to pesticides and its effects on physiology and mortality first appeared in the 1970s, amid a wave of growing concern regarding the effects of organochlorine pesticides (e.g., DDT, DDE, dieldrin, lindane, endosulfan, aldrin) on ecosystems and observations of declining bat populations at high-profile sites such as the Carlsbad Caverns in New Mexico, USA (Clark 1988, 2001). In some cases, DDT and other organochlorines were even applied directly to bat roosts in efforts to exterminate "vermin" (Kunz et al. 1977), and declines in high-profile bat colonies were linked to organochlorine use (Clark et al. 1978; Clark 2001). Even sublethal exposure to pesticides can have negative consequences for bats, resulting in increased metabolic rates (Swanepoel et al. 1998), and ingestion of pesticide residues on arthropods may poses a potential reproductive risk to certain bat species (Stahlschmidt and Brühl 2012).

Organochlorine residues have been documented in bats in a wide variety of both agricultural and non-agricultural landscapes, although several studies have found increased contaminant loads in bats sampled near agricultural areas (Clark and Prouty 1976; White and Krynitsky 1986) or near sites of pesticide manufacture (O'Shea et al. 2001). In some cases, temporal changes in levels of different contaminants reflect shifts in local agricultural practice as farmers adopt new pesticide regimes (Miura et al. 1978; Clark et al. 1980). Organochlorines are notorious for their persistence in ecosystems, and a variety of studies demonstrate that bats continue to harbor these contaminants in their tissues 20–30 years after the use of these pesticides was banned in sampling areas (Clawson and Clark 1989; Guillén et al. 1994; Schmidt et al. 2000; Sasse 2005). In some cases, persistence may reflect the continued use of these pesticides in lower income nations, as may be the case for the migratory *Tadarida brasiliensis* (Thies and Thies 1997; Bennett and Thies 2007). Investigations in India (Senthilkumar et al. 2001) and Benin (Stechert et al. 2014) have detected levels or metabolites of organochlorines in bat samples indicative of continued recent use in these regions, especially to fight against malaria. Furthermore, pesticide standards vary between different countries, application often appears to occur non-selectively, and farmers with limited training (especially in developing countries, where agricultural expansion is greatest) are likely to be unaware of the multitude of negative nontargeted environmental impacts affecting human health and biodiversity (Tilman et al. 2001; Yadav 2010).

Despite the clear negative impacts of organochlorines on bats, the effects of agrochemical classes such as pyrethroids and neonicotinoids remain largely unknown (O'Shea and Johnston 2009; Quarles 2013; Bayat et al. 2014), although recent research demonstrates a negative impact on birds (Hallmann et al. 2014). In North America, pesticide contamination has been implicated in bat mortality associated with the fungal pathogen causing white-nose syndrome (WNS), since pesticide load can lead to immunosuppression and endocrine disruption that could make bats more vulnerable to infection (Kannan et al. 2010). "Back of the envelope" calculations suggest declines in bat populations attributed to WNS could translate into an additional 1320 metric tons of insects escaping predation each year (Quarles 2013). The trickle-down impacts on agricultural production could be substantial, although quantitative evidence is lacking. The effects of GM crops incorporating insecticidal traits have been investigated largely in the context of the provisioning of predation services (Federico et al. 2008; Lopez-Hoffman et al. 2014; see next section); however, declines in pest numbers associated with the use of these crops could result in population declines of insectivorous bats (Lopez-Hoffman et al. 2014).

6.5 Ecosystem Services Provided by Bats in Agricultural Systems

6.5.1 Insectivorous Bats and Pest Limitation

Of the potential ecosystem services provided by bats, their role in consuming insect pests has received the most attention within agricultural systems. Insectivorous bats have a global distribution and have long been identified as key suppressors of arthropod pests in agricultural systems (Kunz et al. 2011). However, surprisingly little evidence exists quantifying the impact of their predation on arthropod populations, plant damage, or its economic value (Boyles et al. 2013; Maas et al. 2013). Several studies have characterized diets of insectivorous bats (reviewed by Kunz et al. 2011), and the recent development of DNA-based methods for dietary analysis provides an unprecedented amount of detail on the composition of bat diets and allows for the identification of individual pest species. Although few studies have documented direct impacts of bat predation on agricultural pests, an increasing body of evidence documents pest consumption, impacts on arthropods, and estimates of direct economic impacts.

We review 15 studies documenting the consumption of known or probable crop pests by insectivorous bats (Table 6.3). The diets of temperate North American insectivores have received particular attention. Many bat species consume lepidopterans, and studies in North America demonstrate bat predation on devastating pests such as corn earworm (*Helicoverpa zea*) and fall armyworm (*Spodoptera frugiperda*) moths (Lee and McCracken 2005; McCracken et al. 2012). Bat species across the world feed on folivorous beetles from a variety of damaging families

Table 6.3 Dietary investigations of insectivorous bat in agricultural areas documenting consumption of pest insect families or species

Study region	Source	Bat species	Crop	Pest insects consumed
Africa (South Africa)	Taylor et al. (2012, 2013a)	Various species	Macadamia nuts	• Hemiptera: *Nezara viridula*
Africa (Swaziland)	Bohmann et al. (2011)	*Chaerephon pumilus*, *Mops condylurus*	Sugarcane	• Hemiptera: Aphidadae, Lygaeidae, Pentatomidae • Lepidoptera: *Eldana saccharina*, *Mythimna phaea*
Asia (Thailand)	Leelapaibul et al. (2005)	*Chaerephon plicatus*	Rice	• Hemiptera: *Sogatella* sp.
Europe (Switzerland)	Arlettaz and Perrin (1995, 1997, 2001)	*Myotis myotis*, *M. blythii*	Agricultural landscape with orchards, pasture	• Coleoptera: *Melolontha* sp.
Latin America (Mexico)	Williams-Guillén (unpublished data)	Various species	Shade coffee	• Coleoptera: *Hypothenemus hampeii*, *Rhabdopterus jansoni* • Orthoptera: *Idiarthron subquadratum*
North America (Canada)	Clare et al. (2011)	*Myotis lucifugus*	Agricultural landscape	• Coleoptera: *Phyllophaga* spp., *Amphimallon majale*, *Phyllobius oblongus*; Curculionidae, Chrysomelidae • Diptera: *Delia antiqua* • Hemiptera: Aphididae • Lepidoptera: *Korscheltellus lupulina*
North America (Canada)	Rambaldini and Brigham (2011)	*Antrozous pallidus*	Grapes	• Coleoptera: Curculionidae, Tenebrionidae • Orthoptera: Acrididae
North America (USA)	Braun de Torrez (2014)	Various species	Pecan	• Lepidoptera: *Acrobasis nuxvorella*

(continued)

Table 6.3 (continued)

Study region	Source	Bat species	Crop	Pest insects consumed
North America (USA)	Lee and McCracken (2005)	*Tadarida brasiliensis*	Landscape with corn and cotton	• Coleoptera: Scarabaeidae • Hemiptera: Cercopidae, Delphacidae, Pentatomidae • Lepidoptera: *Spodoptera frugiperda, Helicoverpa zea*
North America (USA)	McCracken et al. (2012)	*Tadarida brasiliensis*	Corn, cotton	• Lepidoptera: *Helicoverpa zea*
North America (USA)	Storm and Whitaker (2008)	*Eptesicus fuscus*	Agricultural landscape	• Coleoptera: Curculionidae • Hemiptera: Cicadelidae
North America (USA)	Whitaker (1995)	*Eptesicus fuscus*	Agricultural landscape	• Coleoptera: Curculionidae, Scarabaeidae • Hemiptera: Cicadellidae, Pentatomidae

and species, particularly weevils, leaf beetles, and scarab beetles. Bats may also be underappreciated predators of hemipteran pests, with many studies demonstrating consumption of leafhoppers, froghoppers, spittle bugs, and stink bugs. We emphasize that direct consumption alone is not sufficient to prove that bats are limiting insect pests: Damaging insects may comprise a small proportion of the diet, and nearly every study summarized in Table 6.3 also demonstrated consumption of the predatory arthropods that comprise part of the assemblage of natural enemies. Such intraguild predation could counteract the pest-limiting effects of bat insectivory (Brashares et al. 2010), although herbivores generally comprise the majority of diet by volume in investigations using fecal pellet dissections (Kunz et al. 2011). That the relative abundance, diets, and movements of bats may track populations of agricultural pests (Lee and McCracken 2005; McCracken et al. 2012; Taylor et al. 2013b) suggests that many species are indeed preying heavily on herbivorous insects. This has been assessed in mouse-eared bats, *Myotis* spp., that track cyclic, massive local aggregations of cockchafers known since centuries for the damages they cause to fruit trees in Central Europe (Arlettaz 1996; Arlettaz et al. 2001).

During lactation, small bat species consume 75 % to over 100 % of their body weight each night (Kurta et al. 1989; Kunz et al. 1995, 2011), and a single maternity colony of 1 million Brazilian free-tailed bats is capable of consuming over 8 tons of insects per night (Kunz et al. 2011). These numbers suggest the staggering potential for bat predation to limit pest insect populations and provide a valuable ecosystem service for agricultural production. Until recently, surprisingly little work had quantified the impact of bat predation on insect biomass (Maas et al. 2015). Exclosure studies have long been a mainstay for studying the impacts of bird predation; however, it was widely assumed that such methods would not be suitable to measure the impact of bat insectivory, due to the misconception that all insect eating bats take highly mobile, flying prey. However, bats capable of gleaning insect prey from substrates exist throughout the world, and their impacts could be monitored via exclosure studies and disentangled from those of birds. This approach has been used fruitfully in the past five years, demonstrating significant increases in arthropod density when bats are absent, in agroecosystems (Williams-Guillén et al. 2008; Maas et al. 2013), reforestation (Morrison and Lindell 2012), and natural forests (Kalka et al. 2008). In Mexican polycultural shade coffee, arthropod densities on coffee plants during the rainy season nearly doubled in the absence of bats, with marked increases in densities of hoppers, katydids, cockroaches, and beetles (Williams-Guillén et al. 2008). However, no effects on plant damage were observed in that study, perhaps as a result of the short duration of the study or release of spiders and other arthropod predators. In Indonesian shade cacao, excluding bats resulted in a 29 % increase in arthropod numbers (Maas et al. 2013). Although herbivory did not differ significantly between cacao plantations with different levels of shade or proximities to primary habitats within the landscape, exclosure of bats resulted in a significant decrease in yields, with the effects of bird and bat predation together valued at an astonishing US $730 per ha and year (bat predation was valued at US $520 per ha and year). However, the effects of bat predation on crop pests are not universal: An exclosure study in Costa Rican coffee found that excluding bats alone had virtually no effect on the density or damage caused to beans by the devastating coffee berry borer (Karp et al. 2013).

Exclosure studies are not suitable to measure the impact of high-flying insectivores, such as molossids. However, careful extrapolations taking into account bat feeding rates, population sizes, pest reproduction, and survivorship, and the costs of inputs allow for estimation of the economic impact of predation for other bats, particularly molossids forming large colonies. Cleveland et al. (2006) estimate that Mexican free-tailed bats (*T. brasiliensis*) feeding on the cotton bollworm moth in Texas provide pest limitation services worth roughly US $183 per ha and year to cotton growers. Extending these estimates to agricultural areas throughout the USA suggests that bat predation could have a value of nearly US $23 billion annually (Boyles et al. 2011). These benefits hold for both conventional and transgenic cotton (Federico et al. 2008), although the introduction of *Bt* cotton (a genetically modified organism whose tissues produce an insecticide derived from the bacterium *Bacillus thuringiensis*), coupled with reduced area in cotton cultivation, has led to a decline in the overall value of this pest limitation service (Lopez-Hoffman et al. 2014).

Valuation of bat-mediated pest suppression is limited for staple crops and for sites outside the southern USA. In northern Mexico, the impact of *T. brasiliensis* predation on avoided agricultural costs across a variety of staple and commodity crops was estimated at a far more modest $19 per ha and year (Gándara Fierro et al. 2006). In Thailand, the value of wrinkle-lipped bat (*Tadarida plicata*) predation on a major rice pest, the white-back planthopper (*Sogatella furcifera*), was estimated to have a monetary value of $1.2 million annually (Wanger et al. 2014). This estimate results in a seemingly paltry $0.13 per ha and year value considered against Thailand's 8.7 million ha (Redfern et al. 2012) of rice paddies, but in this case an economic approach obscures the true value of the service: This single bat species prevents the loss of nearly 2900 metric tons of rice per year, enough to feed Thailand's entire population of 66.8 million people for a week. Such investigations underscore the potentially grave consequences for human food security should global bat populations continue declining (Kunz et al. 2011).

6.5.2 Nectarivorous Bats and Pollination Services

Pollination services to crops by bats are poorly documented. Bats are key pollinators of wild *Agave* and *Musa* spp. (Kunz et al. 2011). Although these plants are propagated vegetatively under cultivation, bat pollination plays a critical role in sustaining genetic diversity in the wild relatives of these domestic species, a key aspect of maintaining future food security (Hopkins and Maxted 2011). Within the Americas, several bat pollinated cacti are commercially important fruit species (Kunz et al. 2011). Several species of the hemiepiphytic cactus *Hylocereus* (pitahaya, dragonfruit) endemic to the Neotropics are now cultivated worldwide. In Mexico, visitation of *Hylocereus undatus* fruits by bats resulted in significantly higher fruit set than did visitation by diurnal pollinators (Valiente-Banuet et al. 2007). Although *H. undatus* is self-compatible, other species such as *H. costaricensis* (an important fruit crop in southern Mesoamerica) apparently rely on pollination by bats and sphingid moths (Weiss et al. 1994; Le Bellec et al. 2006). Nectarivorous bats, particularly the cave nectar bat (*Eonycteris spelaea*) feed on the flowers of tree beans or petai (*Parkia* spp.) (Bumrungsri et al. 2008a, b, 2013) and durian (*Durio zibethinus*) (Bumrungsri et al. 2008b), pollinating these plants in the process. The economic value of this pollination has been estimated at over US $13 million annually in three provinces of Thailand (Petchmunee 2008).

6.6 The Issue of Ecosystem Disservices of Bats to Agricultural Production

Unfortunately, while the ecosystem services provided by bats are largely invisible, their disservices are obvious. In the Paleotropics, crop raiding by frugivorous pteropodids can cause substantial losses of commercial fruits (see Aziz et al., Chap. 12). For example, in Indian vineyards, *Cynopterus sphinx* damages up to 90 % of the crop along peripheries of plantations and may cause revenue losses of up to US $590 per ha and year (Srinivasulu and Srinivasulu 2002). In the Neotropics, sanguivorous vampire bats can cause substantial economic damage: Estimates for 1968 placed losses at $47.5 million USD for over 512,000 rabies-related cattle deaths in Latin America (Arellano-Sota 1988). Harassment by vampire bats can put cattle off their feed, resulting in annual weight losses estimated at roughly 40 kg/head and milk production loss of 261 L/head (Schmidt and Badger 1979). These estimates fail to take into account the effects of vampire bats on the medium and small domestic animals (e.g., chickens, pigs, goats) that provide critical sources of animal protein for millions of smallholder farmers across the region.

