Chapter 4
Urban Bats and their Parasites

Elizabeth M. Warburton, Erin Swerdfeger, and Joanna L. Coleman

Abstract Understanding host-parasite relationships in urban environments provides information critical for understanding bat ecology in anthropogenically altered landscapes. Although most current evidence comes from bat-virus systems, links between bats and their ectoparasites and endoparasites can provide key examples of how anthropogenic change affects bat health, roosting and foraging ecology, and, ultimately, bat conservation. This chapter examines the current state of knowledge and identifies potentially understudied aspects of urban bats and their parasites. Urbanisation can potentially modulate bat-parasite associations by affecting resource availability, ecophysiology, behaviour, and life history of bats. Urbanisation may also influence how these effects vary among parasites, bat species, and bat age classes. We distinguish between the effects of urbanisation in relation to ectoparasites and endoparasites, with one illustrative case study of each. The first case study examines ectoparasites of little brown bats (*Myotis lucifugus*) along an urban-rural gradient. It found some indications that *M. lucifugus* were more heavily parasitised in the city, likely because this was where the bats were most abundant and because ectoparasitism often rises along with host population density. The second case study investigates how anthropogenic habitat disturbance contributes to shifting helminth communities in big brown bats (*Eptesicus fuscus*). Land cover categories with more intense human activities were most likely to have similar helminth communities, likely because worms that parasitise more ecologically sensitive, intermediate hosts are more prone to extirpation with increasing anthropogenic disturbance. Finally, we conclude by suggesting that the tightly linked nature of the host-parasite relationship provides unique opportunities to

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address key urban ecology questions related to host foraging and roosting in urban areas, host-vector contact rates in disturbed habitat, and host susceptibility in response to anthropogenic stressors.

Keywords Endoparasites · Ectoparasites · Vectors · Chiroptera · Urbanisation

1 Introduction

As cities expand and human populations in urban areas progressively outnumber those in rural areas, bats, like other wildlife, must increasingly contend with more frequent and intense human activities in urban areas relative to other land uses. These activities can drastically alter the amount, configuration, and quality of habitat for bats, especially via replacement of vegetation by built cover. As such, they can also alter bats' relationships with their parasites.

While early definitions of parasitism focus on trophic implications (i.e. parasites 'feed off' their hosts and often include the concept of harming their hosts [e.g. Crofton 1971, cited in [1]]), this trophic focus is a narrow view of parasitism. Indeed, parasites constitute not one but many taxa and must be at least somewhat adapted to their hosts (i.e. to evade immune responses [1]). Thus, parasitism may be viewed through the lens of hosts as habitat, with food sources located within the host habitat [1]. Some of these host-parasite relationships are visually dramatic when encountered in nature, such as with ectoparasites (Fig. 4.1), whereas endoparasites remain hidden inside their bat hosts. This chapter adopts this ecological- and evolutionary-based definition of parasitism.

Studying bats and their host-parasite relationships in cities can provide critical ecological information, such as selection of foraging and roosting sites, that directly impacts bat conservation, as urbanisation is a key extinction threat for bats [2]. Parasitism of wildlife generally is modulated by diverse environmental parameters and linked to the distribution, population dynamics, and health of hosts [3] – all of which may vary with urbanisation. For bats, much evidence comes from virus-related research. For example, certain flying foxes (*Pteropus* spp.) exhibit dramatic behavioural adjustments to recent land use and land cover change in Australia [4, 5]. In their ancestral forest habitat, they migrate over long distances searching for spatially and temporally patchy food resources. However, amid deforestation pushing them out of forests, they have been drawn into cities, where cultivated (native and exotic) trees offer fruit and/or nectar year-round. These conditions favour sedentary behaviour so that there are now permanent, large, aggregations of flying foxes in many cities, where none existed historically [4]. Additionally, pteropodids are the natural reservoirs for Hendra virus (HeV), and modelling suggests that these altered behaviours drive disease dynamics [6]. As bats become more urbanised and sedentary, connectivity between local populations and herd immunity across the metapopulation declines. This results in more sporadic but more intense outbreaks in

Fig. 4.1 This wingless bat fly (Nycteribiidae: *Penicillidia* sp.) nearly covers the entire face of a Mozambican long-fingered bat (*Miniopterus mossambicus*). (Photo credit: Dr. Piotr Naskrecki, Minden Pictures)

urban populations – a phenomenon with significant medical and veterinary implications.

