Chapter 11
Impacts of Wind Energy Development on Bats: A Global Perspective

Edward B. Arnett, Erin F. Baerwald, Fiona Mathews, Luisa Rodrigues, Armando Rodríguez-Durán, Jens Rydell, Rafael Villegas-Patraca and Christian C. Voigt

Abstract Wind energy continues to be one of the fastest growing renewable energy sources under development, and while representing a clean energy source, it is not environmentally neutral. Large numbers of bats are being killed at utility-scale wind energy facilities worldwide, raising concern about cumulative impacts of wind energy development on bat populations. We discuss our current state of knowledge on patterns of bat fatalities at wind facilities, estimates of fatalities, mitigation efforts, and policy and conservation implications. Given the magnitude and extent of fatalities of bats worldwide, the conservation implications of understanding and mitigating bat fatalities at wind energy facilities are critically important and should be proactive and based on science rather than being reactive and arbitrary.

E.B. Arnett (✉)
Department of Natural Resource Management, Texas Tech University, Lubbock, TX, USA
e-mail: earnett@trcp.org

E.F. Baerwald
Department of Biological Sciences, University of Calgary, Calgary, Canada

F. Mathews
College of Life and Environmental Sciences, University of Exeter, Exeter, UK

L. Rodrigues
Instituto da Conservação da Natureza e das Florestas, Lisbon, Portugal

A. Rodríguez-Durán
Universidad Interamericana, Bayamón, Puerto Rico

J. Rydell
Biology Department, Lund University, 223 62 Lund, Sweden

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11.1 Introduction

Developing renewable energy alternatives has become a global priority, owing to long-term environmental impacts from the use of fossil fuels, coupled with a changing climate (Schlesinger and Mitchell 1987; McLeish 2002; Inkley et al. 2004) and because of growing concerns about negative effects from the use of nuclear power (Voigt et al. 2015a). Wind power is one of the fastest growing renewable energy sources worldwide (Fig. 11.1), in part due to recent cost-competitiveness with conventional energy sources, technological advances, and tax incentives (Bernstein et al. 2006). Although presently wind power contributes only about 4 % of the global electricity demand, some countries provide greater than 20 % of their demand from wind (e.g., Denmark [34 %] and Spain and Portugal [21 %]; World Wind Energy Association, www.wwindea.org). By the end of 2013, the Global Wind Energy Council reported that 318,105 MW of wind power capacity was installed worldwide (http://www.gwec.net/wp-content/uploads/2014/04/5_17-1_global-installed-wind-power-capacity_regional-distribution.jpg). The World Wind Energy Association (http://www.wwindea.org) projects that by 2020, more than 700,000 MW could be installed globally.

Wind energy development is not environmentally neutral, and impacts to wildlife and their habitats have been documented and are of increasing concern. Wind energy development affects wildlife through direct mortality and indirectly through impacts on habitat structure and function (Arnett et al. 2007; Arnett 2012; NRC 2007; Strickland et al. 2011). Bats are killed by blunt force trauma or barotrauma and may also suffer from inner ear damage and other injuries not readily noticed by examining carcasses in the field (Baerwald et al. 2008; Grodsky et al. 2011; Rollins et al. 2012; Fig. 11.2). Kunz et al (2007a) proposed several hypotheses that may explain why bats are killed and some of these ideas have subsequently been discussed by others (e.g., Cryan and Barclay 2009; Rydell et al 2010a). Collisions at turbines do not appear to be chance events, and bats probably are attracted to turbines either directly, as turbines may resemble roosts (Cryan 2008), or indirectly, because turbines attract insects on which the bats feed (Rydell et al. 2010b). Horn et al. (2008) and Cryan et al. (2014) provide video evidence of possible attraction of bats to wind turbines.