Not surprisingly, farmers with first-hand experiences of economic losses engendered by bats are more likely to have negative attitudes or report a willingness to destroy bat roosts (Reid 2013). Failure to explicitly address the negative impacts of some bat species likely reduces the efficacy of conservation messages; meanwhile, practical measures to reduce these disservices could benefit multiple bat species by reducing indiscriminate persecution. Different functional groups provide most of the ecosystem services (insectivores, nectarivores) and disservices (frugivores, sanguivores). However, local farmers may not distinguish between these groups. For example, farmers and agricultural technicians in Latin America often attempt to cull vampire bat populations by destroying bat roosts; unfortunately, the widespread belief that all bats are "*vampiros*" frequently results in the destruction of colonies of beneficial bat species (Mayen 2003; Aguiar et al. 2010). If local people perceive the ecosystem services of one bat group as offsetting the damages of another, then an ecosystem service approach could provide a framework for bat conservation more broadly. Unfortunately, the extent to which knowledge of ecosystem services changes attitudes toward bats in developing countries remains unknown.

6.7 Discussion

Our review suggests that in all biogeographic regions investigated, at least some bat species persist in and exploit agricultural areas. In many agricultural systems (e.g., tropical agroforestry or historical landscapes of Europe), bat assemblages maintain richness and may even exceed abundances observed in unmanaged areas. Nevertheless, agricultural intensification has a generally negative effect on bats and thus presumably on the ecosystem services they provide. Our analysis did not address differences between bat taxa in their sensitivity to habitat change and intensification. However, evidence from speciose assemblages suggests that forest-adapted insectivorous species are particularly sensitive to habitat conversion (Medellin et al. 2000; Faria and Baumgarten 2007; Williams-Guillén and Perfecto 2010), implying that in some regions, this valuable ecosystem service could be particularly vulnerable to loss in the face of habitat loss.

Although few investigations have considered the scale of intensification, limited information suggests that less managed systems embedded in regions dominated by intensive agriculture may show depauperate bat faunas (Numa et al. 2005; Faria et al. 2007). Declines in bat populations in agricultural regions are concerning not only from the point of view of biodiversity conservation but also regarding human well-being and food security, especially in many tropical areas where smallholder farming systems are dominant. Ongoing losses of these generalist vertebrate predators could have major impacts on insect pest limitation for a wide variety of staple and commodity crops. However, the smallholder farmers in developing nations who most depend on the ecosystem services provided by bats (due to limited access to manufactured inputs or cultivation of bat pollinated crops) may have highly negative attitudes toward these mammals as a result of visible damages caused to crops and livestock (López del Toro et al. 2009; Reid 2013), whereas beneficial impacts on crop yield productivity and the value of biodiversity (i.e., increased ecosystem resilience) are often unknown or unappreciated (Williams-Guillén, unpublished data). These results suggest a pressing need to reassess common approaches to conservation and agricultural management in the Anthropocene.

6.7.1 Sparing, Sharing, and the Devaluation of Manufactured Capital

Given the anticipated need to nearly double global food production in the twenty-first century, a vigorous debate has emerged with respect to the most viable path to increase production without degrading ecosystem services or reducing biodiversity: land sparing, which posits that increased intensification and yields will reduce pressure to convert non-agricultural lands, versus land sharing, in which agricultural areas are less intensively farmed in order to increase associated biodiversity and habitat permeability (Fischer et al. 2008). Given the vagility and critical role of bats in agricultural production, land sharing approaches might be preferable with respect to the provision of bat-dependent ecosystem services. Many sensitive bat ensembles and species (e.g., many forest-adapted and insectivorous species, e.g., from Phyllostomidae or Vespertilionidae) will require well-structured farmland, i.e., cultivated landscapes including patches of natural and seminatural features for their long-term existence. However, not only do many bat species thrive in diverse agricultural landscapes, but also their loss could affect the provision of pest suppression and pollination services and result in reduced crop productivity. Given the many disadvantages of chemical control of pests, managing agricultural landscapes to maximize the abundance and diversity of bats and other natural enemies must form a key aspect of sustainable agricultural production. However, the design and management of such systems to maximize bat diversity, activity, and ecosystem services is largely unknown, although European conservationists are at the forefront with their strategies to promote biodiversity-friendly farming.

Chemical and mechanical inputs are not the only tools of agricultural intensification. Within recent decades, genetic modification of crops (e.g., *Bt* corn and cotton) has become increasingly prevalent (James 2011). In the short term, adoption of such varieties does reduce the need to rely on bats and other predators for pest limitation (Lopez-Hoffman et al. 2014), resulting in a “devaluation” of the natural capital provided by bats, and undermines arguments for bat conservation that are based exclusively on provision of ecosystem services. However, as is the case with pesticides, insects are rapidly evolving resistance to *Bt* crops across the world, resulting in a rapid devaluation of *manufactured* capital (Lopez-Hoffman et al. 2014). While the value of bats’ natural capital may fluctuate, it likely devalues far less slowly: Bats and insects are engaged in an evolutionary arms race dating back millions of years (Conner and Corcoran 2012). Without bats to buffer the inevitable loss of efficacy of chemical inputs and GM crops, the technological advances that make agricultural intensification possible leave production vulnerable to potentially catastrophic failures to limit pest damage.

6.8 Research Priorities

6.8.1 Filling in Biogeographical Knowledge Gaps

Although the effects of habitat conversion and management have been well investigated in Europe and the Neotropics, the extent to which these processes may differ in other regions of the world remains unknown. We highlight a particular lack of knowledge from Africa and Asia; we did not find any studies from East Asia, although we suspect information exists in the Chinese language literature. Understanding the types and magnitudes of ecosystem services provided by bats in a variety of agricultural systems and regions is particularly important.

6.8.2 Linking Farm Management, Ecosystem Services, and Landscape-Level Processes

The effects of farm-level management on biodiversity and ecosystem services cannot be adequately considered without taking account of landscape-level processes (Tscharntke et al. 2005; Vickery and Arlettaz 2012). Nevertheless, the extent to which local- and landscape-level management interact to shape pest suppression or pollination services is largely uninvestigated. The effect of bats in limiting arthropod pests in agricultural areas is still poorly documented. However, the limited data that exist can demonstrate a vexing degree of divergence in results. For example, bats in Mexican shade coffee have substantial effects on herbivorous insects (Williams-Guillén et al. 2008), while bats in Costa Rican shade coffee had no significant effect on herbivores (Karp et al. 2013). In Indonesian cacao agroforestry systems, insectivorous bats strongly contribute to the suppression of many different pest insect groups and crop yield productivity across gradients of local shade-tree management and forest proximity within the agricultural landscape (Maas et al. 2013). In general, the study sites differ in landscape structure and land use, local farm history and management, habitat dynamics and conversion, intensity of farming practices, and vertebrate insectivore assemblage structure. Elucidating the factors of bat ecosystem service provision is key to managing agricultural areas to sustain bat populations and enhance food production (Maas et al. 2015).

6.8.3 Pest Suppression in the Face of Climate Change, Pesticides, and GM Crops

Not only will warming climates lead to shifts in the areas suitable for agricultural production, but it will also likely lead to range expansions of tropical pests, increases in pest numbers and damage, with a parallel risk of a drop in the efficacy of pest suppression by natural enemies that might be negatively affected by climate change (Thomson et al. 2010; Bebber et al. 2013). Such changes will make the ecosystem services provided by generalist predators like insectivorous bats more valuable than ever before. However, if agricultural adaptation to climate change relies on landscape-level intensification as a strategy, bats are likely to decline further, reducing their provision of pest suppression services. Despite the myriad negative effects of pesticides (i.e., affecting livelihoods, food security, environment, and health; reviewed by Yadav 2010), farmers across the world might turn to agrochemicals as a first response to increases in pest damage (Wilson and Tisdell 2001), with the Old World's rapid development of more environmentally friendly farming practices appearing as an exception in this general move. As reviewed in this chapter, older pesticide classes such as organochlorines have particularly detrimental effects on bat populations. However, the degree to which newer pesticide classes affect bats is largely unknown. The neonicotinoids, once touted for their low toxicity, have now been linked to major declines in bees (Van der Sluijs et al. 2013) and more recently in several species of passerines as a result of insect resource depletion (Hallmann et al. 2014). The extent to which use of next-generation pesticides and GM crops is driving and interacting with bat declines and resultant increases in pest damage is a critical research area.

6.8.4 Quantifying Impact and Value Across Crops and Biomes

Additional valuation of bats' ecosystem services could provide both guidance for bat management priorities in agricultural areas and compelling rationales for conservation. However, valuation efforts have focused almost exclusively on commodity crops quantified along the single dimension of monetary value. Most of the world's smallholder farmers focus on staple crop cultivation and may not have the means to substitute the manufactured capital of pesticides and GM crops for bat predation. As Wanger et al. (2014) demonstrate, valuation based on dollars of damage prevented misses many of the criteria most important to subsistence farmers seeking food security. There is an urgent need to better understand the importance of bat ecosystem services across a variety of crop types, regions, and management approaches. Research also highlights the importance of better quantifying the fluctuations in bat service provision across years and seasons, in relation to population fluctuations, reproductive phenology, and agricultural management (Lopez-Hoffman et al. 2014; Wanger et al. 2014; Maas et al. 2015). This level of local, nuanced knowledge is key to managing pest suppression services in such a way that they are actively used as alternatives to agrochemical inputs and GM crops, and to contribute to more biodiversity-friendly and sustainable land-use practices (Tilman et al. 2002; Maas et al. 2015).

6.8.5 Changing Attitudes and Behaviors Toward Bats in the Developing World

Although the conservation of tropical biodiversity is highly beneficial to global society (Rands et al. 2010), ultimately it is the attitudes and beliefs of farmers and other rural populations that will determine its fate (Brechin et al. 2002; Tscharntke et al. 2012). Throughout the world, bats are subject to misconceptions and poor public perceptions (see Kingston and Barlow, this volume Chap. 17). However, exposure to environmental education can significantly decrease negative attitudes toward bats (López del Toro et al. 2009; Prokop et al. 2009; Reid 2013). These results suggest that reducing bat disservices, conducting environmental education, and building local valuation of beneficial bats could work in concert to improve conservation outcomes. As much as there is a critical need to manage agricultural landscapes to conserve bats, there is a parallel need to understand the local drivers of attitudes toward bats and to develop culturally appropriate, evidence-based interventions that encourage farmers to sustainably manage bat populations and other biodiversity associated with ecosystem services and ecosystem resilience.

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Chapter 7
Dark Matters: The Effects of Artificial Lighting on Bats

E.G. Rowse, D. Lewanzik, E.L. Stone, S. Harris and G. Jones

Abstract While artificial lighting is a major component of global change, its biological impacts have only recently been recognised. Artificial lighting attracts and repels animals in taxon-specific ways and affects physiological processes. Being nocturnal, bats are likely to be strongly affected by artificial lighting. Moreover, many species of bats are insectivorous, and insects are also strongly influenced by lighting. Lighting technologies are changing rapidly, with the use of light-emitting diode (LED) lamps increasing. Impacts on bats and their prey depend on the light spectra produced by street lights; ultraviolet (UV) wavelengths attract more insects and consequently insectivorous bats. Bat responses to lighting are species-specific and reflect differences in flight morphology and performance; fast-flying aerial hawking species frequently feed around street lights, whereas relatively slow-flying bats that forage in more confined spaces are often light-averse. Both high-pressure sodium and LED lights reduce commuting activity by clutter-tolerant bats of the genera *Myotis* and *Rhinolophus*, and these bats still avoided LED lights when dimmed. Light-induced reductions in the activity of frugivorous bats may affect ecosystem services by reducing dispersal of the seeds of pioneer plants and hence reforestation. Rapid changes in street lighting offer the potential to explore

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mitigation methods such as part-night lighting (PNL), dimming, directed lighting, and motion-sensitive lighting that may have beneficial consequences for light-averse bat species.

7.1 Introduction

Anthropogenic change is altering ecosystems at unprecedented rates and humans now dominate most ecosystems (Vitousek et al. 1997; McDonald 2008). Urbanisation in particular has major impacts on bat activity and abundance (Jung and Threlfall 2016), and one aspect of global change that occurs predominately, but not exclusively, in urban areas is increased artificial light at night. Almost a fifth of the global land area was affected by light pollution in 2001 (Cinzano et al. 2001). Although night-time brightness generally increased in Europe between 1995 and 2010, regional patterns are complex, with some localised declines (Bennie et al. 2014). However, the biological impacts of light pollution have only recently been recognised (Longcore and Rich 2004).

Being nocturnal, bats are likely to be affected by light pollution. In this chapter, we review the types of artificial light that bats experience, describe how light pollution has become more widespread in recent years, show how technological changes may lead to significant reductions in light pollution and describe some of the physiological consequences of light pollution that may be relevant to bats. We then discuss how artificial lighting affects the insect prey of bats, and why some bats may benefit from the growth in artificial lighting, whereas others are affected detrimentally. After highlighting some aspects of bat vision, we describe the shift from observational to experimental studies of how bats respond to lighting. Finally, we identify some of the major knowledge gaps and suggest priorities for future research on the effects of artificial lighting on bats.

7.2 Types of Artificial Light

The electromagnetic spectrum encompasses radiation with wavelengths ranging from less than a nanometre (gamma rays) to a kilometre (radio waves) (Campbell 2011). While humans perceive wavelengths between 400 and 700 nm as 'visible light' (Purves and Lotto 2003), birds, fish and invertebrates can detect light in the ultraviolet (UV) range (10–400 nm). Recent work suggests that UV sensitivity may be widespread among mammals (Douglas and Jeffery 2014), and snakes and beetles can detect spectral emissions in the infrared range (700–1000 nm) (Schmitz and Bleckmann 1998; Land and Nilsson 2012).

Artificial lighting has infiltrated all aspects of human life both indoors and outside (Gaston et al. 2012). Here, we focus on street lighting because of its universal use and potential for ecological impacts (Gaston et al. 2012). Different types of street light have distinct spectral signatures (Fig. 7.1); their primary emissions

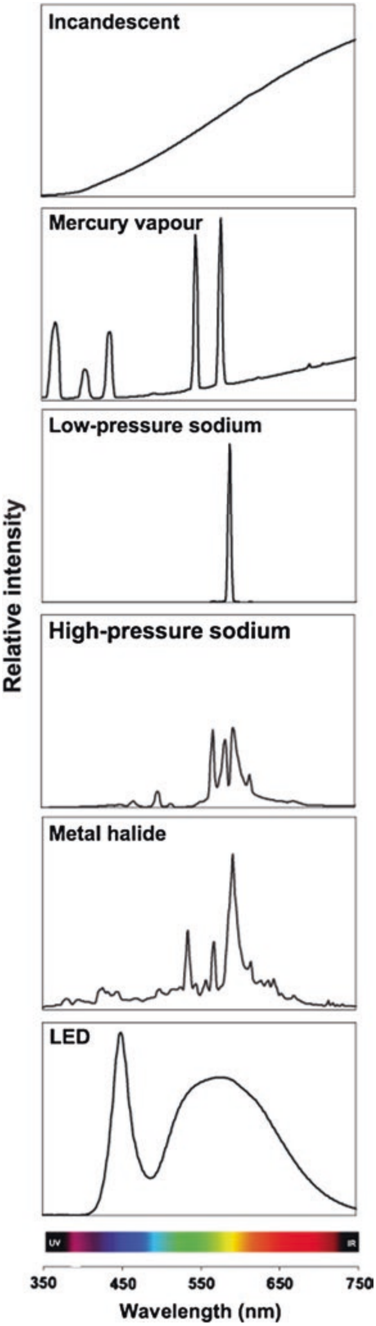

Fig. 7.1 The spectral content of different light types varies considerably. The spectral composition of common lighting technologies is shown. From Gaston et al. (2013)

depend on the type of reactive material or coating in the lamps (Buchanan 2006). Incandescent lamps, developed by Thomas Edison in 1880, mainly emit long wavelengths with a maximum intensity between 900 and 1050 nm (Elvidge et al. 2010). Despite improvements such as the quartz halogen lamp, which uses an inert gas to preserve the tungsten filament, incandescent lamps are still relatively inefficient because their emissions are predominantly near the infrared spectrum and so largely invisible to humans (Elvidge et al. 2010).