Though the above example focuses on a virus, it illustrates the generalised, expected effect of higher host densities increasing host-parasite contact rates [7 and others therein], including parasites that present zoonotic disease risks. Pteropodids are not the only bats whose distributions and population dynamics may vary with urbanisation, which may ultimately influence bat-parasite dynamics. Other species may be more abundant in cities, especially synanthropes that readily exploit subsidised food resources or anthropogenic roosts [see also 8]. Moreover, species such as Kuhl's pipistrelle [*Pipistrellus kuhlii*; 9] and little brown bats [*Myotis lucifugus*; 10] may exhibit altered fecundity in relation to urbanisation – a phenomenon that could modulate bat-parasite dynamics by altering the relative availability of pups and juveniles. The naïve immune systems of young bats and their reduced ability to self-groom may make them more susceptible to parasitism. Alternatively, parasites may prefer adult hosts, given their higher overwintering survival [11 and others therein]. Thus, altered host age structure could affect parasite populations.

Urban-associated pollutants and other stressors in cities may compromise immune function or other aspects of host health with possible parasitological consequences. For example, adult female and juvenile *Pipistrellus kuhlii* foraging over a more polluted reservoir in the Negev Desert harboured more ectoparasites compared to individuals foraging over cleaner ponds [12]. However, the focus of this study was not urban pollutants, and a lack of site replication makes it difficult to conclusively attribute differential parasitism to water quality. Other taxa offer additional evidence of these phenomena. Serieys et al. [13] investigated the causes of a deadly outbreak of Notoedric mange, a parasitic skin disease that decimated an urban population of bobcats (*Felis rufus*) in California, United States of America (USA). Comparison of blood samples from *F. rufus* along an urbanisation gradient showed that exposure to rodenticides and urban land use was linked to reduced immune function and skin health and higher susceptibility to mange.

Although understanding bat-parasite relationships is relevant to bat biology and ecology, only 21% of 570 publications on bat parasites identified in our literature search were in the topic areas (defined by Web of Science) of ecology and conservation (Fig. 4.2). Other dominant research foci and/or motivations were biodiversity discovery and phylogeny (39%) and zoonoses (19%). Studies of these associations in urban areas are rare, i.e. a total of 29 potentially relevant papers – all but 4 published since 2015 and strongly biased towards the Neotropics (18 studies) and zoonotic questions (16 studies). The nearly universal approach has been to document parasites of bats in urban areas and sometimes compare findings with published data from non-urban areas, as opposed to conducting simultaneous comparisons (e.g. along urban gradients), which could help elucidate the urban ecology of bats and their parasites. As such, this chapter examines the current state of knowledge and identifies potentially understudied aspects of urban bats and their parasites. The central theme is urbanisation modulating the dynamics of bat-parasite associations via its effects on resource availability, ecophysiology, behaviour, and life history of bats. These impacts can vary among parasites, bat species, and bat cohorts; consequently, bat ectoparasites and endoparasites are discussed in detail with one illustrative case study each.

2 Ectoparasites

Bats host a huge diversity of ectoparasitic arthropods that spend their whole lives on the outside of bats' bodies and/or in their roosts and often have high host specificity [14]. Thus, their diversity and abundance are inexorably linked to aspects of bat