Regardless of causal mechanisms, bat fatalities raise serious concerns about population-level impacts because bats are long-lived and have exceptionally low reproductive rates, and their population growth is relatively slow, which

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R. Villegas-Patraca
Unidad de Servicios Profesionales Altamente Especializados,
Instituto de Ecología, Coatepec, Veracruz, Mexico

C.C. Voigt
Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research,
Berlin, Germany

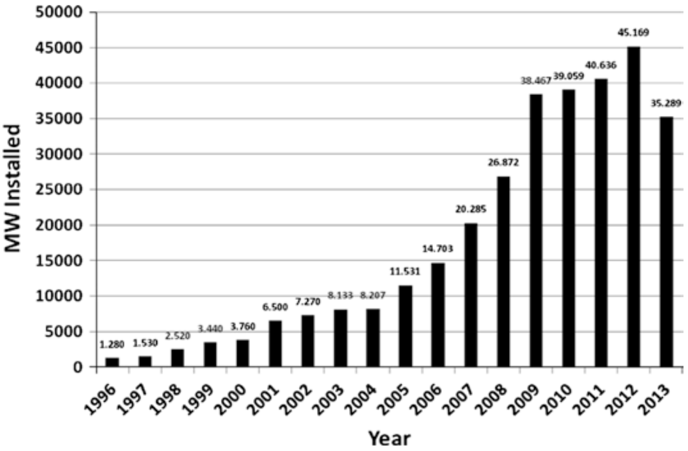

Fig. 11.1 Annual installed global wind energy capacity (MW) from 1996–2013 (modified from the Global Wind Energy Council, http://www.gwec.net/global-figures/graphs/)

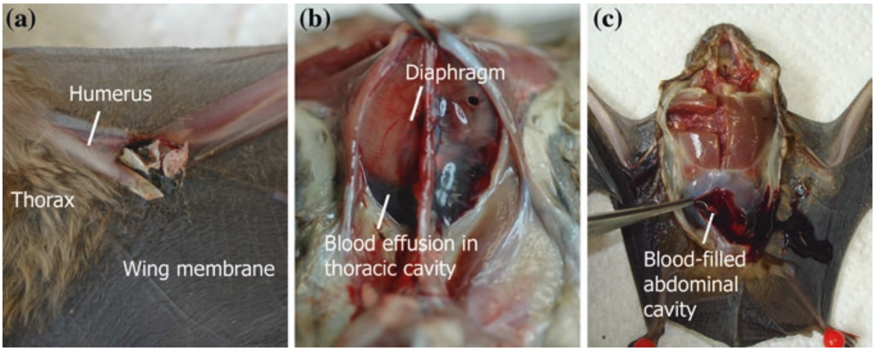

Fig. 11.2 Blunt force trauma (**a**) and barotrauma (**b**, **c**) in three noctule bats (*Nyctalus noctula*) killed at wind turbine in Germany. **a** Ventral view of an open fracture of the left humerus at the height of the elbow joint. **b** Ventral view of the opened abdominal cavity with blood effusion in the thoracic cavity visible behind the diaphragm (hemothorax). **c** Ventral view of opened carcass without bone fractures, but severe bleeding in the abdominal cavity (hemoabdomen) (picture courtesy: Gudrun Wibbelt, IZW)

limits their ability to recover from declines and maintain sustainable populations (Barclay and Harder 2003). Additionally, other sources of mortality cumulatively threaten many populations. For example, white-nosed syndrome causes devastating declines in bat populations in the USA and Canada (e.g., Frick et al. 2010), and national programs for improving insulation of buildings, particularly in Northern Europe, cause losses of roosting opportunities for bats such as the common pipistrelle (*Pipistrellus pipistrellus*; Voigt et al. 2016). Thus, high wind turbine mortality poses a serious threat to bats unless solutions are developed and implemented (Arnett and Baerwald 2013). In this chapter, we build on previous reviews of existing information (e.g., Arnett et al. 2008; Rydell et al. 2010a; Arnett and Baerwald 2013; EUROBATS 2014), synthesize information on bat fatalities at wind energy facilities worldwide, discuss unifying themes and policy and conservation implications, and offer insights for future directions of research and mitigation of bat fatalities at wind facilities.