Gas discharge lamps, developed by the mid-twentieth century, produce light by passing electric arcs through gas-filled bulbs (Elvidge et al. 2010). These are further classified as low-pressure discharge and high-intensity discharge (HID) lamps (Elvidge et al. 2010). Low-pressure discharge lamps include the compact fluorescent lamp (CFL) and low-pressure sodium (LPS) lamps. Fluorescent lamps produce distinct emission peaks, which combine to emit a ‘white’ light (Royal Commission on Environmental Pollution 2009; Elvidge et al. 2010), whereas LPS lamps have a narrow spectral signature, emitting monochromatic orange light with a peak intensity of 589 nm (Fig. 7.1) (Rydell 2006; Elvidge et al. 2010).

HID lamps include high-pressure mercury vapour (HPMV) lamps, which produce a bluish-white light, and high-pressure sodium (HPS) and metal halide lamps that have broader spectral emissions (Fig. 7.1) (Davies et al. 2013). Emissions from HPMV lamps extend into the UV range (Rydell 2006; Elvidge et al. 2010), whereas HPS lamps emit yellow-orange light and metal halide lamps ‘white’ light (Royal Commission on Environmental Pollution 2009; Davies et al. 2013; Gaston et al. 2013). The colour rendering index (CRI) compares how accurately a light source replicates the full range of colours of an object viewed in natural light on a scale of 0–100, where 100 is equivalent to natural light (Schubert and Kim 2005; Elvidge et al. 2010; Davies et al. 2013). HPS lamps typically have a CRI between 7 and 32, whereas metal halide lamps have a CRI ranging from 64 to 100, reflecting their ability to render colour more suited for human vision (Elvidge et al. 2010; Gaston et al. 2012).

Gas discharge lamps replaced incandescent lamps because of their energy efficiency and improved longevity (Schubert and Kim 2005), and LPS (44 %) and HPS (41 %) lamps came to dominate street lighting in the UK (Royal Commission on Environmental Pollution 2009) and elsewhere. The luminous efficacy (LE) (amount of light produced per watt of electricity) of gas discharge lamps is five times higher than incandescent lamps (Schubert and Kim 2005; Elvidge et al. 2010). However, with pressure to reduce energy use and CO_2 emissions, the lighting industry is now turning to light-emitting diodes (LEDs) (Elvidge et al. 2010; Gaston et al. 2012). LEDs have broad spectral signatures, typically 400–700 nm, with very few emissions in the UV range (Elvidge et al. 2010). This is achieved mainly through the use of cerium-doped yttrium aluminium garnet (YAG:Ce) phosphors with a gallium nitride (GaN) which converts monochromatic blue to ‘white’ light. However, more recently LEDs are able to produce light by combining multiple monochromatic sources (red, green and blue), which allows for greater control over spectral emissions (Narendran et al. 2004; Gaston et al. 2012, 2013; Davies et al. 2013). LED lamps have comparable CRI scores to metal halide lamps (65–100) (Elvidge et al. 2010) but benefit from lower running costs (Gaston et al. 2012); low energy consumption (Elvidge et al. 2010); controllability of spectral, temporal and intensity of emissions; reduced CO_2 emissions (Hölker et al. 2010a); and smart lighting capabilities that enable dimming in response to weather, traffic and lunar conditions (Bennie et al. 2014).

7.3 The Growth of Light Pollution

Light pollution is defined as the changing of natural light levels in nocturnal landscapes (nightscapes) through artificial lighting sources (Falchi et al. 2011; Kyba and Hölker 2013). Here, we focus on ecological light pollution, i.e. the direct ecological effects of light as opposed to astronomical light pollution, which describes the light that disrupts viewing of stars and other celestial matter (Longcore and Rich 2004). Ecological light pollution can be caused by glare (extreme contrasts between bright and dark areas), over-illumination, light clutter (unnecessary numbers of light sources), light trespass (unwanted light) and skyglow, where artificial light is directed towards the sky, scattered by atmospheric molecules and reflected back to earth (Royal Commission on Environmental Pollution 2009; Gaston et al. 2012; Kyba and Hölker 2013).

Artificial lighting has increased as a result of urbanisation, population growth, economic development and advances in lighting technologies and provides numerous economic, commercial, recreational and security benefits (Riegel 1973; Hölker et al. 2010a; Davies et al. 2012). However, light pollution is now of global concern: the accelerated use of electric lighting, growing at 6 % per year, has escalated light pollution to threat status (Hölker et al. 2010a, b). Satellite images suggest that 19 % of the global land surface surpassed the threshold for acceptable lighting levels (Cinzano et al. 2001). However, satellites are unable to capture all illumination from light sources (Bennie et al. 2014). While light pollution is currently more apparent in developed nations (Fig. 7.2), projected increases in industrial and urban growth suggest that light pollution will become more spatially heterogeneous both locally and regionally (Cinzano et al. 2001; Gaston et al. 2012; Hölker et al. 2010b; Bennie et al. 2014).

In the UK, street lighting consumes approximately 114 Twh of energy annually (International Energy Agency 2006) and is growing at 3 % per annum (Royal Commission on Environmental Pollution 2009). The number of lighting installations is increasing (Gaston et al. 2012), and the change in emissions due to increased use of broad spectrum technologies is also likely to affect light pollution as these sources emit higher levels of blue light. This scatters more into the atmosphere than green or red light, ultimately making a bigger contribution to skyglow (Benenson et al. 2002; Falchi et al. 2011; Kyba and Hölker 2013). The growth in light pollution will be further exacerbated because, as LEDs become cheaper, non-essential uses, such as advertising and architectural lighting, may increase (Schubert and Kim 2005).

Fig. 7.2 Artificial lighting is currently most widespread in the developed world. Global use of lighting at night in 2000. From NASA Earth Observatory/NOAA NGDC (2012)

7.4 Projected Changes in Technology

International lighting policies are prioritising energy-efficient technologies to reduce costs and CO_2 emissions. The European Ecodesign Directive, for instance, encourages moves from energy-intensive technologies such as incandescent, LPS and HPMV lamps (Hölker et al. 2010a) to 'whiter' lighting with higher colour rendering capabilities (Gaston et al. 2012). This may reduce CO_2 emissions in the EU by as much as 42 Mt per year. A number of pilot studies in cities around the world (including Adelaide, Hong Kong, London, Mumbai, New York, Sydney and Toronto) have compared LED lamps against existing lighting technologies. After a three-year trial, the City of Sydney Council agreed to switch to LEDs on 6500 outdoor lights due to their reduced energy consumption, cost-effectiveness and improved illuminance (The Climate Group 2014).

Future research will focus on increasing the efficiencies of LEDs: the LE of a LED is 60–90 lm/W, compared to 80–120 lm/W for HPS lamps (California Lighting Technology Center 2010). More effective ways of producing light are also being investigated, such as combining multiple monochromatic sources as opposed to using phosphors: this will increase control over spectral emissions (Schubert and Kim 2005; Gaston et al. 2012).

7.5 The Biological Effects of Light Pollution

The number of studies revealing negative consequences of artificial night lighting on a multitude of both diurnal and nocturnal vertebrates and invertebrates is increasing rapidly (reviewed in Rich and Longcore 2006). Most negative effects are due to the disruption of natural circadian and circannual cycles, which in turn can affect a whole range of species interactions, physiological processes and behaviours.

7.5.1 Impacts of Light Pollution on Intra- and Inter-specific Competition

Light-induced changes in circadian activity patterns can alter competition both within species (e.g. for mates) and between species (e.g. interference and exploitation competition). These are best documented for birds. For instance, early singing may be a signal of male quality in songbirds and increases the rate of extra-pair copulations, which are usually higher in older males. In territories affected by artificial light, males of several songbird species start singing earlier at dawn and thereby gain access to about twice as many extra-pair mates (Kempenaers et al. 2010; Nordt and Klenke 2013; Dominoni et al. 2014). The effect of artificial light on paternity gain is even stronger in yearlings than in adults, and so street lights might result in maladaptive mate choice of females by artificially increasing the extra-pair success of yearlings (Kempenaers et al. 2010). Whether similar maladaptive effects occur with nocturnal species is less clear.

Artificial light can affect niche partitioning by extending the activity of diurnal species, bringing them into inter-specific competition with nocturnal species (Longcore and Rich 2004; Rich and Longcore 2006). The scissor-tailed flycatcher *Tyrannus forficatus*, for example, will catch insects at street lights until at least 3 h after sunset (Frey 1993); this may increase exploitation and interference competition with insectivorous bats. Light pollution may also cause inter-specific competition between bats, with light-sensitive bat species excluded from illuminated resources exploited by light-tolerant species (Arlettaz et al. 2000).

7.5.2 Effects of Artificial Light on Physiological Homeostasis

Light-induced changes in circadian rhythms may induce physiological aberrations. For instance, exposure of captive mice to light at night disrupts metabolic signals, leading to increased body mass and decreased glucose tolerance (Fonken et al. 2010). Dim night-time light can also impair learning and memory, affect stress hormone levels, compromise immune function and cause depressive-like behaviour in rodents (Bedrosian et al. 2011, 2013; Fonken et al. 2012). In humans, depression, obesity and cancer risk relate to light pollution and associated disruptions of the circadian system (Fonken and Nelson 2011; Kronfeld-Schor and Einat 2012; Haim and Portnov 2013).

Light pollution can also result in a decoupling of seasonal behaviours and physiological adaptations from the optimal time of year. So, for instance, reproduction might be desynchronised from peak food availability; even very low light levels at night advance avian reproduction (Dominoni et al. 2013) so that birds breed earlier close to street lights than in darker territories (Kempenaers et al. 2010). Light-induced decoupling can even reverse an animal's seasonal phenotype, so that it exhibits a long-day phenotype in winter and vice versa. In sheep, 1 h of light during the dark phase is enough to mimic a long-day during short-day conditions (Chemineau et al. 1992). Also in primates, artificial light at night can induce a long-day phenotype; these animals had higher core body temperatures, showed less locomotor activity during the nocturnal activity period and had fainter torpor bouts compared with short-day photoperiod acclimated animals (Le Tallec et al. 2013). Voles that experienced light interference at night showed reduced winter acclimatisation of their thermoregulatory system to such a degree that they reduced heat production and died under winter field conditions (Haim et al. 2004, 2005). Thus, light pollution may have deleterious impacts on survival when animals expend too much energy during winter (Haim et al. 2004): this may be relevant for hibernating bats.

7.5.3 Interference of Light Pollution with Nocturnal Navigation

A well-documented effect of light pollution not mediated through circadian rhythms is the impact on movement decisions of visually orienting animals. Nesting attempts of female sea turtles are disrupted by artificial light, and light attracts or confuses the hatchlings, rendering them more vulnerable to predation, exhaustion and dehydration (Salmon 2006; Perry et al. 2008; Berry et al. 2013).

Birds migrating at night often approach bright lights instead of following their normal migration route, possibly because the light interferes with their magnetic compass (Poot et al. 2008). Birds may also be trapped within the sphere of light, milling around illuminated objects until they die through collisions or exhaustion (Gauthreaux and Belser 2006; Montevecchi 2006; Spoelstra and Visser 2014). This may have relevance to bats, which also use magnetic compasses for navigation (Holland et al. 2006).

Similarly many insects, particularly moths (Lepidoptera), use artificial lights rather than the moon for orientation and die of exhaustion when circling a lamp or following a collision with the hot cover. Artificial light also provokes a 'dazzling effect': many insects become immobilised when approaching a lamp and rest on the ground or in vegetation, becoming easy prey (Eisenbeis 2006). Light pollution may even be a driver of an insect biodiversity crisis (Conrad et al. 2006). The 'vacuum cleaner' effect, i.e. the long-distance attraction of light-susceptible species to lamps, removes large numbers of insects from the ecosystem, even resulting in local extinctions. This flight-to-light behaviour strongly depends on spectral output of the lighting: white HPMV lamps have a high UV proportion of their spectrum, and so four times as many moths are captured at HPMV lights compared to yellow/orange HPS lights (Eisenbeis 2006). Warm-white and cool-white LED lights induce less flight-to-light behaviour than HPS lights (Huemer et al. 2010; Eisenbeis and Eick 2011), and the virtually monochromatic deep-orange LPS lights are least attractive to insects (Rydell 1992; Blake et al. 1994; Eisenbeis 2006; Frank 2006).

Several spiders, amphibians, reptiles, birds and bats focus their foraging on insects accumulated at street lights (Rich and Longcore 2006). For bats, this can also be advantageous because artificial light disrupts the evasive behaviour of most nocturnal Lepidoptera, rendering them more vulnerable to bat attacks (Svensson and Rydell 1998; Acharya and Fenton 1999).

7.6 Bat Vision

Vision is important in the lives of many bats; see reviews in Suthers (1970), Altringham and Fenton (2003) and Eklöf (2003). A number of species rely on vision to a large extent (Altringham 2011). Since vision is important to both bats and their predators, we briefly summarise some key recent findings relevant to bats' perception of artificial lighting.

Most pteropodids do not echolocate and use vision to locate fruit and flowers. Some echolocating bats use vision to complement auditory information when hunting (Eklöf and Jones 2003) and, if vision and echolocation provide conflicting information, visual information is used in preference (Orbach and Fenton 2010). Vision can also be more effective than echolocation over long distances (Boonman et al. 2013), and the California leaf-nosed bat *Macrotus californicus* relies more on vision when hunting prey under low levels of illumination equivalent to a moonlit night (Bell 1985).

Recent research on bat vision has focussed on the molecular evolution of light-sensitive pigments (Jones et al. 2013). As for most nocturnal mammals, bat retinas are dominated by rods: they are highly sensitive under low light and confer monochromatic vision. The opsin DNA sequences of rhodopsin (the opsin in rods) were intact in 15 bat species (Zhao et al. 2009a) and wavelengths of maximum absorbance were 497–501 nm.

Colour vision in mammals results in part from opsins in the cones that are sensitive to short and medium wavelengths. Zhao et al. (2009b) sequenced a short-wavelength sensitive opsin gene (*Sws1*) that is most sensitive to blue-violet wavelengths, and a medium-to-long-wavelength sensitive opsin gene (*M/lws*) in a range of bat species; maximum absorbance of red light wavelengths by the *M/lws* opsin was at 545–553 nm. Although many bats resemble diurnal mammals in having the potential for dichromatic vision, with both genes being intact, *Sws-1* was pseudogenised in all the rhinolophid and hipposiderid bats studied and in some pteropodids, especially cave-roosting taxa. Immunohistochemistry suggests that the primary visual cortex may not respond to stimulation by UV light in these taxa (Xuan et al. 2012a), and behavioural responses to UV were also lacking (Xuan et al. 2012b). The lesser Asiatic yellow bat *Scotophilus kuhlii* and Leschenault's rousette *Rousettus leschenaultii* showed behavioural (Xuan et al. 2012b) and immunohistochemical responses in the primary visual cortex (Xuan et al. 2012a) to UV light at 365 nm. Two phyllostomid species (Pallas's long-tongued bat *Glossophaga soricina* and Seba's short-tailed bat *Carollia perspicillata*) possess significant cone populations and express opsins that are sensitive to short and long wavelengths. The short-wavelength opsin is sensitive to UV and may be advantageous for the detections of UV-reflecting flowers (Winter et al. 2003; Müller et al. 2009). Other bat species with intact *Sws1* genes may be UV sensitive, as ancestral reconstructions suggest UV sensitivity, with maximal sensitivity close to 360 nm (Zhao et al. 2009b).