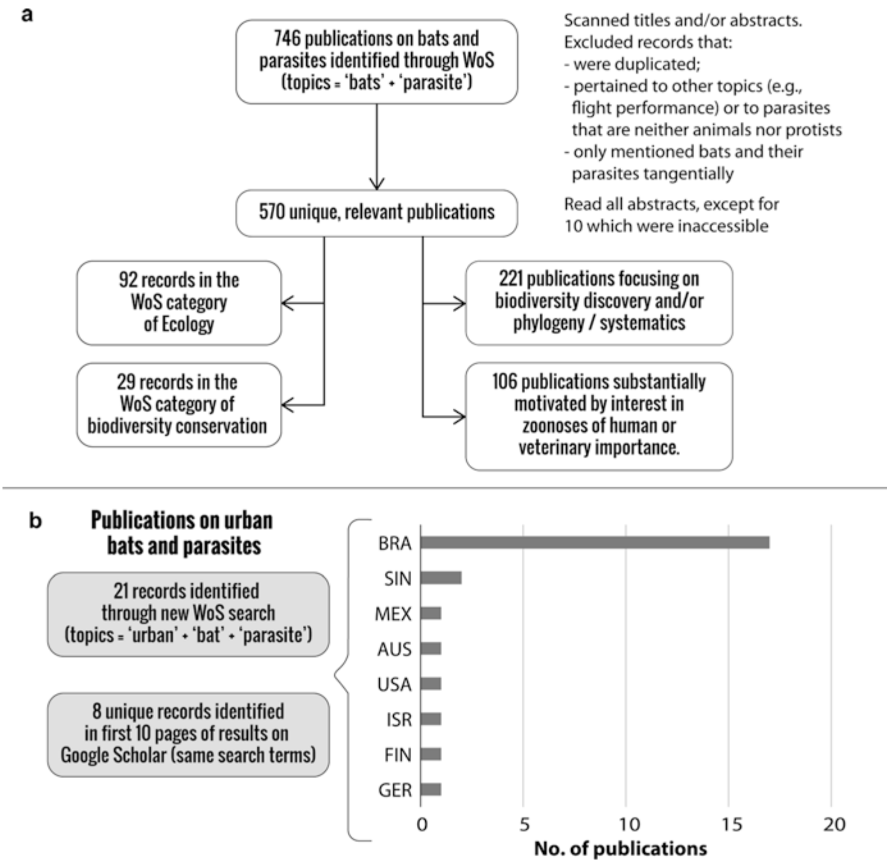

Fig. 4.2 Results of a literature search on 27 April 2021. (**a**) In step 1, we searched Web of Science (WoS) with the search terms 'bats' and 'parasite' in the topics. Scanning all titles and abstracts allowed us to exclude 176 records. We then read the 560 accessible abstracts of the resulting unique, relevant records and examined their distribution among WoS categories (in WoS analytics) and 2 research foci: (1) biodiversity discovery and phylogeny/systematics (i.e. species checklists, taxonomic revisions, evolution) and (2) zoonoses of human and veterinary importance, i.e. abstracts prominently mention diseases of humans, pets, or livestock). (**b**) In step 2, we performed a new WoS search with the search terms 'urban', 'bat', and 'parasite' in the topics and supplemented this with a Google Scholar search to identify other unique records (not indexed in WoS) in the first ten pages of results. We retained studies that reported original fieldwork (as opposed to meta-analyses) and classified these by location to explore geographic clustering of studies. (Histogram, country ISO codes on y-axis)

health, ecology, and behaviour that should be responsive to urbanisation. Additionally, various urban-related environmental changes (e.g. climate, pollution) may affect these ectoparasites independently of their hosts. Finally, these parasites may be disease vectors. Therefore, studying ectoparasitism in relation to urbanisation could help answer timely questions in urban ecology and bat roost selection, two key components of bat conservation.

2.1 What Are the Parasitological Consequences of Altered Roosting Behaviours By Urban Bats?

In most biomes, urban development reduces the availability of natural roosts while increasing that of anthropogenic structures. Therefore, any bat species' urban adaptedness is at least somewhat predicted by flexible roosting habits. Indeed, divergent behaviours between urban and non-urban bat populations are well-documented. These include shifts to commensal roosting, as in Brazil, where 84 species that inhabit cities mainly use built elements, especially buildings [15]. Other shifts include increased roost fidelity, as in the case of Indiana bats (*Myotis sodalis*), which switch less often at the edge of a developing urban area than in contiguous forest [16].

Both shifts have parasitological implications. First, not only does frequent roost switching correlate with reduced ectoparasitism, which may have evolved as an anti-parasitic strategy, but also this roost-switching declines in commensal roosts [7 and others therein]. Next, commensal roosts, being generally larger and more permanent than natural ones, favour larger colonies and tighter social networks among bats, and thus parasite transfers between individuals [7]. They also promote reproduction of insects (e.g. bat flies: Diptera, Streblidae, Nycteribiidae) that complete part of their life cycles in roosts [17]. Finally, ectoparasites may exhibit greater host specificity in commensal roosts occupied by a single bat species. For instance, four bat fly species parasitise a single species in Singapore, where their bat hosts use commensal roosts, but use multiple hosts elsewhere in Southeast Asia, where they roost with other bat species in caves [17].

2.2 Does Urbanisation Have Linked Fitness and Parasitological Implications for Bats?

Urbanisation could modulate either the prevalence or the intensity of ectoparasitism by impacting various indicators of bat fitness or affect bat fitness by modulating ectoparasitism factors. One indicator of this modulation is bat body condition, which may vary with urbanisation [3, 10] and often correlates with ectoparasitism – sometimes positively [e.g. various parasites on *M. lucifugus*; 18], sometimes negatively [e.g. bat flies on fruit bats; 17]. Yet, while the ectoparasites clearly gain resources, for example, by consuming the blood or lymph of their hosts, whether they directly and substantially reduce body condition is debatable [14] because establishing cause and effect is difficult. For example, finding that bats in better body condition harbour fewer parasites could indicate either that fitter individuals are better able to cope with parasites (e.g. have more energy to groom) or that they are not preferred hosts.