11.2 Composition and Estimates of Bat Fatalities

We present information on estimates of bat fatalities as reported in published literature or publically available reports, but caution that studies had varying levels of effort, used different estimators (e.g., Huso 2011; Korner-Nievergelt et al. 2013) and different methods to quantify bias (Arnett et al. 2008; Strickland et al. 2011), thus biasing estimates. Also, most estimators fail to adequately account for unsearched area near turbines (Huso and Dalthorp 2013), which further biases estimates. Some studies report fatalities/turbine and others fatalities/MW of installed capacity. As such, data presented here offer a general and relative sense of fatalities within and among continents and do not represent quantitative comparisons.

11.2.1 North America

From 2000 to 2011 in the USA and Canada, annual bat fatality rates were highest at facilities located in the Northeastern Deciduous Forest (6.1–10.5 bats/MW; Fig. 11.3) and Midwestern Deciduous Forest-Agricultural (4.9–11.0 bats/MW) regions defined by Arnett and Baerwald (2013: 438). Average fatality rate in the

Fig. 11.3 Wind energy facilities on forested ridges in the eastern USA have consistently documented high fatality rates of bats (photograph by E.B. Arnett)

Great Plains region was moderately high (6 bats/MW, 95 % CI: 4.0–8.1 bats/MW), while the Great Basin/Southwest Desert region (1.0–1.8 bats/MW) consistently reports the least variable and lowest fatality rates for bats (Arnett et al. 2008; Arnett and Baerwald 2013; Johnson 2005). Wind energy facilities in this region occur in habitats generally offering few roosting resources, possibly (but untested) poor foraging opportunities, and may not be in migratory pathways, thus rendering these sites less risky to bats (Arnett and Baerwald 2013). However, facilities in other regions report high fatality rates of bats where there are large expanses of prairie and agricultural lands with few roosting resources, foraging opportunities, and likely migratory routes (e.g., Summer view Alberta, Canada, 8–14.6 bats/MW; Baerwald et al. 2008). Thus, current patterns in the Great Basin/Southwest region reported by Arnett and Baerwald (2013) may simply reflect biased reporting and an absence of evidence as opposed to evidence of absence (Huso and Dalthorp 2013).

Twenty-one of the 47 species of bats known to occur in the USA and Canada have been reported killed at wind energy facilities, and fatalities are skewed toward migratory species often referred to as “tree bats” that include hoary bats (*Lasiurus cinereus*; 38 %), eastern red bats (*Lasiurus borealis*; 22 %), and silver-haired bats (*Lasionycteris noctivagans*; 18.4 %) that comprise a total of 78.4 % of the recovered bat turbine fatalities in the USA and Canada (Arnett and Baerwald 2013). However, other species also are affected, sometimes seriously. Fatalities of the cave-living Brazilian free-tailed bats (*Tadarida brasiliensis*) are quite frequent in the southern USA during the maternity period in summer (Miller 2008; Piorkowski and O’Connell 2010). In the USA, two species listed as threatened or endangered under the Endangered Species Act also have been killed by turbines, the Indiana bat (*Myotis sodalis*) and Hawaiian hoary bat (*Lasiurus cinereus semotus*; Arnett and Baerwald 2013).

In the Oaxacan Isthmus region of Mexico, 32 of the 42 species of bats known to occupy this region (García-Grajales and Silva 2012; Briones-Salas et al. 2013) were found killed (Villegas-Patraca et al. 2012). These bats belonged to five different families (Mormoopidae, Molossidae, Vespertilionidae, Phyllostomidae, and Emballonuridae), although 52 % of the fatalities belonged to just two species, Davy’s naked-backed bat (*Pteronotus davyi*; 40.2 %) and the ghost-faced bat (*Mormoops megalophylla*; 11.9 %), both of the family Mormoopidae. These two species are particularly abundant in the area studied and form colonies with thousands of individuals in caves (García-Grajales and Silva 2012). Both are aerial-hawking and relatively fast-flying bats (Bateman and Vaughan 1974; Adams 1989). Also, unlike those species killed most frequently in Holarctic regions of North America, these species do not tend to roost in trees. Ninety-seven percent of bat fatalities found at wind turbines are resident species. This differs considerably from the USA, Canada, and parts of northern Europe, suggesting that wind turbines are equally dangerous to resident cave bats assumed to be non-migratory as to migratory tree-roosting species. The common theme is rather that the most frequently killed species are adapted to flight and echolocation in the open air (e.g., bats that have a relatively high wing loading).