Whether differences in UV sensitivity among bat taxa affect how species with intact and pseudogenised *Sws1* genes respond to different types of lighting remains unknown. Nevertheless the findings are of interest given that the wavelengths of maximum absorbance in bat opsins lie close to some of the peak emissions of wavelengths in a range of light types (Davies et al. 2013). Moreover emerging LED lighting technologies do not emit UV wavelengths, whereas older technologies, especially HPMV lamps, emit wavelengths that extend into the UV range and so HPMV lights may have been particularly conspicuous to horseshoe bats.

7.7 Observational Studies on Bats at Street Lights

Bats have been observed foraging around lights ever since artificial lighting became pervasive (Shields and Bildstein 1979; Belwood and Fullard 1984; Barak and Yom-Tov 1989; Acharya and Fenton 1999). Artificial light attracts many positively phototactic insects (Rydell 1992; Eisenbeis 2006), and most insectivorous bats are probably opportunistic feeders. Thus, they quickly identify and exploit insect accumulations such as swarming termites (Gould 1978) and insect clusters at artificial lights (Fenton and Morris 1976; Bell 1980; de Jong and Ahlén 1991). So some insectivorous bats probably profit from street lights because resource predictability and high insect densities increase foraging efficiency (Rydell 1992, 2006). For instance, 18 of 25 Neotropical insectivorous bat species which could be detected by acoustic monitoring were observed foraging around street lights in a small settlement. While more species were recorded in mature forest, total bat activity was lowest in forest but highest around street lights (Jung and Kalko 2010).

Bats prey on relatively large insects at street lights, mostly moths (Fenton and Morris 1976; Belwood and Fullard 1984; Acharya and Fenton 1992; Acharya 1995; Hickey et al. 1996; Acharya and Fenton 1999; Jacobs 1999; Pavey 1999; Fullard 2001). While moths are the most numerous insects around artificial lights (Huemer et al. 2010; Eisenbeis and Eick 2011), their contribution to a bat's diet can be much higher than expected from their relative abundance at street lights

(Belwood and Fullard 1984). This implies that bats focus on larger moths rather than smaller prey at street lights. Although moths were only captured in 36 % of attacks, northern bats *Eptesicus nilssonii* probably gain more than twice as much energy when feeding on moths at street lights than smaller dipterans in woodlands (Rydell 1992).

Aggregations of large insects around lamps enable bats to reduce foraging time and hence energy costs while maximising energy returns (Acharya and Fenton 1999; Jung and Kalko 2010). Big brown bats *Eptesicus fuscus*, for instance, spend less than half as much time outside the roost where in habitats where they forage at street lights than where they do not use lamps for hunting (Geggie and Fenton 1985). Hence, foraging at lights might be beneficial when a high foraging efficiency compensates for the potentially higher predation risk.

Bat activity and foraging efficiency at street lights are mainly determined by the number and size of prey insects available, both of which are strongly affected by the spectral characteristics of the light (Blake et al. 1994). Thus, the type of light indirectly influences bat activity. The light's attractiveness for insects increases with its UV spectral content. Aerial-hunting long-legged myotis *Myotis volans* and California myotis *M. californicus* consistently preyed on insects clustered in the cone of experimental black (UV) lights in North America (Bell 1980). While black light is not used for street lighting, similar results are seen with street lights that produce UV emissions. Thus, bat density can be an order of magnitude higher in towns illuminated by HPMV compared with those illuminated by HPS lights and road sections illuminated by HPMV rather than deep-orange LPS lights (Rydell 1992). In Britain, mean bat activity, likely to be mainly common pipistrelles *Pipistrellus pipistrellus*, is usually equal to or lower along roads lit by LPS lights than in dark sections, whereas bat activity is higher under HPMV than LPS lights or sections with no light (Fig. 7.3; Blake et al. 1994).

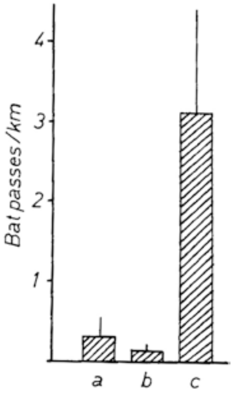

Fig. 7.3 Bat activity varies according to the type of artificial lighting. Activity of pipistrelle *Pipistrellus* spp. bats (mean and SD) along a 28 km stretch of road near Aberdeen, Scotland. *a* rural sections of the road without streetlamps, *b* village sections with sodium (*orange*) lamps and *c* a village with high-pressure mercury vapour lamps. From Rydell and Racey (1995)

7.8 Experimental Studies on Bats at Street Lights

Drawing conclusions from observational studies can be difficult, especially since confounding factors other than the presence of street lights can affect bat activity. Experimental field studies have demonstrated species-specific impacts of street lighting. Two 70 W HPS (DW Windsor Ltd, UK) lights, spaced and orientated to replicate street lights, were installed along preferred commuting routes of lesser horseshoe bats *Rhinolophus hipposideros*. The commuting activity of *R. hipposideros* (Fig. 7.4) and *Myotis* spp. was significantly reduced, and the onset of commuting delayed, on lit nights (Stone et al. 2009; Stone 2011). The following year the experiment was repeated on the same routes using white LED lights (Monaro LED, DW Windsor Ltd), at low (3.6 lux), medium (6.6 lux) and high (49.8 lux) light intensities. Activity of both *R. hipposideros* and *Myotis* spp. was significantly reduced during all lit treatments, and for *R. hipposideros,* the effect size at 49.8 lux was the same as that under HPS illumination. So both HPS and LED light disturbance caused spatial avoidance of preferred commuting routes by *R. hipposideros* and *Myotis* spp. (Stone et al. 2009), with no evidence of short-term habituation. Further work is needed to test for long-term habituation. In contrast, there was no significant change in bat activity under HPS and LED light treatments for *P. pipistrellus*, and for bats in the genera *Eptesicus* and *Nyctalus* (Fig. 7.5).

R. hipposideros and many other slow-flying species rely on linear habitat features for shelter from wind, rain and predators; acoustic orientation; and foraging

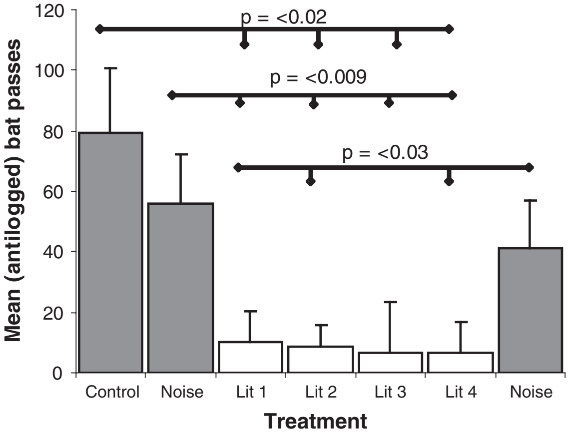

Fig. 7.4 Light-averse bat species show reduced activity along commuting routes subjected to high-pressure sodium (HPS) lighting. Activity of lesser horseshoe bats *Rhinolophus hipposideros* (mean passes and SE) in relation to lighting treatment. Significant within-subject differences with *p* values are shown. Treatments were control nights (no lighting treatment or generator), noise controls (HPS light units installed but switched off, generator running at night), 4 nights where lighting was switched on and powered by the generator (Lit 1 to Lit 4) and a final noise control. From Stone et al. (2009)

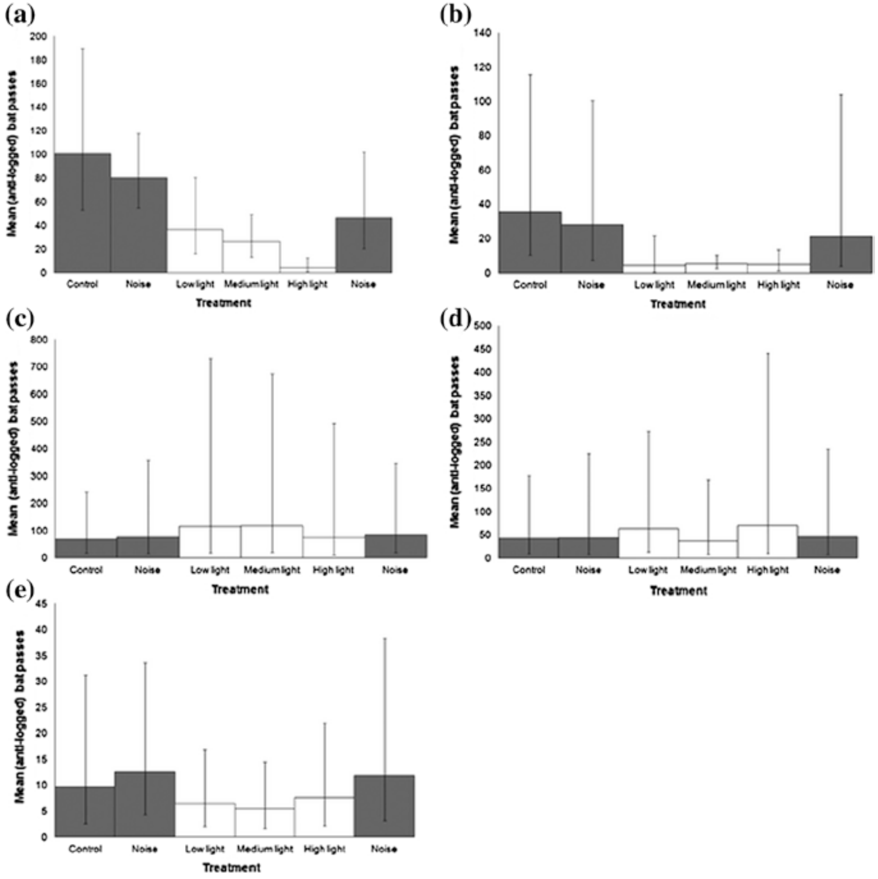

Fig. 7.5 Bats respond in different ways to LED lighting. Although the light-averse *Rhinolophus hipposideros* showed higher activity under more dimmed treatments compared with less dimmed ones, activity was still less than under unlit conditions. *Myotis* spp. showed negligible activity under all dimmed treatments. Geometric mean and confidence limits for bat passes along treatment hedges subjected to LED illumination at different light intensities are illustrated. Treatments were control nights (no lighting treatment or generator), noise controls (LED light units installed but switched off, generator running at night), 3 nights where illumination levels were modified (low light mean = 3.6 lux; medium light mean = 6.6 lux; and high light mean = 49.8 lux), and a final noise control. Bat passes were monitored on Anabat bat detectors and are shown for **a** *Rhinolophus hipposideros*, **b** *Myotis* spp., **c** common pipistrelle *Pipistrellus pipistrellus*, **d** soprano pipistrelle *Pipistrellus pygmaeus* and **e** *Nyctalus/Eptesicus*. From Stone et al. (2012)

(Verboom and Spoelstra 1999; Verboom et al. 1999). Using suboptimal routes with reduced cover to avoid artificial lighting may increase vulnerability to aerial predators and energetic costs due to increased exposure to wind and rain. So bats may have to travel further to reach foraging areas, reducing foraging time and increasing energetic losses, with consequential negative effects on reproduction rates and fitness. For example, juvenile growth rates were suppressed in the grey bat

Myotis grisescens with increased travel distance to foraging grounds (Tuttle 1976). Compensating for energetic losses by increasing foraging time may not be possible if, for instance, emergence and/or commuting is delayed by light pollution (Stone et al. 2009). Such delays also increase the risk that bats will miss the dusk peak in insect abundance, reducing the quality of foraging time. Delayed emergence could therefore affect the fitness of both individuals and the roost as whole.

Light disturbance along the commuting routes may isolate bats from their foraging grounds if the energetic costs of using alternative routes exceed the benefits. The commuting costs for *P. pipistrellus* become prohibitive when foraging areas are more than 5 km from the roost (Speakman 1991). Since bats select roosts based on the quality of surrounding habitat features, including linear connectivity (Jenkins et al. 1998; Oakeley and Jones 1998), maintaining optimal commuting routes is paramount. Whether fitness, or likely proxies of fitness, is affected by lighting needs further evaluation.

7.9 Winners and Losers: Light-Tolerant and Light-Averse Bats

Bats show variable responses to light pollution. Insectivorous bats that hunt in open spaces above the canopy (open-space foragers) or along vegetation edges such as forest edges, tree lines or hedgerows (edge foragers) are the species most tolerant of artificial lighting. They have evolved traits advantageous for foraging in sparsely structured habitats (Norberg and Rayner 1987; Neuweiler 1989) and so are preadapted to foraging in urban habitats (Rydell 2006; Jung and Kalko 2010; Jung and Threlfall 2016). Open-space foragers, such as the noctule *Nyctalus noctula*, typically have long narrow wings with a high aspect ratio, often combined with a high wing loading (weight/wing area). They have to fly fast to remain airborne and so use high-intensity, low-frequency narrowband echolocation calls that facilitate long-range detection of insects (Norberg and Rayner 1987; Rydell 2006; Kalko et al. 2008). When foraging at street lights, open-space foragers typically fly above the lamps, diving into the light cone to catch insects (Jung and Kalko 2010).

Edge foragers generally use echolocation calls with a conspicuous narrowband component, but usually also include a frequency-modulated ‘broadband’ component during the search phase, which is advantageous for ranging when flying close to obstacles. They comprise relatively fast-flying species with above-average aspect ratio and wing loading (e.g. *P. pipistrellus*), and species with an average aspect ratio and wing loading (e.g. *E. nilssonii*). Edge foragers tend to be more manoeuvrable than open-space foragers (Norberg and Rayner 1987; Kalko et al. 2008), and some can even conduct circuits inside the light cone when hunting insects at street lights (Jung and Kalko 2010).

Though most edge foragers fly with agility and speed (Norberg and Rayner 1987), they differ in their degree of synanthropism. While Kuhl’s pipistelle

Pipistrellus kuhlii is recorded almost exclusively at street lights in southern Switzerland, *P. pipistrellus* forage to a similar extent both at lights and at least 100 m from lights (Haffner and Stutz 1985). Even within a species, foraging activity at lamps can be highly variable depending on the quantity of insects available: Geggie and Fenton (1985) never observed *E. fuscus* foraging around street lights in an urban environment, whereas in rural habitats feeding activity was greater at lights than in areas without lights. In spring and autumn, when artificial lights attract numerous insects in Sweden, *E. nilssonii* activity is about 20-fold higher in towns with street lighting than in non-illuminated towns, forest and farmland (de Jong and Ahlén 1991; Rydell 1991), with the bats flying back and forth above the street lights, regularly diving to within 1 m of the ground to catch insects.

Although fast-flying species adapted to forage in open areas, particularly bats of the genera *Eptesicus*, *Nyctalus* and *Pipistrellus*, may benefit from the increased foraging opportunities provided at lamps that attract high densities of insects, Stone et al. (2009, 2012) found no significant increases in bat activity for these ‘light-tolerant’ species during lit treatments. This could be due to two factors. First, HPS lights are less attractive to insects than white lights because their spectral content has less UV (Blake et al. 1994); for example, HPS street lights attracted fewer insects than white lights in Germany (Eisenbeis and Eick 2011). Second, the experimental nature of the study may have affected the results, since bats may need time to find and recognise newly installed lights as an attractive foraging source.