Another indicator of fitness that could vary with urbanisation is reproductive output. Evidence remains scant, but in Italy, as urban land cover around building maternity roosts of *Pipistrellus kuhlii* increases, so do numbers of pups per female [9]. Higher urban proportions of immature bats could, as mentioned, have either positive or negative effects on ectoparasitism levels, depending on their host age-class preferences. Additionally, these *P. kuhlii* give birth earlier in more urbanised roosts [9]. For temperate zone bats, earlier parturition is a fitness gain – it leaves more time for mothers and juveniles to accumulate fat reserves needed to overwinter. Earlier parturition could also be detrimental to various ectoparasites by reducing their optimal reproduction window. For example, two nycteribiid flies, one wing mite (*Spinturnix psi*) and one hard tick (*Ixodes simplex simplex*), on Schreiber's bat (*Miniopterus schreibersii*) in Portugal mainly reproduce on adult females and volant pups and mostly during pregnancy and lactation [19]. This is likely because pregnant females and pups have reduced behavioural and immune defences, and lactation enhances opportunities for vertical transmission while reducing the mother's available energy to groom [19].

2.3 Do Urban Abiotic Changes Modulate Bat-Ectoparasite Relationships?

Compared to surrounding areas, most cities are warmer and less humid, with altered precipitation and dampened seasonality – this is the urban heat island (UHI). For ectoparasites of bats, especially ones that live part of their lives off their hosts, such shifts could alter survival, reproduction, and/or host-seeking behaviour. Though this possibility has not been tested specifically in relation to the UHI, temperature and precipitation do affect bat flies parasitising bats in Venezuela, albeit differentially depending on the bat species [20]. Additionally, the UHI in Poland seemed linked to reduced abundance of *Ixodes ricinus* [21], which rarely parasitise bats but are in the same genus as other hard ticks that do.

Cities also tend to have high levels of various forms of pollution. One is heavy metal contamination, and evidence from a small sample of Daubenton's bats (*Myotis daubentonii*) in Finland [22] suggests that it might disrupt bat-ectoparasite associations. The likelihood that an individual harboured wing mites rose with its cadmium and copper exposures but declined with lead exposure, while arsenic and cobalt levels were negatively correlated with the presence of bat flies. Another urban issue is the presence of light and noise pollution. The implications for bats and their ectoparasites are unknown but may be worth studying given strong evidence that both stressors disrupt associations between túngara frogs (*Engystomops pustulosus*) and the *Corethrella* midges that bite them, namely, by reducing midge abundance [23].

2.4 Could Urban Changes in Ectoparasite Loads Alter the Risk of Disease?

Bats are a species-rich order [24] and, as such, host a wide diversity of microparasites and macroparasites, increasing the likelihood of parasite co-occurrence within the same host. This intra-host parasite diversity creates opportunities for one parasite to be a vector for another. Indeed, several ectoparasites transmit pathogens between bats, and bat species that host more ectoparasite species also host greater viral richness [25]. Consequently, if urbanisation alters bat-ectoparasite associations, it could also alter dynamics of pathogen transmission.

One such pathogen of concern is the fungus *Pseudogymnoascus destructans*. This fungus causes white nose syndrome, a disease that mainly kills bats during hibernation and has pushed some North American species to the brink of extinction [26]. Recently, it was detected on spinturnicid mites collected from bats in Kentucky, USA, raising the possibility that ectoparasites are involved in spreading the disease [27]. The fact that these bats were sampled in late summer further suggests that bats might transport the fungus from summer habitats, which may be urban, to their hibernacula, where mating occurs, during which time ectoparasites may move between hosts. Thus, the urban ecology of bat-ectoparasite associations may have conservation implications.

Box 4.1 Ectoparasites of Bats in Relation to Urbanisation

The following case study is extracted from unpublished data from Coleman JL, Swerdfeger E and RMR Barclay.

Problem

Only 29 of the 570 relevant studies identified (Fig. 4.2) assessed bat-parasite relationships along urbanisation gradients, and none did so for colonial insectivorous bats in temperate zone cities. As outlined above, examination of bat ectoparasites in urban environments could be key to understanding host roosting behaviour and fitness.

Methodology

Ectoparasites on *M. lucifugus* were documented in relation to urbanisation in Calgary, Alberta, Canada. The urban gradient consisted of three zones: urban (within city limits and surrounded by development), rural ($\geq$ 40 km from city limits), and transition (from city limits out to 40 km, 11 sites). Each zone had at least nine replicate sites (11 urban, 11 transition, 9 rural), all located in treed, riparian areas to minimise confounding effects of habitat. From May to mid-September in 2007 and 2008, the authors captured 884 bats by mist-netting and recorded their body condition, demographics, and ectoparasites. The authors considered three cohorts (adult females, adult males, and juveniles) and calculated total ectoparasite prevalence (percentage of bats infested), total

(continued)

Box 4.1 (continued)

ectoparasite intensity (ectoparasites per infested bat), and intensity and prevalence per parasite taxon. Associations between zone and infestation (total ectoparasite prevalence and per parasite taxon) were assessed using two-way contingency tables. The influence of urbanisation on intensity (total ectoparasite intensity and per taxon) was compared for each bat cohort using negative binomial generalised linear mixed models. Finally, non-parametric measures of associations between individual parasite load and body condition were determined.