11.2.2 Europe

Rydell et al. (2010a) synthesized data from 41 sites in 5 countries in northwestern Europe and found that the Black Forest region in Germany ($n = 10$) had the highest annual fatality rates, averaging 10.5 bats killed/MW. Some regions in Germany had relatively low estimated annual fatality rates, averaging around 1.1–1.2 bats/MW (Rydell et al. 2010a), yet some of these studies did not control for carcass removal and searcher efficiency. The single comprehensive study that covered most parts of Germany did take the aforementioned field biases into account when estimating annual fatality rates of 10–12 bats per wind turbines, translating to 6–8 bats per MW produced (Korner-Nievergelt et al. 2013). Studies from mostly agricultural areas of Austria ($n = 3$), Switzerland ($n = 3$), and England ($n = 1$) yielded mean annual fatalities rates of 2.5, 5.3, and 0.6 bats killed/MW, respectively (Rydell et al. 2010a). In France, some particularly dangerous sites are located near water along the river Rhone in the east (Dubourg-Savage et al. 2011) and on the Atlantic coast in the west (Rydell et al. 2010a). In Spain, bat fatalities from 56 wind facilities ranged from 0.00 to 0.80 bats/MW per year (Camina 2012), but most studies did not correct for scavenger removal and searcher biases and therefore underestimate fatalities. In Portugal, annual fatality rates at 28 facilities ranged from 0.07 to 11.0/MW (L. Rodrigues, Instituto da Conservação da Natureza e das Florestas, unpublished data). Generally, data from Europe are inconsistently collected, rendering comparisons and generalizations across countries difficult. Nevertheless, it is clear that bats are frequently killed at wind turbines throughout the continent, with some facilities experiencing considerably higher fatality rates relative to others.

Members of EUROBATS recently synthesized data from several countries and reported 6429 documented bat kills of 27 species collected at wind facilities in Europe from 2003 to 2014 (EUROBATS 2014), but some studies used to derive estimates of fatality rates did not incorporate field bias or area corrections. The species of bats found most frequently at wind facilities across northern Europe were the common pipistrelle, common noctule (*Nyctalus noctula*), Nathusius' pipistrelle (*Pipistrellus nathusii*), and Leisler's bat (*Nyctalus leisleri*). In Germany, nearly 70 % of recorded deaths represent the latter three species and the particolored bat (*Vespertilio murinus*), all of which are long-distance migrants (Hutterer et al. 2005). Owing to its central geographical location on the European continent, Germany appears to provide ecological stepping stones for many long-distance bat migrants from northeastern populations (Steffens et al. 2004; Voigt et al. 2012). However, resident species or short-distance migrants, including common pipistrelle and northern bats (*Eptesicus nilssonii*), also are frequently killed in northern Europe (Rydell et al. 2010a). The majority (>90 %) of bats killed at wind turbines in southern Europe belong to the various pipistrelle and noctule species: common pipistrelle, Nathusius' pipistrelle, soprano pipistrelle (*Pipistrellus* *pygmaeus*), Kuhl's pipistrelle (*Pipistrellus kuhlii*), and Savi's pipistrelles (*Hypsugo savii*) and the common noctule, giant noctule (*Nyctalus lasiopterus*) and Leisler's bat (*Nyctalus leisleri*). Some of these are long-distance migrants (e.g., Nathusius' pipistrelle and common noctule) that often roost in tree holes, while others are resident and usually house-living species that do not migrate long distances (e.g., Kuhl's pipistrelle and Savi's pipistrelle). Rare species, such as the barbastelle (*Barbastella barbastellus*) and the *Myotis* and *Plecotus* spp., also are killed occasionally, but in smaller numbers. Thus, bats killed at wind turbines in southern Europe generally belong to the same genera as those in northern Europe (*Pipistrellus* and *Nyctalus* spp.), but include several non-migratory species such as Kuhl's and Savi's pipistrelles.