Though a relatively high proportion of aerial insectivorous bats may forage in suburban habitats, bat activity and the number of bat species decrease significantly towards highly urbanised areas. This is probably because both roosts and appropriate insect habitats are lacking, and those insects which are present might not aggregate at street lamps because the pervasive artificial lighting in city centres causes a dilution effect, rendering the lights less attractive for bats (Gaisler et al. 1998; Avila-Flores and Fenton 2005; Frank 2006; Rydell 2006; Jung and Kalko 2011; Jung and Threlfall 2016). In Panama, 18 of 25 insectivorous bat species frequently foraged around street lamps in a settlement bordering mature forest; the reduced vegetation cover in town constrained strictly forest-dwelling species from hunting at lamps (Jung and Kalko 2010). Yet, even some closely related and ecologically similar species may differ in their tolerance of urban habitats, and their potential to adapt to anthropologically altered habitats is best viewed from a species-specific perspective.

As compared to open-space foragers, bats at the other end of the wing shape spectrum, such as many horseshoe bats (Rhinolophidae) with their low aspect ratio wings and a low wing loading, rarely forage near artificial lights (Rydell 2006; Stone et al. 2009, 2012). They are mostly forest-dwelling and their short broad wings facilitate the high manoeuvrability needed for hawking insects in a cluttered environment (Norberg and Rayner 1987). However, their morphology only allows slow flight speeds, which might render them more vulnerable to predators when flying in a sphere of light away from protective vegetation cover (Jones and Rydell 1994; Rydell et al. 1996). Most forest-dwelling bat species emerge from their roosts relatively late in the evening, presumably to minimise predation risk from diurnal birds of prey (Jones and Rydell 1994) and so may be 'hard-wired' to be light-averse. Furthermore, slow-hawking bats use echolocation calls that are adapted for short-range prey detection among clutter (Norberg and Rayner 1987), and so these may not be suitable for orientation in semi-open habitats where most street lights are positioned.

Myotis spp. in Canada and Sweden and brown long-eared bats *Plecotus auritus* in Sweden were only recorded away from street lights (Furlonger et al. 1987; Rydell 1992). In Australia, the chocolate wattled bat *Chalinolobus morio* avoided parks when lights were switched on (Scanlon and Petit 2008). Despite having street-lit areas in their home range, they were never utilised by greater horseshoe bats *Rhinolophus ferrumequinum* (Jones and Morton 1992; Jones et al. 1995). Artificial light reduced the foraging activity of pond bats *Myotis dasycneme* over rivers in the Netherlands (Kuijper et al. 2008), and commuting activity of *R. hipposideros* and *Myotis* spp. was reduced under LED and HPS street lights (Stone et al. 2009, 2012). It is likely that the *Myotis* spp. in Stone et al.'s studies were Natterer's bats *Myotis nattereri* (Stone 2011). *M. nattereri* emerges from roosts relatively late (Jones and Rydell 1994), at median light levels (3.5 lux, Swift 1997), lower than those recorded for *R. hipposideros* (Stone et al. 2009). *M. nattereri* and *R. hipposideros* use different echolocation strategies (Parsons and Jones 2000) but have similar flight and foraging patterns. *M. nattereri* has broad wings, prefers foraging in woodlands and is slow-flying and manoeuvrable, often foraging close to vegetation to glean prey (Arlettaz 1996; Swift 1997). This suggests that light-dependent predation risk limits the ability of these bats to take advantage of illuminated areas. Nevertheless, one large-eared horseshoe bat *Rhinolophus philippinensis* was repeatedly observed traversing 200 m of open grassland to forage extensively around artificial lights in Australia. The same lights were also used by eastern horseshoe bats *Rhinolophus megaphyllus* (Pavey 1999).

Extinction risk is highest in bat species with low aspect ratios (Jones et al. 2003; Safi and Kerth 2004), which are the species that show aversion to artificial lighting. Thus, species that may suffer most from light pollution are likely to be already threatened taxa.

7.10 Effects of Light Pollution on Ecosystem Services Provided by Bats

The impacts of lighting go far beyond changing the physiology, behaviour and/or distribution of individual species. Since congeners interact with each other as well as their prey and predators, light pollution is likely to have far-reaching consequences for the entire biome and the ecosystem services that bats provide. Insectivorous bats, for instance, significantly reduce the number of insects that cause damage to flora and fauna (Ghanem and Voigt 2012). The value of insectivorous bats to the US agricultural industry by reducing insect populations was estimated to be $23 billion/year (Boyles et al. 2011).

Most studies to date have been on temperate-zone insectivorous bats. However, many tropical bats feed on nectar and fruits, thereby pollinating flowers and dispersing seeds of several hundred species of plants (Ghanem and Voigt 2012). Consequently, frugivorous bats are key for succession and maintaining plant diversity, especially in fragmented Neotropical landscapes (Medellin and Gaona 1999; Muscarella and Fleming 2007). However, very little is known about the impact of light pollution on this feeding guild. Southern long-nosed bats *Leptonycteris yerbabuenae*, a nectar- and fruit-eating species, used areas of relatively low light intensity when commuting (Lowery et al. 2009) and Oprea et al. (2009) rarely captured frugivorous bats along roads, although some were present in municipal parks. However, neither study could disentangle the influence of lighting from other factors related to urbanisation, such as altered vegetation cover or increased noise levels. Lewanzik and Voigt (2014) provided the first experimental evidence for light avoidance by frugivorous bats. They found that Sowell's short-tailed bat *Carollia sowelli*, a specialist on fruits of the genus *Piper*, harvested only about half as many fruits in a flight cage compartment lit by a sodium vapour street light than in a dark compartment, and free-ranging bats neglected ripe fruits that were experimentally illuminated (Fig. 7.6). Lewanzik and Voigt (2014) concluded that artificial light might reduce nocturnal dispersal of pioneer plant seeds. Since

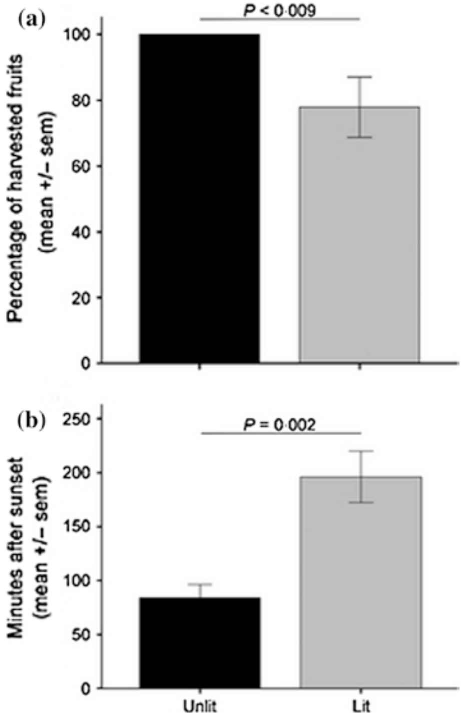

Fig. 7.6 Artificial lighting reduces and delays feeding behaviour on pepper plants by a frugivorous bat. **a** Percentage of harvested infructescences of *Piper sancti-felices* among 14 marked plants harvested by Sowell's short-tailed bats *Carollia sowelli* in non-illuminated conditions (*black*) and under conditions where plants were illuminated by a street lamp (*grey*) in the field, **b** time after sunset when infructescences were harvested. From Lewanzik and Voigt (2014)

bat-mediated seed intake is particularly important during the early stages of succession (Medellin and Gaona 1999; Muscarella and Fleming 2007), light pollution might slow down the reforestation of cleared rainforests (Lewanzik and Voigt 2014).

7.11 Knowledge Gaps, Future Challenges and Mitigation Strategies

7.11.1 Knowledge Gaps

Light pollution has only recently been acknowledged as a threat to biodiversity (Hölker et al. 2010b), and there are still many unknowns about the interactions between bat species and artificial lighting sources (Hölker et al. 2010a). Most studies have focused on specific ecological behaviours such as foraging (Rydell 1992; Blake et al. 1994), predator–prey interactions, particularly with moths (Rydell et al. 1995; Svensson and Rydell 1998), commuting routes (Stone et al. 2009, 2012) and roost emergence (Downs et al. 2003). No long-term studies have been carried out to determine whether any of these behavioural changes have fitness consequences (Beier 2006; Stone et al. 2012). The only indication of potential population-level responses has been shown in Hungary on *Myotis* species, where juveniles roosting in illuminated buildings had a lower body mass than their counterparts in unlit roosts (Boldogh et al. 2007). However, this study did not establish whether a lower body mass in these juveniles reduced their survival rate after hibernation. It is particularly important to understand higher level responses for bat species because they have low fecundity rates, usually only producing one pup per year (Dietz et al. 2009), and so populations are sensitive to sudden changes (Stone et al. 2012).

Further studies are needed to address the impact of artificial lighting at the community level (Davies et al. 2012). The current literature highlights that artificial lighting causes species-specific responses (Rydell 1992; Stone et al. 2009, 2012; Jung and Kalko 2010), which could cause light-tolerant species to exclude light-averse species (Polak et al. 2011; Stone et al. 2012). Such competitive interactions have been proposed as the driving force behind changes in bat populations in Switzerland, where decreases in photosensitive *R. hipposideros* have been linked to increases in light-tolerant *P. pipistrellus* (Stutz and Haffner 1984; Arlettaz et al. 2000). It is believed that by avoiding street lights, *R. hipposideros* are foregoing profitable prey sources exploited by *P. pipistrellus* (Arlettaz et al. 1999, 2000).

So far research has focussed largely on insectivorous bats in temperate zones. Further research in tropical ecosystems is needed. For example, the forested areas of South-east Asia contain a high diversity and abundance of horseshoe bat species that are likely to be negatively affected by light pollution, and the impact of light pollution on pollination and seed dispersal in the tropics and subtropics needs further investigation.

Research on the impacts of different light spectra in emerging technologies on bat activity and reproduction will be valuable; this is currently being investigated in the Netherlands as part of a large-scale investigation exposing a wide range of taxa to white, red and green LED lighting (see http://www.lichtopnatuur.org). With the current plans to switch to broader spectrum lighting sources, it is important to understand more about the spectral sensitivities of bats (Davies et al. 2012, 2013), especially given the recent findings on opsin genes highlighted above. Determining if there are spectral and intensity thresholds for different species would aid mitigation strategies and improve conservation initiatives (Stone et al. 2012; Gaston et al. 2013).

7.11.2 Mitigation Strategies

The most effective approach to reduce the detrimental effects of artificial lighting is to limit the growth of lighting by restricting unnecessary installations or removing them from areas already saturated with artificial lighting sources. This has the greatest potential to reduce light pollution and minimise ecological effects (Gaston et al. 2012). Turning off lights in areas commonly used by light-averse bats to forage, commute or roost during key times such as reproduction (Jones 2000) may be effective. Bats are faithful to maternity roosts due to the specific conditions they provide, and so conserving them is important for maintaining bat populations (Lewis 1995; Mann et al. 2002). However, some photosensitive bats may be disrupted even if areas were only lit for a short period of time (Boldogh et al. 2007), and switching off lighting may be challenged if it is perceived to jeopardise public safety (Lyytimäki and Rinne 2013).

Reducing the duration of illumination through part-night lighting (PNL) schemes could also help limit the adverse effects of light on nocturnal animals (Gaston et al. 2012). This has already been adopted by a number of local authorities in the UK, which switch off lights in specified areas between midnight and 05.30 to reduce CO_2 emissions and save money (Lockwood 2011). Since April 2009, lights along sections of motorways have also been switched off between these hours (Royal Commission on Environmental Pollution 2009). While this may help to reduce light pollution, it is unlikely to have significant ecological benefits since the lights remain switched on in the early part of the night, when bats and other nocturnal species undertake key activities such as foraging and commuting (Gaston et al. 2012). Intelligent lighting schemes, such as the use of motion sensors, have already been implemented in Portugal and may have more ecological benefits. The lights remain switched off unless needed and so still provide all the perceived public safety benefits (Royal Commission on Environmental Pollution 2009). However, these fluctuations in lighting levels may also be damaging to bats (Longcore and Rich 2004).

It is also important to reduce the trespass of artificial lighting to minimise the impact on bats. Newer technologies such as LEDs produce more directional light (Gaston et al. 2012), preventing the horizontal or upward emissions which contribute most to light pollution (Falchi et al. 2011). Effective luminaire design, installation of shielding fixtures and correct column height can also help focus light and avoid wasteful emissions (Royal Commission on Environmental Pollution 2009). In Lombardia, Italy, for example, 75 % of light pollution was due to poorly designed luminaires; the other 25 % was unavoidable reflection from road surfaces (Falchi 2011). Vegetation canopies such as hedgerows can also help decrease light trespass, which is crucial for many bat species that use linear features as commuting routes (Rydell 1992; Fure 2006). Diminishing trespass could create dark refuges, providing corridors for bats to forage in fragmented habitats (Longcore and Rich 2004; Stone et al. 2012; Gaston et al. 2012).

Light intensity has a significant effect on bat activity (Stone et al. 2012) and delays roost emergence (Downs et al. 2003). If bats delay foraging, they risk missing the peak abundance in insects that occurs shortly after dusk, so may not meet their energy requirements, which in turn could reduce fitness (Jones and Rydell 1994; Stone et al. 2012). In addition to implementing PNL, many local authorities are also dimming lights in specified areas (Gaston et al. 2012). This relies on local authorities already having lights such as LEDs that have the necessary centralised management system (International Energy Agency 2006). These schemes are more environmentally friendly and cost-effective (Gaston et al. 2012). However, dimming lights may not be beneficial to all bat species; Daubenton's bats *Myotis daubentonii*, for instance, only emerge from their roosts at very low light levels (less than 1 lux) (Fure 2006) and *R. hipposideros* and *Myotis* spp. avoid commuting routes illuminated to 3.6 lux (Stone et al. 2012). Since illumination levels of street lights are usually between 10 and 60 lux (Gaston et al. 2012), it may not be feasible to dim lighting to such low intensities without compromising public perceptions of safety (Stone et al. 2012; Lyytimäki and Rinne 2013).

7.11.3 Future Challenges

With a number of changes to street lighting planned in the coming years, including dimming, PNL and modifications to luminaire design to reduce light pollution, energy expenditure and greenhouse gas emissions, nightscapes could increase in heterogeneity, making it even more challenging to understand the impacts of artificial lighting on biodiversity (Gaston et al. 2012).

This is further complicated because current metrics for measuring emissions from light sources omit key biological information (Longcore and Rich 2004; Gaston et al. 2012). Illumination is measured in lux, which is defined as the brightness of a light according to human spectral sensitivities; spectral sensitivities of other taxa are often very different from ours (Peitsch et al. 1992; Briscoe and Chittka 2001). In bats, for example, many species can detect wavelengths in the UV range (Winter et al. 2003; Wang et al. 2004; Müller et al. 2009). So HPS and LPS lamps could have the same intensity of light, e.g. 50 lux, but HPS lamps emit UV wavelengths, whereas LPS lamps do not, thereby affecting both bats and their insect prey in different ways (Longcore and Rich 2004). Since lux is commonly used as a metric by lighting engineers, designers and environmental regulators, migrating from this measure may thwart interdisciplinary communication (Longcore and Rich 2004).

Another challenge is to find more effective ways of quantifying the impact of artificial lighting on bat species. Current methods use acoustic survey methods to quantify bat activity; this underestimates the activity of bats that use low-intensity echolocation calls (O'Farrell and Gannon 1999). Crucially, we also need to determine whether artificial lighting has fitness consequences (Stone et al. 2012). A decrease in bat activity may have no relevance for fitness if, for example, the bats are able to utilise equally suitable alternative sites nearby.