Findings

The relationship between urbanisation and ectoparasites of *M. lucifugus* reveals a complex response that varies among parasite taxa, over time, and with demographics and body condition. Most bats (60%) harboured at least one ectoparasite (Fig. 4.3), including various mites (Acarina: Macronyssidae, Spinturnicidae), bat fleas (*Myodopsilla* spp., G. Chilton, pers. comm.), bed

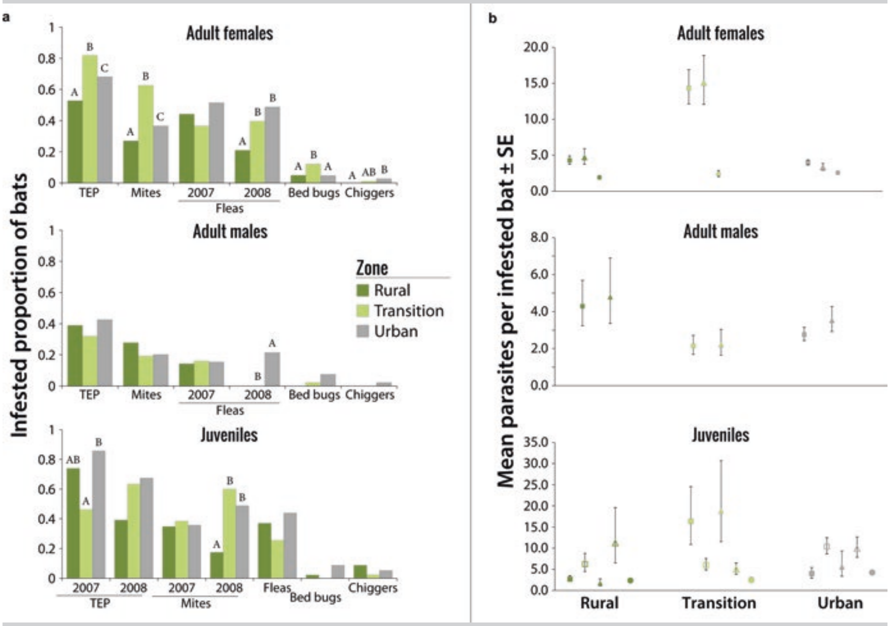

Fig. 4.3 Variation in ectoparasitism on three cohorts of little brown bats, *Myotis lucifugus*, with urbanisation in Calgary, Alberta, Canada. Upper charts for adult females, middle charts for adult males, lower charts for juveniles, different colours for different zones. (**a**) Differences in ectoparasite prevalence (total ectoparasite prevalence = TEP). Different letters above columns indicate significantly different values – columns with no letters are not different. (**b**) Variation in intensity of parasites. Symbols represent total ectoparasites (squares), triangles (mites), and circles (fleas). On the chart for juveniles, closed symbols are 2007 values and open symbols are 2008 values. For adult females and juveniles, values are means over both years. All values are least-squared means with back-transformed standard errors

(continued)

Box 4.1 (continued)

bugs (*Cimex* spp.), chiggers (Trombiculidae, H. Proctor, pers. comm.), and soft ticks (Argasidae). Intensities and yearly variation were generally low, especially in the urban population (Fig. 4.3b). Links between urbanisation and ectoparasitism were obvious in adult female bats. Maximal prevalence (except for fleas in 2007; Fig. 4.3a) and total ectoparasite intensity (Fig. 4.3b) occurred in the transition zone. Total ectoparasite intensity also peaked on lactating females and in 2008. For fleas, intensity differed between years (but not during pregnancy) and with reproductive status in 2008, but not with urbanisation (Fig. 4.3b). Body condition was positively correlated with ectoparasitism (total ectoparasite intensity and intensities of mites and bed bugs) but only on adult females. For adult male bats, the only link between urbanisation and ectoparasitism was that urban males were the only ones with fleas in 2008 (Fig. 4.3a).

Juvenile bats' ectoparasite associations mirrored those of adult females in some respects. For example, they had higher total ectoparasite and mite intensities in 2007, and rural juveniles were less likely to harbour mites in 2008 (Fig. 4.3). Prevalence and intensity measures for other juvenile bat-ectoparasite associations either did not vary with urbanisation or varied inconsistently between years (i.e. significant year-zone interactions).

Synthesis

By some measures, *M. lucifugus* were more parasitised in the city. This is likely because bats were most abundant there [10] and ectoparasitism often rises along with host population density [28]. However, for adult females, parasitism increased in the transition zone. This could reflect divergent roosting ecology along the urban-rural gradient. Urban and rural bats mainly roosted in large, enclosed, built structures, while those in the transition zone roosted in tree cavities or under shingles. Though switching among tree roosts can reduce infestations [29], it could also facilitate some dispersal of temporary parasites through passive transport between roosts [30]. Additionally, urbanisation could affect body condition, which was best in the transition zone, and increased parasitism with better body condition is predicted by the hypothesis that parasites prefer healthier hosts [31]. The near lack of variation in ectoparasite associations of adult males along the gradient may simply reflect the fact that they are widely dispersed in summer and harbour few parasites.