11.2.3 Africa

Little work has been done on wind energy facilities in Africa, and prior to 2012, no studies had been published from the continent. During a pilot study at a single turbine located in the Eastern Cape of South Africa, Doty and Martin (2012) found 18 carcasses of 2 species of bats—the Cape serotine (*Neoromicia capensis*) and Egyptian free-tailed bat (*Tadarida aegyptiaca*). No estimates of fatality rates were provided, likely because of small sample size of recovered carcasses and no bat carcasses were used during field bias trials. In the Western Cape of South Africa, Aronson et al. (2013) reported only one carcass of a Cape serotine. These studies confirm at least some species of bats are vulnerable to wind turbine mortality in South Africa, which could have implications for ecosystem function and conservation of bats in this region.

11.2.4 New Zealand and Australia

In Australia, Hall and Richards (1972) were the first to report bat fatalities at a wind facility in the world, and 22 white-striped free-tailed bats (*Tadarida australis*) were found over a 4-year period. Little work had been done in the region since this pioneering discovery, until Hull and Cawthen (2012) surveyed two wind facilities in Tasmania, where they recorded 54 bat fatalities from two species, Gould's wattled bats (*Chalinolobus gouldii*) and an unknown *Vespadelus* sp. More recently, Bennett (2012) found white-striped free-tailed bats at two turbines located in Victoria. While no estimates of fatality rates were provided for these studies, they indicate that some species of bats are at risk of wind turbine mortality in this part of the world.

11.2.5 South America, Central America, and the Caribbean

Few studies have been done in Latin American regions on bat fatalities caused by wind turbines. Puerto Rico hosts 13 species of bats of five families. Five of these 13 species belong to the family Phyllostomidae, which feed on fruits and nectar and forage in the understory and canopy (Gannon et al. 2005). It was originally speculated that these species would be at low risk for mortality caused by wind turbines based on their life histories and foraging patterns. Species in the family Molossidae also occur in Puerto Rico, and conversely, these species have been considered to be at higher risk to turbine collisions because they fly high in open spaces. Species from both families of bats have been detected during preconstruction surveys in areas where wind facilities were proposed. Twenty months of ongoing post-construction surveys in Puerto Rico revealed 30 carcasses from 11 of the 13 species, for a corrected mortality rate of about 10 bats/turbine /year (Rodríguez-Durán, Universidad Interamericana, unpublished data). Aside from the expected mortality of species in the family Molossidae, it was surprising that fruit and nectar feeding species of phyllostomids were followed in number of fatalities given their flight and foraging patterns. One important hazard for bats in this region relates to their use of hot caves as roosts (Rodríguez-Durán 2009; Ladle et al. 2012). Although little studied, these systems may be ubiquitous throughout parts of México, Panamá, Colombia, Venezuela, Brazil, and the Greater Antilles. Phyllostomids and mormoopids (family Mormoopidae) form large aggregations in hot caves and commute to foraging areas flying long distances at high altitude. This reliance on hot caves may place them at risk from wind facilities located near their feeding sites or along their commuting routes.