A transdisciplinary approach needs to be adopted to minimise the impact of light on biodiversity, reduce CO_2 emissions, increase energy efficiency and reduce costs (Hölker et al. 2010a; Gaston et al. 2012). Scientists, policymakers and engineers need to work together to implement successful strategies (Stone et al. 2012). Moreover, it is vital to find ways to broaden awareness of light pollution and its ecological impacts. Since the public plays an integral part in agreeing mitigation schemes such as dimming lights, their support is pivotal in moving forward (Hölker et al. 2010a).

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Chapter 8
Bats and Water: Anthropogenic Alterations Threaten Global Bat Populations

Carmi Korine, Rick Adams, Danilo Russo, Marina Fisher-Phelps and David Jacobs

Abstract Natural bodies of open water in desert landscapes, such as springs and ephemeral pools, and the plant-life they support, are important resources for the survival of animals in hyper arid, arid and semi-arid (dryland) environments. Human-made artificial water sources, i.e. waste-water treatment ponds, catchments and reservoirs, have become equally important for wildlife in those areas. Bodies of open water are used by bats either for drinking and/or as sites over which to forage for aquatic emergent insects. Due to the scarcity of available water for replenishing water losses during roosting and flight, open bodies of water of many shapes and sizes may well be a key resource influencing the survival,

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activity, resource use and the distribution of insectivorous bats. In this chapter, we review the current knowledge of bats living in semi- and arid regions around the world and discuss the factors that influence their richness, behaviour and activity around bodies of water. We further present how increased anthropogenic changes in hydrology and water availability may influence the distribution of species of bats in desert environments and offer directions for future research on basic and applied aspects on bats and the water they use in these environments.

8.1 General Introduction

Dryland environments which include hyper-arid, arid and semi-arid regions can be highly complex and diverse, despite being occasionally perceived as simple ecosystems supporting low species diversity (Ayal et al. 2005). Aridity is described by ratio of precipitation to potential evapotranspiration ratio (P/ETP) (UNESCO 1979, Fig. 8.1) and dryland environments are ecosystems in which typically food availability is low, precipitation is limited and unpredictable, ambient temperature is high, humidity is low, and drinking water is scarce (Noy-Meir 1973). Consequently, there are large variations in primary production by plants that can strongly affect overall species diversity and interactions (Evenari et al. 1971). Furthermore, the distribution, abundance and persistence of several desert-dwelling mammal species is affected by water availability, especially during dry summer months, when the challenges of minimizing energy use and water losses is greatest (Calder 1984; Morton et al. 1995; Lovegrove 2000; Marom et al. 2006).

In desert environments, bats are an important component of the mammalian fauna. Carpenter (1969) asserted that, based on the number of species and abundance, bats are one of the most successful desert mammals, although they are outnumbered by rodents in the driest parts of the Sahara and the Namib Desert (Findley 1993). In the deserts of Israel, insectivorous bats are the most diverse

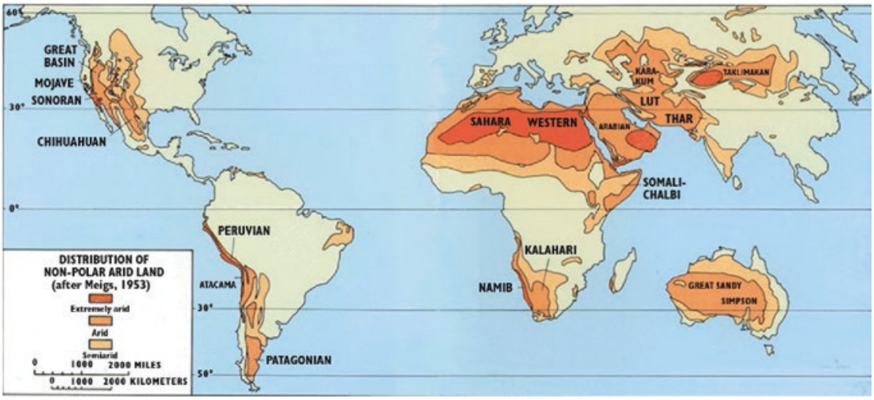

Fig. 8.1 The arid lands of the world (U.S. Geological Survey, science information services)

Fig. 8.2 A drinking event of the lesser horseshoe bat (*Rhinolophus hipposideros*) from a spring in the Dead Sea, Israel. Photo by Jens Rydell

group of mammals (Mendelssohn and Yom-Tov 1999), with 12 species recorded in the Negev Desert (Korine and Pinshow 2004) and 17 species in the Dead Sea area (Yom-Tov 1993). Benda et al. (2008) recorded 14 species of insectivorous bats in Sinai, highlighting the diversity of these mammals in desert environments. The dryland regions of South America are the most species-rich habitats of the region and have the highest number of endemic species, even when compared to the tropical lowland Amazon forest (Mares 1992; Ojeda and Tabeni 2009; Sandoval and Barquez 2013). In the Yungas dry forest of Argentina, 55 % of the bat species may be endemics (Sandoval et al. 2010). However, this area is severely under-protected and very little research has been conducted on the bat fauna (Mares 1992; Sandoval and Barquez 2013) In Mongolia, more than half of the bat species only occur in arid and semi-arid regions (Nyambayar et al. 2010).

Most bats, and in particular desert-dwelling bats, use open water sources for drinking water and/or as a foraging site (Vaughan et al. 1996; Grindal et al. 1999; Ciechanowski 2002; Campbell 2009, Fig. 8.2) with various studies reporting high levels of bat activity over open bodies of water (Rydell et al. 1994; Walsh et al. 1995; Young and Ford 2000; Mickeviciene and Mickevicius 2001; Ciechanowski 2002; Russo and Jones 2003; Korine and Pinshow 2004; Williams and Dickman 2004; Anderson et al. 2006; Davie et al. 2012; Monamy et al. 2013), making even small springs, ephemeral pools and waterholes key foraging areas for insectivorous bats worldwide (Racey 1998). Water availability was even proposed as a mechanism for elevational patterns of species richness of bats in arid mountains (McCain 2007).

In this chapter, we review our current knowledge of bats and water across regionally different semi-arid and dryland environments, and the factors that may influence their richness, behavior and activity around bodies of water. We discuss how anthropogenic development may influence water availability and thus the distribution of species of bats in desert environments. Dryland environments are also predicted to be particularly sensitive to climate change, and we will discuss patterns by which climate disruption may further reduce water availability in arid regions. Finally, we offer directions for future research on basic and applied aspects on bats and the water they use in these environments.

8.2 Ecology of Bats and Water in Drylands Environments

8.2.1 Water Sources Used by Bats

Permanent and ephemeral pools are the central characteristic of many watersheds in dry, arid and semi-arid regions. Temporary pools have largely been ignored in management programs due to their relatively small size and apparent lack of benefit for human use (Schwartz and Jenkins 2000). However, during spring and early summer, temporary pools may serve as important foraging grounds for aquatic and terrestrial species, some of which are regionally or locally rare and/or endemic (Nicolet et al. 2004). Temporary pools in the Negev Desert had equivalent levels of species richness of bats and activity to permanent pools (Razgour et al. 2010) and the activity of bats was reduced significantly when bodies of open water were dried (Korine and Pinshow 2004), highlighting the importance of pools of all shapes and sizes to desert wildlife. In the arid regions of Mongolia, even suboptimal water sources such as small human-dug wells and salty lakes are used by bats and are an important resource for their continued survival (Nyambayar et al. 2010). Conservation efforts should therefore focus on those sources offering only temporary water availability because although they support similar bat species richness and activity levels as permanent pools, they are less likely to be protected due to their ephemeral nature.

That said, the importance of permanent pools can be underestimated if landscape availability of water is not considered through time. Geluso and Geluso (2012) analyzed 34 years of data in relation to capture rates gathered at a single drinking site, which was sampled once yearly, in the San Mateo Mountains of New Mexico. They found that in non-drought years capture success was significantly lower because bats were more dispersed across the landscape. However, in drought years, capture rates at the only available water source skyrocketed, thereby indicating the importance of open-water to local species of bats.

Data gathered on foraging patterns of bats in Utah indicated a strong affinity by *Myotis* bats for riparian and edge habitats as compared to other surrounding areas (Rogers et al. 2006). Similarly, Grindal et al. (1999) showed that bat activity levels were significantly greater in riparian versus upland areas in British Columbia and capture rates were higher for females than for males indicating that female bats may be more dependent on water-driven attributes of a particular area. Williams et al. (2006) sampled across 22.5 km of the Muddy River floodplain in the Mojave Desert in Nevada, which was highly disturbed by long-standing flood control, livestock grazing, and the invasion of non-native plant species, and found that the riparian woodland habitat, which represents less than 1 % of the area, accounted for greater than 50 % of all bat activity. Areas of historically less disturbed mesquite bosque habitat maintained higher bat activity than more disturbed areas. Fortunately, restoration of habitats can increase local species richness. In Arizona, red bats (*Lasiurus blossevillii*), which had not been reported before, were captured along riparian-restoration areas of the lower Colorado River. The Arizona myotis (*Myotis occultus*), presumed extirpated, was also captured after restoration (Calvert 2012).

In Africa, there is evidence that bat activity is higher around bodies of water than in adjacent areas. For example, in two regions in southern Africa, bat abundance was higher in riverine habitat than in adjacent, dryer savannah (Rautenbach et al. 1996; Monadjem and Reside 2008). Differences in species richness and diversity between riverine and savannah habitats were not the same in the two regions. In the Kruger National Park, there was no difference in bat species richness or evenness between riverine habitat and savannah (Rautenbach et al. 1996). In contrast, at another site in Swaziland, the riverine habitat had higher species richness and diversity (Monadjem and Reside 2008). In both regions, the two assemblages differed in the relative densities of the various species, with the savannah assemblages forming a subset of the riverine assemblages (Rautenbach et al. 1996; Monadjem and Reside 2008). This reinforces the notion that bat assemblages in less mesic regions are extensions of bat assemblages in more mesic regions, but that not all species are inclined to make use of less mesic habitats when conditions are favorable. Some of them, particularly fruit eating bats (e.g. *Epomophorus crypturus*; Thomas and Fenton 1978) may be restricted to riverine habitats (Monadjem and Reside 2008).

Australian studies also indicate high levels of bat activity around bodies of water (Lumsden and Bennett 1995; Williams and Dickman 2004; Griffiths et al. 2014a). Young and Ford (2000) found that species richness of bats, abundance, and capture success in the semi-arid Idalia National Park was greatest in areas adjacent to water, with 97 % of captures occurring at sites with water. Bats in Uluru National Park and the north-eastern edge of the Simpson Desert predominantly use oasis habitats that have permanent or temporary water sources even in years with higher than average annual rainfall (Coles 1993; Williams and Dickman 2004). Multiple species of Australian insectivorous bats have even been recorded flying, foraging, and perhaps drinking over hypersaline environments (Laegdsgaard et al. 2004; Gonsalves et al. 2012; Griffiths et al. 2014a, b). *Pteropus* species in New Guinea have been recorded drinking seawater (Iudica and Bonaccorso 2003) but the prevalence of bats drinking hypersaline water in arid environments is not understood, despite natural hypersaline water bodies being common in arid and semi-arid areas in Western Australia (Halse et al. 2003; Timms 2005). In the arid regions of Mongolia, bats are mostly frequently found in association with water (Dolch et al. 2007; Davie et al. 2012).

8.2.2 Bodies of Water as a Drinking Source

Water sources that are used by bats are likely to be pools in streams, lakes, ponds, slow-flowing streams and rivers and artificial bodies of water with similar properties such as farm and urban dams (Jackrel and Matlack 2010; Sirami et al. 2013), canals (e.g. Lisón and Calvo 2011), cattle troughs, swimming pools and settling ponds at waste water treatment facilities (Vaughan et al. 1996; Abbott et al. 2009; Naidoo et al. 2013, 2014) and mines having natural seepage (Donato et al. 2007; Griffiths et al. 2014a).

Both the size and accessibility of the water source influence whether a bat can drink from it. Bats drink water by swooping over a water source while lapping at the surface (Harvey et al. 1999). Because bats drink on the wing, small and more maneuverable bats are able to drink from smaller pools, whereas less maneuverable bats need a large surface area of water to skim (Tuttle et al. 2006). In the Negev Desert, Razgour et al. (2010) found that both within and between pools, species richness of bats and activity significantly increased with pond size. Furthermore, manipulations that decreased pond size led to a significant reduction in species richness and activity and affected the bat assemblage composition. The size and situation of artificial water sources similarly affect their use by bats. In the arid Texas Panhandle, USA, bats preferentially drank water from larger livestock tanks that were full and had only light vegetation around. They tended to avoid smaller, half-full tanks with denser vegetation around them (Jackrel and Matlack 2010). Although there are many anecdotal observations (Nickerson and O'Keefe 2013) of bats drinking from swimming pools there have been no formal studies of this.

Despite the central nature of drinking and water availability for bats, there are a surprisingly small number of studies addressing this topic in Europe, even though many species do drink at open water sources regularly to rehydrate (e.g. Russo et al. 2012). Some appear more sensitive than others to water deprivation because of their stricter dependence on water habitats. For instance, in water-denial experiments Daubenton's bat, *Myotis daubentonii*, a species selectively dwelling in riparian habitat and above bodies of open water, has been found to undergo a greater body mass loss and to show signs of dehydration earlier than the brown long-eared bat, *Plecotus auritus*, a forest bat (Webb et al. 1995). Drinking sites are also of chief importance for European bats outside the semiarid Mediterranean region. In the Bavarian Forest, Germany, oligotrophic, acidic ponds are used by over a dozen species of bats for drinking (Seibold et al. 2013). Likewise, in the Italian Apennines, water cattle troughs built for traditional livestock breeding are frequently used to drink by over a dozen species of bats. Such small (often less than 15 × 1.5 m) pools of water are locally of extreme importance (Russo et al. 2010, 2012) for several threatened species (Fig. 8.3). These pools also concentrate insects, so bats occasionally forage there, but their importance for drinking is overwhelming (Russo et al. 2012). The disappearance of traditional livestock breeding due to rural depopulation in many Apennine areas has led to the abandonment of the cattle troughs, implying an unstudied yet potentially high cost for bat

Fig. 8.3 Cattle troughs used by drinking bats in the Italian Apennines. Photo by Luca Cistrone

populations (Fig. 8.3). In Italian forests, bats also drink from the small ephemeral pools which form following heavy rain and only last few days or weeks (D. Russo, pers. obs.). Eavesdropping on other drinking bats is likely to play an important role in locating such sites and this behaviour is typical of species with manoeuvrable flight such as the barbastelle bat, *Barbastella barbastellus*, and the greater horseshoe bat *Rhinolophus ferrumequinum*.

8.2.3 Bodies of Water as a Foraging Habitat

The tendency for higher insect abundance near water sources attracts bats to use water sources as foraging habitats. Furthermore, calm surface water provides a less cluttered acoustic signal return from the echolocation pulses (Mackey and Barclay 1989; Siemers et al. 2001), and there is some evidence, at least for echolocating bats, that activity over calm pools of water is higher than that over fast-flowing riffles (von Frenckell and Barclay 1987). Bat activity in a transect from dry woodland savannah to riverine habitat in southern Africa was correlated with insect abundance—both bat activity and insect abundance were higher in riverine habitat (Rautenbach et al. 1996) suggesting that bats were attracted to this habitat because of the feeding opportunities it provided.