For juveniles, low variation in intensities may reflect age-biased parasitism. On one hand, the transition zone, where reproductive output peaks [10], presumably offers ectoparasites the greatest availability of young, vulnerable hosts [28]. On the other, because juveniles experience the highest overwinter mortality, permanent parasites should avoid independent young prior to winter [11] regardless of urbanisation.

Box 4.1 (continued)

Overall, this case demonstrates that ectoparasitic associations and their links to urbanisation can vary widely among conspecific cohorts. This highlights how the ecology of colonial bats can differ within as well as among species. It also illustrates that short-term studies might not reveal the full picture of urbanisation-mediated ectoparasitism. In some ways, parasitism did differ between years but it was most consistent in the city. This could reflect the potential for reduced urban seasonality (i.e. UHI) affecting parasites directly, by influencing their survival or, indirectly, by influencing host population dynamics and movements [28]. Ultimately, this case underscores the importance of multi-year investigations of multiple infestation metrics and parasitic taxa along urbanisation gradients to elucidate the role of urbanisation in mediating bat-ectoparasite relationships.

3 Endoparasites

As human encroachment on bat habitat grows, so do worries about bats acting as reservoirs for parasites, including some of public health concern. However, bat parasites that do not infect humans or domestic animals can provide key clues to ecological differences between urban and non-urban bats, such as feeding and roosting preferences. Additionally, comparing parasite diversity between urban and non-urban bats can help elucidate whether key phenomena, such as biological homogenisation, occur at multiple scales within anthropogenically disturbed habitat. Eukaryotic bat endoparasites, typically single-celled protozoans and worm-like helminths, represent both tropically transmitted and vector-borne groups. Thus, these parasites can reveal the influence of land use and land cover change on host susceptibility, parasite contact rates, and transmission pathways and the potential consequences of land use and land cover change on biodiversity at the scales of the host and parasite.

3.1 Protozoan Parasites and Host-Vector Contact Rates

Blood-borne parasites in the genera *Trypanosoma* and *Leishmania* (phylum Euglenozoa) are transmitted by hematophagous insects. Although both New and Old World *Leishmania* spp. have been documented infecting bats [e.g. 32 and others therein], only New World *Trypanosoma* spp. have been found in bats [33, 34]. One such species, *T. cruzi*, which causes Chagas disease in humans, infects various mammals, and there are concerns that bats could act as reservoirs of this parasite. Indeed, the prevalence of *Trypanosoma* spp. infecting Jamaican fruit-eating bats (*Artibeus jamaicensis*) is higher in forest fragments in a residential and agricultural matrix than in continuous tropical forest in Panama [34]. Likewise, trypanosomes were isolated from five bat species within rainforest fragments and surrounding farms in Espirito Santo, Brazil, but not from 20 other species of wild mammals [33]. The prevalence of *Leishmania* spp. within urban and peri-urban bats may be relatively high. For example, over 59% of common pipistrelle (*Pipistrellus pipistrellus*) sampled in and around Madrid harboured *L. infantum* [32], whereas *Miniopterus schreibersii* in Spanish wildlands demonstrated no evidence of *Leishmania* infection [35]. Although the dichotomous findings of these studies could reflect differences in tissues examined (i.e. the spleen [32] versus peripheral blood [35]), human-modified landscapes provide phlebotomine sandflies, the vectors of *Leishmania* spp., with hospitable habitat [36], and these flies can feed successfully on multiple species of bats [37]. Thus, an increase in phlebotomine sandflies in urban areas could be responsible for higher urban infection rates. Given that both parasite genera (*Leishmania* and *Trypanosoma*) have generalist species and generalist arthropod vectors, urbanisation could increase parasite contact rates for urban bats.

Members of the phylum Apicomplexa parasitise a wide variety of birds and mammals, including bats, and some are of zoonotic concern [38]. Apicomplexans can enter hosts via a hematophagous arthropod vector (e.g. *Plasmodium*) or through faecal-oral transmission (e.g. *Eimeria*). Therefore, effects of urbanisation in this phylum could vary with the life cycle and vector. For instance, Indian flying foxes (*Pteropus medius*) were slightly more likely to host *Hepatocystis* sp., vectored by mosquitos, and *Babesia* sp., vectored by ticks, in peri-urban than in rural areas of Bangladesh [39]. Meanwhile, the prevalence of *Polychromophilus* sp., vectored by bat flies, in Australian bent-wing bats (*Miniopterus orianae*) was up to 1.9 times higher at sites that retained ≤18% of their original habitat than at sites with ≥45% [40]. Thus, land use changes may promote apicomplexan infections, perhaps by increasing vector-host contact rates and/or susceptibility of hosts.