11.2.6 Asia

On the island of Taiwan off the Chinese mainland, wind facilities have been established along the western coastline, predominantly in former mangrove wetlands. Bat fatalities have been recorded at three of these facilities (C.H. Chou, Endemic Species Research Institute, unpublished data). Carcass searches and acoustic monitoring indicated regular feeding activity of bats near turbines in summer, and 51 dead bats were found. However, the study is ongoing and no field bias correction experiments have been conducted yet, so corrected fatality estimates are not available. The Japanese pipistrelle (*Pipistrellus abramus*), which is a non-migratory open-air foraging bat, was killed most frequently ($n = 39$). Six other species have also been found killed, although in smaller numbers (1–4 individuals for each species), namely Horikawa's brown bat (*Eptesicus serotinus horikawai*), common house bat (*Scotophilus kuhlii*), Chinese noctule (*Nyctalus plancyi velutinus*), Taiwanese golden bat (*Myotis formosus flavus*), a recently described mouse-eared bat (*Myotis secundus*), and Japanese long-fingered bat (*Miniopterus fuliginosus*).

Three other species have been observed foraging around the turbines, but have not yet been found during carcass searches. These species are the yellow-necked sprite (*Arielulus torquatus*), Taiwanese tube-nosed bat (*Murina puta*), and East Asian free-tailed bat (*Tadarida insignis*). Several of these species (e.g., yellow-necked sprite, Taiwanese golden bat, Taiwanese tube-nosed bat, Chinese noctule, Horikawa's brown bat, and *M. secundus*) are all island endemics, some of which occur in sparse and probably small and vulnerable populations. Nevertheless, the pattern conforms to that of most regions around the world, since the mortality predominantly (but not exclusively) affects species that feed in the open air (C.H. Chou, Endemic Species Research Institute unpublished data).

11.2.7 Conclusions

Bats are killed at wind turbines worldwide, and those fatalities are not restricted to migratory species at high latitudes, as previously suggested (e.g., Kunz et al. 2007a; Arnett et al. 2008). Hence, the bias toward tree-roosting migrants observed in North America and to some extent also in northern Europe is not consistent elsewhere. An emerging hypothesis is that bats that regularly move and feed in less cluttered and more open air-space are most vulnerable to collisions with wind turbines, regardless of continent, habitat, migratory patterns, and roost preferences. The species most often killed at wind turbines throughout Europe belong to aerial-hawking and relatively fast-flying, open-air species, and this is consistent with the pattern found in North America and Mexico. However, other species, including gleaning insectivores and even fruit feeders, also are killed occasionally. The vulnerability of tropical bat faunas is a potentially serious problem that must be addressed immediately and preferably before extensive wind facilities are planned and constructed.

While fatalities of endangered species like the Indiana bat are important from a legal perspective, they currently appear to be biologically irrelevant in comparison with those for hoary and eastern red bats, for example. However, fatalities of listed species worldwide may become increasingly important as wind energy development expands.

The paucity of studies in most regions of the world is alarming, particularly in Mexico, Central and South America, the Caribbean, Africa, New Zealand, and Australia. Notably, we could not find information on bat fatalities at wind facilities from mainland Asia, but the data from Taiwan indicate that the bat fauna of eastern Asia may be highly vulnerable at wind turbines. Turbine fatalities may be a serious threat to bats in, for example, China where wind energy development is substantial (Global Wind Energy Council, http://www.gwec.net/global-figures/graphs/#). This situation is further complicated by the fact that in most countries information gathered is sequestered either by wind energy companies or government agencies and not made readily available. The importance of having access to this information cannot be overstated for all regions of the world.