Drought is known to reduce the abundance of insects in temperate zones (Frampton et al. 2000) and thus affect reproduction in insectivorous bats (Rhodes 2007). An eight year study by Bogan and Lytle (2011) on aquatic insects living in two study pools of a formerly perennial desert stream in the Whetstone Mountains of Arizona, USA, showed that complete water loss followed by intermittent flow caused a catastrophic regime shift in community structure that did not recover to the pre-drying configuration even after four years. Ledger et al. (2011) found significant reduction in and suppression of secondary productivity by drought that could have severe constraining effects on terrestrial vertebrate predator populations, and Love et al. (2008) found similar effects in Arkansas, USA. Furthermore, desert bats in Arizona responded to artificial-light-induced food patches (Fenton and Morris 1975) and one would presume this would be similar when small pools of water create swarms of high insect density. All of these data together suggest that small water sources with intermittent flow are vitally important as foraging sites to at least some insectivorous desert bat species.

In Europe, three species of bats are aquatic habitat specialists: Daubenton's bat, *M. daubentonii*, the long-fingered bat, *Myotis capaccinii*, and the pond bat, *Myotis dasycneme.* Besides taking insects in flight by aerial hawking, they typically forage very close to the water surface, from which prey is gaffed with their large feet or the inter-femoral membrane and transferred to the mouth while on the wing (Kalko and Schnitzler 1989; Siemers et al. 2001). Chironomidae and Trichoptera are frequent prey items of these bats (e.g. Biscardi et al. 2007; Krüger et al. 2012). *M. capaccinii* may seize adult chironomids from the water surface as they emerge from pupal casings. Trawling bats mainly forage over calm water whose surface is free from ripples (Rydell et al. 1999) as echoes from clutter interfere with prey detection (Siemers and Schnitzler 2004). On windy nights, *M. capaccinii* and *M. daubentonii* are less active (Russo and Jones 2003), presumably because wind reduces prey density and generates ripples on the water surface affecting target detection. In such circumstances, bats forage at sheltered sites where water is calmer (Lewis and Stephenson 1966; Lewis 1969).

Several other species of bats frequent riparian habitats to forage and/or drink, especially the soprano pipistrelle, *Pipistrellus pygmaeus* (e.g. Nicholls and Racey 2006), Nathusius' pipistrelle, *Pipistrellus nathusii* (Flaquer et al. 2009), and other *Pipistrellus* spp. (Scott et al. 2010), Schreiber's bat *Miniopterus schreibersii* (Serra-Cobo et al. 2000) and noctules, *Nyctalus* spp. (Rachwald 1992; Racey 1998; Vaughan et al. 1997). The stricter reliance on riparian habitats is one of the main ecological factors distinguishing *P. pygmaeus* from its sibling *P. pipistrellus* (but see Warren et al. 2000) and allowing interspecific niche partitioning and thus coexistence (Oakeley and Jones 1998; Nicholls and Racey 2006; Davidson-Watts et al. 2006; Sattler et al. 2007). However, local factors such as elevation or landscape composition may influence differences across species. At larger scales, the presence of main rivers and wetland areas are important as migratory paths and offer important stopover sites to migrating bats across Europe (Flaquer et al. 2009). Rivers and riparian vegetation also constitute important linear landscape elements used for navigation by several European bats (Serra-Cobo et al. 2000; Russo et al. 2002).

As might be expected given the above, the quality of foraging areas lacking water is influenced by their distance to water. In Portugal, proximity to a drinking water source increased foraging habitat quality for Mehely's horseshoe bat *Rhinolophus mehelyi* and *M. schreibersii* (Rainho and Palmeirim 2011). Similarly, a radio-tracking study of *R. mehelyi* in Spain showed that although this species hunted predominately in forest, the foraging areas were always within 500 m of a water source (Salsamendi et al. 2012), possibly to allow for easy rehydration between foraging bouts or perhaps to take advantage of water-emergent forest insects. In historic landscape parks of England (Glendell and Vaughan 2002) as well as in German forests (Kusch and Idelberger 2005) the relative area of available water surface is an effective proxy for levels of bat activity.

Australian bats have also been documented preferentially foraging around water sources. When compared to other habitat types in the Simpson Desert, more feedings buzzes were recorded around permanent and temporary water sources (Williams and Dickman 2004). Bats will also forage over hypersaline water bodies but more feeding buzzes are recorded over freshwater sites (Griffiths et al. 2014b). There is also evidence (e.g. Aldridge and Rautenbach 1987; Schoeman and Jacobs 2003, 2011; Naidoo et al. 2011, 2013) that insects associated with freshwater habitats (e.g. Plecoptera, Ephemeroptera and Trichoptera) occur in the diet of southern African bats.

8.2.4 Water, Roosts and Reproduction

The propensity for female bats to choose roost sites that are relatively high in ambient temperature is thought to help them save metabolic energy by allowing for continued gestation of the young during torpor (Speakman et al. 1991; Adams and Thibault 2006; Daniel et al. 2010). The cost of such a choice in roost sites in arid regions, however, is the propensity for high-levels of evaporative water loss during the diurnal roosting cycle (Webb 1995) and this is further exacerbated when females are lactating (Kurta et al. 1990). The only quantitative field study to assess the need for drinking water by lactating female bats in drylands used PIT-tagged lactating and non-reproductive females from a maternity colony of fringed myotis (*Myotis thysanodes*) in Colorado, USA. Adams and Hayes (2008) found that lactating females visited to drink an average of seven times more per night than did non-breeding adult females. In addition, lactating females visited to drink consistently night after night regardless of daily relative humidity and temperatures, whereas non-reproductive females visited more when temperatures were high and relative humidity low (Adams and Hayes 2008).

In addition, Adams (2010) synthesized 13 years of capture data from the same field sites in Colorado, USA and found that summer mean precipitation had the highest correlation with reproductive frequency followed closely by mean stream discharge rates. Of these two, the latter showed the most abrupt effect on bat reproduction. When stream discharge rates were lower than 7 m/s, the frequency of reproductively active females captured plummeted, in some years by as much as 50 %. When female reproductive condition was plotted against mean stream discharge, the frequency of lactating females tracked the amount of available water, whereas the frequency of pregnant females was not correlated. This suggests that during drought years pregnant females may give birth, but do not have access to enough drinking water to support lactation. O’Shea et al. (2010) using mark/recapture of big brown bats, *Eptesicus fuscus*, at maternity colonies in Ft. Collins, Colorado, USA found that first year survival was lowest in bats born during a drought year, although other factors were also at play.

Several species of bats have been found to roost close to bodies of water to minimize the energy expenditure required to reach important drinking or foraging sites (Racey 1998; Korine et al. 2013). The need to drink directly after emerging from the roosts may be the main factor determining the proximity of roosts to water, especially for maternity colonies (Racey 1998). *M. daubentonii*, whose foraging strictly depends on water habitat, often uses bridges over rivers, as well as buildings or cavity-bearing trees in the immediate surroundings of riparian biotopes (Racey 1998; Parsons and Jones 2003; Lučan and Radil 2010; Encarnação 2012). Several other species, such as Natterer's bat (*Myotis nattereri*), pipistrelles (*Pipistrellus* spp.) and brown long-eared bat, also tend to roost in landscapes comprising bodies of water that provide drinking and foraging opportunities (Racey 1998; Entwistle et al. 1997; Oakeley and Jones 1998). Floodplain forests of central Europe host important reproductive colonies of tree-roosting noctule bat *Nyctalus noctula* (Görföl et al. 2009). *Myotis macropus*, an Australian species, has a variable roosting behaviour but the primary force behind roost selection is proximity to waterways (Campbell 2009).

8.3 Threats to Water Sources Used by Bats

In drylands, where water resources are scarce, any loss of or degradation to open water source, such as a reduction in water quality, may create cascading affects that will be harmful to the wildlife that depends on it. When bats drink from a polluted source they ingest toxins directly and during foraging they indirectly ingest toxins that may have bio-accumulated within their insect prey. For example, if insect larvae feed on microorganisms in polluted water, they concentrate the pollutants in their bodies and when they metamorphose into adults these are consumed by bats. The effect of environmental chemical containments on bats was reviewed in 2001; most studies have occurred in Europe (~50 %) and North America (~34 %) mostly pertaining to organochlorine insecticides (58 %), metals (30 %), and polychlorinated biphenyls or PCBs (13 %) (Clark and Shore 2001). There are hardly any reports on the effect of polluted water on bat activity and richness in the drylands of North Africa, the Middle East and South America. Levels of bat activity in the Negev Desert were very high over wastewater treatment ponds (Korine and Pinshow 2004), however species richness was low and the majority of the activity was attributed to Kuhl's pipistrelle (*Pipistrellus kuhlii*). Pilosof et al. (2013) showed that sewage pollution in the Negev desert affected the immune response of Kuhl's pipistrelle and Naidoo et al. (2014) reported on DNA damage to bats that forage at wastewater treatments work.

8.3.1 Loss of Sources of Water

An estimated two-thirds of Earth's freshwater flowing to oceans is obstructed by anthropogenic development (Nilsson and Berggren 2000), with approximately 75,000 dams in the USA alone and the majority of natural wetlands having been destroyed as well. Although not the scope of this chapter, it is important to mention that for bats, wetlands provide critical foraging habitat (Johnson et al. 2008; Rainey et al. 2006) with absolute area and connectivity of wetlands being important components for foraging (Lookingbill et al. 2010).

Indeed, a recent report on total wetland loss in the USA from 2004–2009, showed a 25 % reduction from the previous reporting period. In addition, a total of 95,000 acres of saltwater wetlands and 265,720 acres of freshwater wetlands were lost (Dahl and Stedman 2013). The situation is exacerbated in the western USA, where livestock grazing has damaged at least 80 % of stream and riparian ecosystems (Belsky and Matzke 1999). The consequences for bats are illustrated by observed declines in bat activity as related to flow-reduction and drying along the San Pedro River in Arizona. Moreover, these declines corresponded to declines in insect availability at perennial sites and both bat activity and insect activity declined to imperceptible levels in areas where the river dried up (Hagen and Sabo 2012).

European rivers, lakes and wetlands are among the most seriously altered ecosystems. Human impact has caused a major structural or chemical degradation of such ecosystems with fatal repercussions for their associated biota (e.g. Abel 1996). Alteration of European rivers has often led to the loss of channel features, floodplain connectivity and structure of bank vegetation. A threatened vespertilionid, *M. capaccinii*, selects foraging sites where water is less polluted and riparian vegetation better preserved. Along with the loss or disturbance of suitable cave roosts (Papadatou et al. 2008), riparian habitat alteration poses the main threat to this bat (Biscardi et al. 2007).

Australian rivers have the highest variation in flow and flooding in the world (Williams 1981; Puckridge et al. 1988). Anthropogenic activities such as extraction and diversion of water have had adverse impacts on rivers in the arid-zone of Australia (Walker 1985; Kingsford and Thomas 1995). High natural variation in water availability coupled with anthropogenic activities and climate change has the potential to catastrophically affect arid-species that depend on water availability (Roshier et al. 2001; McKenzie et al. 2007; Saunders et al. 2013).

A major concern associated with natural rivers and lakes in urban areas is that they may be polluted by runoff from roads or other sources. When bats drink from these sources, they ingest these pollutants directly or indirectly by feeding on aquatic-emergent insects. Sources of pollution of farm and golf course dams include feces from livestock and wild animal, nitrate and phosphate in fertilizers, metals, pathogens, sediments and pesticides. Unfortunately, little research has been done on the use of polluted urban water sources by bats and the probable health impacts on bats. The little evidence that does exist suggests that at least some species of bats may not avoid polluted bodies of water in arid areas (Pilosof et al. 2013; Korine et al. 2015). In Durban, South Africa bat abundance and species richness were higher over a polluted than over an unpolluted river and bat feeding activity (measured by feeding buzzes in the echolocation sequences) was also higher at the polluted river. There was, however, no difference in insect diversity between the two rivers (Naidoo et al. 2011) and, with the exception of a single species, Rufous mouse-eared bat, *Myotis bocagii*, proportions of prey items in the diets of bats did not correspond to their proportion in the insect fauna. *M. bocagii* fed predominantly on Diptera and this was also the most abundant insect in the insect light traps (Naidoo et al. 2011).

8.3.2 Mining

Mining is a major anthropogenic source of environmental destruction and contamination globally. Toxins associated with extensive mining operations, in particular, gold mining is well documented. Cyanide used to extract gold from ore is commonly stored in open ponds, some of which are 200 acres in size. The actual numbers of bats, and other wildlife killed by drinking at these ponds is poorly understood and very difficult to track as many affected individuals either become submerged, or die from drinking contaminated water after leaving the site. Between 1980 and 1989, 34 % of all known mammals killed at cyanide ponds used for mining gold in California, Nevada, and Arizona were bats (Clark and Hothem 1991).

Other heavy metals used in mining operations such as arsenic, cadmium, chromium, copper, lead, mercury, methyl mercury, nickel, and zinc have been found in bat carcasses. In Arizona, USA where at least 20 % of bat populations are in decline (King et al. 2001), Mexican free-tailed bats (*Tadarida brasiliensis*) living 8 km from a major copper smelting mine had accumulated significant levels of atmospheric mercury in their tissues (Petit 2007). In another study in Arizona, pallid bats (*Antrozous pallidus*), western pipistrelles (*Parastrellus hesperus*), and *T. brasiliensis* had elevated mercury levels in their liver and muscles that they most likely acquired via drinking from contaminated free-water sources (Reidinger 1972; see also Syaripuddin et al. 2014).

Besides contaminated ponds, natural water flows through thousands of abandoned mines in the western USA (used by bats for hibernaculum and maternity roosts) may be highly contaminated with heavy metals. For example, at Sheep Tank Mine overlooking the Colorado River in Arizona, barium, manganese and zinc were detected in soil samples at concentrations 10 times normal levels and *E. fuscus* captured at the site had higher concentrations of these elements than those collected from three other sites (King et al. 2001). Other species included in the study had high arsenic levels as well as other contaminants (copper, lead, barium, manganese, and zinc) (King et al. 2001). Bats and other terrestrial vertebrates can also be exposed to high levels of contaminants by ingesting aquatic emergent insects living in toxic streams and High levels of bioaccumulated cadmium and zinc are known to occur as far as 381 km downstream from the pollution source, whereas lead was found to be transferred from sediments to chironomids (midges) only as far as 40 km downstream (Cain et al. 1992). Thus, large stretches of streams and rivers far from the point source of contamination pose threats to bats and other aquatic and terrestrial wildlife.

Bats are also known to fly and possibly forage/drink over gold mines in Australia (Donato and Smith 2007; Smith et al. 2008). High bat activity was recorded over gold mine water bodies containing cyanide (Griffiths et al. 2014a). Griffiths et al. (2014b) suggested that elevated salt levels in water bodies at gold mines may decrease bat activity, foraging, and drinking. Bats, including the Vulnerable (IUCN 2014) ghost bat, *Macroderma gigas*, have also been recorded around an Australian copper mine in the Great Sandy Desert, although the mine's effects on individuals or the population is unknown (Read 1998).

Africa is rich in mineral resources and this makes mining activities relatively common so likely a serious threat to water quality and therefore to bats. A matter of grave concern is that no research has been done in Africa in this regard. This situation prevails despite evidence that mining activities do pollute surface water in Africa (Olade 1987; Naicker et al. 2003).