3.2 Helminths Provide Insights into Host Foraging

Although roundworms (Nematoda) and spiny-headed worms (Acanthocephala) infect bats, flukes (Trematoda) and tapeworms (Cestoda) often dominate bat helminth communities [41]. Many of these parasites have complex life cycles involving one or more invertebrate intermediate hosts. Whereas bat trematodes require two aquatic intermediate hosts (freshwater snails and larval insects; Fig. 4.4), cestodes have fully terrestrial life cycles, with arthropods, e.g. beetles, acting as single intermediate hosts [42]. Thus, habitat diversity of bat helminth life cycles varies, and anthropogenic disruption of any of these habitats may shift helminth communities. Urbanisation can affect both parasite community diversity and host traits, e.g. body condition and immune function. It could also cause ecologically sensitive intermediate hosts to decline, while more resilient taxa could become dominant [43]. Similarly, certain urban stressors could increase host susceptibility via

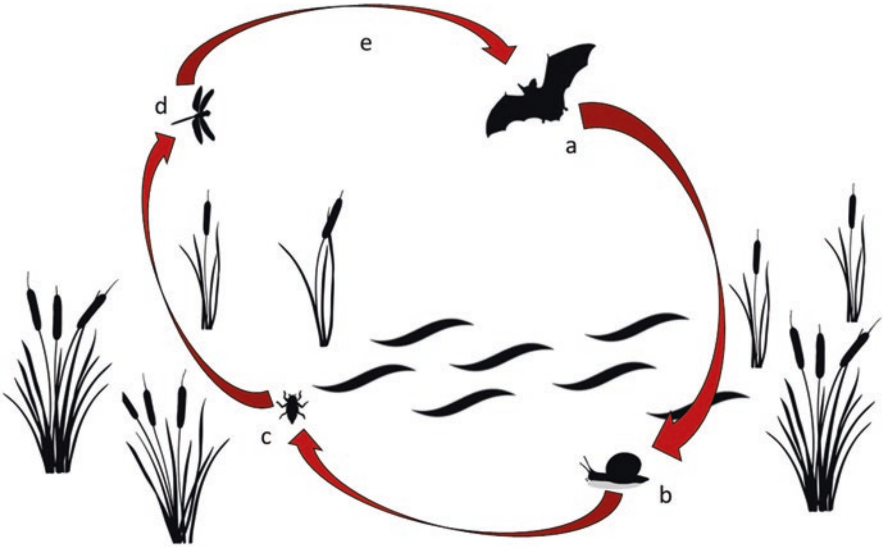

Fig. 4.4 Representative life cycle diagram of a trematode belonging to Lecithodendriidae, a family that almost exclusively parasitises bats. Trematode eggs are passed with faeces as a bat flies over a body of freshwater, such as when drinking (**a**). They then infect a snail where larvae metamorphose, grow, and exit their host as another free-swimming larval stage (**b**). These larvae swim until they contact a larval insect (e.g. a dragonfly nymph) and encyst within it (**c**). When the dragonfly metamorphoses into an adult, it carries the encysted trematode larvae (**d**). When a bat ingests the adult dragonfly, the encysted larvae break free and grow into adult worms in the bat's intestine, where they begin shedding eggs with the bat's faeces (**e**)

physiological processes [44]. Ultimately, understanding urban-related shifts in helminth communities may reveal the responses of bat hosts to extreme habitat disturbance.

Box 4.2 The Link Between Bat Helminth Communities and Anthropogenic Land Use

This information is extracted from Warburton et al. (2016) [41].

Problem

The ecology of endoparasite communities that inhabit bats is understudied not only in relatively undisturbed settings but also in relation to urbanisation. These helminth communities exist across a variety of environmental conditions, including not only 'natural' but also highly altered land covers, such as urbanised ones. Biological communities are typically thought to exhibit a distance-decay relationship where their species compositions become increasingly dissimilar with increasing physical distance. However, environments

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Box 4.2 (continued)

themselves, especially anthropogenically altered ones, can also shift the species composition of biological communities. Further, understanding how parasite communities change with urbanisation may elucidate how bat hosts function in cities by revealing key aspects of bat foraging ecology in urban environments.

Methodology

To understand how anthropogenic habitat disturbance contributes to shifting parasite communities, *Eptesicus fuscus* from a three-state region (Michigan, Indiana, and Kentucky) in the Midwestern USA were captured, and their helminth communities were assessed. Two hundred sixty bats consisting of adult and juvenile members of both sexes were captured from 13 maternity colonies with a mean inter-roost distance of 315.7 km (range = 6.9–660.7 km). The authors used GIS layers from the US National Land Cover Database and National Wetlands Inventory to quantify the area covered by 16 land cover categories, including designations such as barren land, croplands, forests, wetlands, and city centres, within 12-km radii of each colony (i.e. the maximum recorded foraging distance for *E. fuscus*). Using redundancy analysis, an extension of multiple linear regression that accounts for multiple response and explanatory variables, the effects of physical distances between roosts and land cover on helminth communities were assessed.

Findings

Helminth community composition was largely predicted by land cover around roosts. Indeed, land cover categories with more intense human activities had similar helminth communities. The effect was most significant ($p < 0.004$) in developed open spaces (e.g. parks, golf courses) and high-impervious cover sites (e.g. central business districts) and approached significance ($p = 0.0504$) in cultivated land covers (e.g. croplands, orchards). However, more urbanised sites did not have less species rich or less diverse helminth communities; instead, their species composition changed. Certain helminths, e.g. the cestode *Hymenolepis roudabushi* and the trematode *Paralecithodendrium swansoni*, were more closely associated with more developed land cover, while others, e.g. the nematodes *Rictularia lucifugus* and *Litomosoides guitaresi*, were more closely associated with cropland. Still other species, e.g. the trematode *Acanthatrium eptesici*, were associated with relatively undisturbed habitats such as woody wetlands.

Synthesis

These shifts in the helminth communities of bats in different land covers likely reflect shifts in intermediate host community composition and structure. Parasites with ecologically sensitive intermediate hosts, such as mayflies, might be more prone to extirpation with increasing anthropogenic

(continued)

Box 4.2 (continued)
disturbance. However, instead of producing a net loss in parasite species richness, the ecological niches left vacant by such extirpations could be filled by other helminths whose intermediate hosts are more resilient, such as chrysomelid beetles. Thus, understanding how helminth communities change in urban areas can reveal bats use resources in anthropogenically altered landscapes.

4 Concluding Perspectives

After surveying the literature, there is clearly still much to learn about bat-parasite relationships in the context of urbanisation. This knowledge gap is unfortunate, although perhaps not surprising given that bats and parasites are high-diversity groups, and they occur in many cities around the world. Further, the tightly linked nature of the host-parasite relationship provides excellent opportunities to address key urban ecology questions.

Questions about host foraging and roosting habits in urban areas, host-vector contact rates in disturbed habitat, and host susceptibility in response to anthropogenic stressors can be readily addressed within urban bat-parasite systems. For example, many ectoparasites contact bat hosts in roosts, whereas many helminths of bats are tropically transmitted. As such, comparing the diversity of ectoparasite and endoparasite communities between urban and non-urban bats can provide insight into how urban bats use resources in response to anthropogenic disturbance.

Additionally, certain human activities could increase transmission pathways, but this phenomenon is largely unexamined for most parasitic taxa. In one well-known example [5], urban planting of ornamental trees increased aggregations of flying foxes and consequently led to increased HeV transmission. Given that HeV relies on faecal-oral transmission, parasites with faecal-oral transmission (e.g. coccidia) could increase in these cities as well. Other human activities, such as draining wetlands for residential or agricultural use, should eliminate transmission pathways for trematodes that use aquatic intermediate hosts. However, anthropogenic effects on transmission pathways are poorly studied for most parasitic taxa, including those parasitising bats, and represent key knowledge gaps that require further investigation.

Urban bat-parasite systems could also be useful for examining broader ecological hypotheses. One is the diversity dilution hypothesis, which predicts increasing parasitism with declining diversity of hosts. Although evidence is equivocal [45], some findings in anthropogenically disturbed habitats [46–48] support key aspects of the hypothesis, namely, that preserving biodiversity in urban areas can reduce disease incidence.

Because parasitic associations are strong selective forces on both partners [14], urbanisation could have evolutionary implications for hosts and parasites. For example, pigeons (*Columbia livia*) exhibit hereditary variation in colouration along the urban gradient in Paris, France – variation that apparently reflects divergent strategies to cope with urban-related changes in blood-parasite pressure [49]. Although urban evolutionary ecology studies have not yet focused on bats and their parasites, doing so could elucidate the role of cities as drivers of evolution.

Research on urban bats and their parasites could also have important ecotoxicological applications as diverse parasites are increasingly perceived as useful bioindicators of habitat quality [50]. Finally, the potential effects of anthropogenic stressors, such as light pollution and roost disturbance, on the immune system of urban bats are not well known. These stressors could have a negative impact on disease susceptibility in urban bats, thereby increasing parasite prevalence or abundance. Thus, future work linking environmental health, anthropogenic activities, and host susceptibility could shed more light on our understanding of urban bat-parasite systems.

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