8.3.3 Agriculture

Organochlorine pollution of streams and rivers, and other sources, is of major concern for bats (see Bayat et al. 2014 for review). Experimental testing of organochlorine insecticides such as DDT on two species widely distributed throughout the USA, found that *Myotis lucifugus* was approximately twice more sensitive than were *E. fuscus*. Furthermore, juvenile *E. fuscus* were 1.5 times more sensitive than adults (Clark et al. 1978). In addition, tests showed that individuals of *T. brasiliensis* poisoned with DDT survived for some time but later died of DDT poisoning mobilized from fat during active flight after being starved (Clark et al. 1975). Laboratory studies also show that presence of organochlorine in tissues can accelerate the catabolism of fat, causing DDE-dosed bats (*M. lucifugus*) to lose weight faster than control bats (Clark and Stafford 1981). Although banned in the USA in 1972, significant levels of DDT and DDE have been documented in tissues collected from bats foraging and drinking at the Rocky Mountain Arsenal Superfund Site (O'Shea et al. 2001). High DDT concentrations are also found in *M. lucifugus* tissues in the Eastern United States (Kannan et al. 2010). Furthermore, post-ban persistence of DDT in USA bats has been verified by sampling guano at roost sites (Clark et al. 1982; Reidinger and Cockrum 1978; Bennett and Thies 2007). DDT has also been found in bat tissues in Australia despite being banned since 1987 (Mispagel et al. 2004; Allinson et al. 2006). DDT for agricultural use was essential banned worldwide in 2001, but recent work from Africa showed that DDT is probably still being used and accumulating in the tissues of multiple species of bats (Stechert et al. 2014).

The two most common agricultural pollutants are nitrogen and phosphorus and sources of these pollutants include inorganic and organic fertilizers, leguminous crops, septic tanks, farm and municipal waste water treatment facilities, and, in the case of phosphorous, run-off from groundwater discharge and atmospheric deposition. An excess of these nutrients is the leading cause of aquatic eutrophication (Shabalala et al. 2013). Inorganic pollutants such as metals from agricultural and industrial run-off can also accumulate in these sites as well as in the tissues of insects using these bodies of water. Bats feedings on such insects are thus at risk of ingesting high levels of toxic metals such cadmium, chromium and nickel (see Naidoo et al. 2013).

8.3.4 Waste Water

European bats foraging in aquatic habitats are known to be largely exposed to toxic heavy metals which bioaccumulate in their insect food (Pikula et al. 2010). Organic pollution of rivers is also known to affect bat foraging, but its effects are variable. A British study compared the differences in bat activity found respectively upstream and downstream from sewage outputs and showed that downstream activity of pipistrelle bats decreased whereas that of *M. daubentonii* increased relative to upstream sites (Vaughan et al. 1996). The latter species is thought to benefit from the higher downstream abundance of pollution-tolerant prey such as chironomids. However, an Irish study obtained opposite results, with *P. pygmaeus* being more common downstream of sewage effluent discharges than *M. daubentonii* (Abbott et al. 2009). Park and Cristinacce (2006) compared the effects of two types of sewage treatment works for foraging bats: those with percolating filter beds, often hosting many insects potentially important for bats, and the "activated sludge" system—gradually replacing the former—in which sewage and bacteria-laden sludge are mixed and agitated so that they prove inhospitable for the invertebrate fauna. The study showed that both insect biomass and bat activity were higher at percolating filter beds and that bat activity there was comparable to that recorded at nearby natural foraging habitats. However, bats may run serious risks when foraging at such sewage treatment works: endocrine disrupting chemicals, which may alter the endocrine functions in exposed animals, have been found to concentrate in bat insect prey at percolating filter beds, with potentially harmful effects on foraging bats (Park et al. 2009).

There has been very little research in Africa on the concentration of pollutants in tissues of bats and no work on the long and short term effects of these pollutants on the health of bats. There is some evidence of the presence of the toxic metals cadmium, chromium and nickel in tissues of African bats foraging at sites downstream of waste water treatment plants (Naidoo et al. 2013). Furthermore, bats foraging over waste water treatment facilities display increased haematocrit and DNA damage and decreased antioxidant capacity in muscle tissue compared to bats that forage over unpolluted sites. Although these effects were not lethal they may result in long-term negative effects on the health of bats (Naidoo et al. 2014). These metals were probably ingested by bats via their insect prey.

There is evidence that aerial insects developing in sewage sludge and waste water at sewage treatment plants can accumulate pollutants that could disrupt endocrine functioning (Park et al. 2009). However, a similar study on the activity of the insectivorous bat, the banana bat, *Neoromicia nana*, at three urban rivers systems above and downstream of where sewage effluent enters these rivers revealed that the relative abundance and feeding activity of *N. nana* were higher at polluted sites downstream of where sewage entered the system than at the unpolluted sites upstream (Naidoo et al. 2013). In this case the bats may have been attracted by the higher abundance of dipterans over the polluted sites. Diptera were the dominant prey items in both the insect fauna at the polluted sites and in the diets of the bats (Naidoo et al. 2013). This also appeared to be the case for *M. bocagii* which also fed predominantly and opportunistically on Diptera (Naidoo et al. 2011).

The response by bats to rivers affected by waste water treatment effluent may vary both between and within species. In North America (Kalcounis-Rueppell et al. 2007) and England (Vaughan et al. 1996), some species were more active upstream from where waste water effluent entered the rivers while others were more active downstream. It appears that these differences arise from the differential effects of euthrophication on insect prey as well as on the responses of bats. Some species take advantage of eutrophication that causes an increase in the abundance of their preferred prey, and other species which apparently do not feed on insects that are affected by eutrophication, prefer to forage in less polluted habitats. Furthermore, these differences may also result from differences in the foraging behavior of the same species at different sites. For example, *N. nana* fed opportunistically on the small abundant dipterans at wastewater polluted sites, but at unpolluted river sites fed selectively on insects from other orders (Naidoo et al. 2013).

Another major anthropogenic compound found in open bodies of water in the USA is polychlorinated biphenyl or PCB, a common industrial waste product that was banned by the United States in 1979 and the United Nations in 2001. PCB poisoning in pregnant *M. lucifugus* led to stillborn young (Clark and Krynitsky 1978). Aquatic-emergent insects are key exporters of contaminants to terrestrial ecosystems (Menzie 1980; Runck 2007) and data show significant lateral transfers of PCBs to terrestrial riparian predators such as spiders, reptiles and amphibians (Walters et al. 2008). High concentrations of PCB's have been found in fat tissues of *M. lucifugus* in New York and Kentucky (Kannan et al. 2010). Along the fresh water tidal river, the Biesbosch, in the Netherlands, direct transfer from river sediments to chironomids to pond bats occurred in concentrations known to cause negative reproductive effects in mink (Reinhold et al. 1999). Frick et al. (2007) investigated the effects of an accidental chemical spill (metam sodium) on Yuma myotis (*Myotis yumanensis*) in California and found reduced female juvenile survival, but not adult female survival. The spill-affected population declined significantly during the first years of the study. Although the population increased in year four, this also coincided with an end to an extensive regional drought. Controlled experimental exposure to Lindane (an organochlorine used in wood preservatives) at sublethal levels in *P. pipstrellus* increased 24 h metabolic rates of a 7.3 g individual by 15 % and in a 6.3 g individual by 23 %, thereby posing a significant threat to survivorship of free-living individuals (Swanepoel et al. 1999) and showing that sub-lethal exposure can affect energetic balance.

8.4 Mitigation and Restoration

Both the availability and distribution of water in drylands have been drastically altered by natural processes such as decline in annual precipitation, and by anthropogenic developments such as irrigation for agriculture, over exploitation of groundwater and human-induced climate changes.

8.4.1 Restoration of Water Sources and Related Habitats

Most wetlands have been altered globally due to anthropogenic disruption, pollution, and outright destruction. In some, but too few, places, humans have begun to restore some of those wetlands. For example, in the USA, the Sierra Nevada Conservancy is working in cooperation with State Parks, the Department of Toxic Substances, California State University Chico and others, to identify mercury sources and potential remediation strategies for an abandoned hydraulic mine discharging sediment and heavy metals into the Yuba River and removing mercury from dredged sediment that have accumulated in the Combie Reservoir.

In California, restoration of the Cosumnes River floodplain re-established bat activity that broadly corresponded with flooding and an increase in aquatic emergent insects (Rainey et al. 2006). Furthermore restoration of riparian habitat, frequently damaged by cattle as well as other anthropogenic uses, and wetlands commonly destroyed by human development, is essential and is occurring in some areas, but well below necessary levels for bat conservation (Goodwin et al. 1997).

Despite some of the negative effects highlighted in the previous section concerning waste water effluent, wastewater reclamation is an important process especially in areas where water is scare (Anderson et al. 2001). Wastewater can be used to construct artificial wetlands that provide habitat for wildlife if the water is properly treated (Greenway and Simpson 1996; Fujioka et al. 1999; Greenway and Woolley 1999; Greenway 2005). Some studies have found that increased nutrient loads, such as those caused by wastewater effluent may have a positive effect on insect and bat abundance both in US and European streams (Kokurewicz 1995; Vaughan et al. 1996; Abbott et al. 2009). One US study found that bat activity and foraging levels were the same up-stream and down-stream of wastewater discharge but community structure was altered, with the riparian-specialist *Perimyotis subflavus* being more abundant (Kalcounis-Rueppell et al. 2007).

8.4.2 Artificial Water Sources

One way to overcome the diminishing of natural water sources in many drylands is the development of artificial catchments which are widely used for wildlife management (Krausman et al. 2006). There has long been controversy regarding the effects of catchments on local wildlife, in which critics argue that these developments do not yield expected benefits to game species and may have opposing impacts such as predation (O'Brien et al. 2006).

Small artificial ponds may be of utmost importance for wildlife (Russo et al. 2012). The large-scale expansion of intensive agriculture in semiarid Mediterranean climates has often been sustained by hydraulic engineering works, to cope with the scarcity of natural irrigation water. In southeastern Spain, Lisón and Calvo (2011) studied the effects on bats of a water transfer channel and a related network of irrigation ponds in a mixed landscape of traditional and intensive agricultural landscape. In general, artificial bodies of water had a positive effect on bat activity, but this mainly regarded common, generalist species (*P. pipistrellus* and *P. pygmaeus*) most likely because of the absence of foraging habitats suitable for more specialized species (those bearing a higher conservation value) such as riparian vegetation. In Catalonia, rice paddies sustain high bat activity, providing large amounts of insect prey. However, roost availability was the main limiting factor and installing bat boxes represents a valuable strategy to increase bat populations (Flaquer et al. 2006). In the arid Ikh Nart Nature Reserve in Mongolia, significantly more bats were caught at natural springs relative to human-made wells and no bats were captured at sites without water (Davie et al. 2012). This suggests that at least for this area, replacing lost natural water sources with artificial ones may not be as effective for preserving bat populations as conserving natural water sources.

Paradoxically, the creation of large water reservoirs may prove harmful to the entire bat community. Rebelo and Rainho (2009) looked at the effects on bats of the largest reservoir in Europe, created by construction in 2001 of the Alqueva dam, in Alentejo, Southern Portugal. The project led to the deforestation and submersion of an area of ca. 250 km^2. Consequently, bat populations were affected by the sudden disappearance of ca. 200 km of riparian habitat, together with large-scale roost loss and the replacement of important habitat with a vast homogeneous one which was not used by foraging bats. Noticeably, bat activity showed a strong decline in the submerged areas but increased in the surrounding unaffected habitat.

The expansion of Mediterranean species into surrounding arid wildlife communities may have a negative impact on local populations such as competition for the use of pools for drinking and foraging. Nine of the 12 Negev species of bats (Korine and Pinshow 2004) are associated with arid areas, and the Kuhl's pipistrelle, the European free-tailed bat (*Tadrida teniotis*), and the rare lesser horseshoe bat (*Rhinolophus hipposideros*)—are Mediterranean species that have expanded their distribution into the Negev in the twentieth century (Yom-Tov and Mendelssohn 1988). The most common bat in some desert habitats and in particular at artificial water sites in the Negev is Kuhl's pipistrelle (Korine and Pinshow 2004). The expanded distribution is probably linked to human settlements and in particular to artificial bodies of water since non-desert species of bats must drink on a daily basis and drink more frequently compared with desert-dwelling bats (Razgour 2010). Kuhl's pipistrelle competes for the use of pools for drinking and foraging, resulting in temporal and spatial partitioning between local desert bat species (Razgour et al. 2011). The documented competition between Kuhl's pipistrelle and desert-dwelling bat species (Polak et al. 2011; Razgour et al. 2011), combined with the increasing development of bodies of open water in the Negev and other drylands, may lead to further resource competition resulting in loss to the region's biodiversity. Korine et al. (2015) have shown that species richness and activity of desert dwelling bats did not differ between artificial and natural bodies of water in the Negev desert, however several species of bats drank or foraged only at natural bodies of water.

8.5 Conclusion and Future Directions

Human population growth, land use change and habitat loss have led to massive habitat alterations and destruction, particularly of water sources in arid regions. The availability of water (temporary/permanent) appears to have a strong positive influence on species of bats richness and activity. This suggests that large temporary pools are important for the conservation of bats in arid environments. A reduction in the availability of temporary pools, due to intensification of arid conditions, is expected to predominantly affect species of bats that forage over water, and will most likely increase interspecific competition for foraging space above the pools. These problems are likely be exacerbated in species of bats that are able to extend into arid areas because of their association with humans. Studies on the distribution of bats in drylands on a large scale should be the focus of future research to understand how climate change and introduction of artificial bodies of water effect species distribution, activity and richness. Studies are strongly needed in arid regions to understand the best and most efficient way to provide safe artificial water sources for bats that can mitigate increased incidences of drought due to climate change and, in some cases, the total loss of available water, especially in the more temperate arid regions with shorter growing seasons. For example, placement of artificial water sources near maternity roosts is instrumental in arid temperate areas with shorter growing seasons (Adams 2010). However, the introduction of artificial bodies of water may promote invasion by non-native species and range expansion of others, leading to resource competition. In regions of Europe likely to become water-stressed because of human induced climate changes, bats may be affected as they may lack the physiological means to cope with water limitation (Sherwin et al. 2013).

Africa, as well as other arid areas such as the Negev and the Mongolian deserts, has a high diversity of bats but compared to other areas of the world its bat fauna has been little studied. Fundamental research is most needed throughout Africa and other arid zones on how often bats need to drink and whether this varies across species, geographically and seasonally. Comparative studies on bats with distributions restricted to arid regions and species that have populations in mesic and arid regions would be particularly informative in this regard. For example, the diversity of renal capacities and habitat use amongst African species of bats of the same family (Happold and Happold 1988), and the emergence of robust family level phylogenies (e.g. Stoffberg et al. 2010) provide an excellent opportunity to study the evolution of renal form and function in African bats in an ecological context. Special focus should be placed on research determining the extent to which African bats are reliant on artificial water sources. Such research should target arid zone species of bats, especially those species that live in close association with humans because these are the species likely to be impacted by insufficient or polluted water sources.

Research is also needed on whether all water sources are used for both drinking and foraging and how bats respond to decreases in water quality as a result of pollutants. Do certain species of bats avoid drinking from low quality bodies of water as shown by Korine et al. (2015)? Would bats still use polluted bodies of water for feeding but not for drinking? If so, how do they detect low quality water, do they do so before they are adversely affected by it and do they have alternative water sources? How are desert-dwelling bats affected by pollutants in water or by waterborne toxins and pollutants in the insect fauna, and are such bats able to deal with such pollutants physiologically?

Although least is known about bats and water in sub-Sahara Africa, studies thus far in other regions of the world are in their infancy in terms of understanding the long-term effects of decreased water availability on bat and other wild populations. Due to human destruction of wetlands and riparian habitats as well as unsustainable human population growth that more and more is utilizing greater amounts of fresh water, availability of fresh water to sustain wildlife populations are reaching critically low levels, especially in areas suffering from extended droughts due to human-induced climate disruption. Because water is a key ingredient of all life, focus on this topic needs to increase and because bats act as ‘canaries in a global coal mine,’ studies concerning bats and water are key to better management of water resources in natural and artificial areas.

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