11.3 Patterns of Bat Fatality

11.3.1 Temporal Patterns

In the temperate Northern Hemisphere, most bat fatalities occur during late summer and early autumn. In the USA, fatalities peak in mid-July through early September in most parts of the country (Johnson 2005; Arnett et al. 2008; Baerwald and Barclay 2011; Arnett and Baerwald 2013). Studies from Europe demonstrate a similar pattern (e.g., in Germany, where most (about 90 %) bat fatalities at wind turbines occur between mid-July and the end of September; Brinkmann et al. 2011; Lehnert et al. 2014). Some studies from northern Europe and North America demonstrate smaller peaks of fatalities during spring (Arnett et al. 2008; Rydell et al. 2010a). In Greece and on the Iberian Peninsula of Spain and Portugal, the pattern is similar, with most (>90 %) fatalities in late summer (Georgiakakis et al. 2012; Camina 2012; Amorim et al. 2012), but in some places, particularly at high elevation sites, fatalities occur from May to October and without any obvious concentration in the late summer period (Dubourg-Savage et al. 2011; Camina 2012). Such consistent temporal patterns of fatality are helpful when predicting high-risk periods and applying some mitigation measures such as raising turbine cut-in speed (Arnett et al. 2011, Baerwald et al. 2009). Hull and Cawthen (2012) noted that fatalities predominantly occurred in autumn in Tasmania, where the climate is temperate. However, in the tropical Isthmus of Tehuantepec in Mexico, while 46 % of bat fatalities were found in the summer rainy season, no clear pattern in bat deaths associated with any season emerged.

In summary, while there are clear temporal patterns and a distinct late summer fatality peak in high-latitude temperate regions (north Europe and North America), the pattern becomes less obvious in warmer climates at lower temperate latitudes (south Europe) and temporal patterns may dissipate entirely in tropical regions (e.g., southern Mexico).

11.3.2 Spatial Patterns

Arnett and Baerwald (2013) noted that the spatial context of bat kills, both among turbines within a facility and among different facilities, could be useful for developing mitigation strategies. They hypothesized that if, for example, kills were concentrated at specific turbines, then curtailment, removal, or relocating that turbine may reduce bat deaths. However, if fatalities are broadly distributed, then facility-wide mitigation strategies would be necessary (Arnett et al. 2008). Thus far, studies worldwide have failed to detect specific turbines responsible for most fatalities at any given facility.

Other patterns at scales beyond individual turbines have been reported that may assist with assessing risk. Baerwald and Barclay (2011) found no differences in fatalities on the east vs. west side of a facility in southern Alberta, but the fatality rate was higher at the north end. Baerwald and Barclay (2011) hypothesized that because fall migrations are from north to south, higher fatality rates could be expected at the more northerly turbines first encountered by migrating bats. At a landscape scale, Baerwald and Barclay (2009) found both higher activity and fatality rates of bats at wind facilities near the foothills of the Rocky Mountains as compared to eastward prairie grasslands. They speculated that turbine proximity to stopover and roost sites in foothills habitat significantly increased fatality rates assuming that geographical landmarks are used for navigating migration routes and that bats judge nightly travel distances between suitable diurnal roosting sites.

11.3.3 Habitat Relationships

Relationships between bat fatalities and habitat or topographic characteristics may be useful for developing mitigation strategies (e.g., to avoid placing turbines near places where many bats move or forage, such as near open water sources, wetlands, or known roosts; Arnett et al. 2008; Arnett and Baerwald 2013; Rydell et al. 2010a). Johnson et al. (2004) did not find a significant relationship between the number of bat fatalities and any of the 10 cover types within 100 m of turbines at facilities in Minnesota or any relationship between fatalities and distance to nearest wetland or woodlot. In assessing the type of vegetation present in areas where the fatalities were found in wind facilities in the Isthmus of Tehuantepec, 79.6 % occurred in agricultural areas. In Oklahoma in 2004, Piorkowski and O'Connell (2010) found that turbines in eroded ravine topography accounted for higher fatality rates than those in areas of low topographic relief and reported some evidence that turbines in mixed cedar/pasture habitats killed more bats than those in cropland and prairie habitats. However, these patterns were not repeated in 2005 or for both years of the study when combined, and Piorkowski and O'Connell (2010) speculated that bats may have exhibited different habitat use patterns in different years or they did not measure factors better explaining annual differences they observed. Interestingly, Grodsky (2010) found that bat fatalities were actually lower near the Horicon Marsh in Wisconsin. Hull and Cawthen (2012) found no relationships between bat fatalities and proximity of turbines to the coast or vegetation. Hence, correlating high-risk locations with particular habitat types or topographic patterns has proven difficult and inconsistent.

Analyses of fatalities reported from Spain and Portugal, where most wind facilities are located on top of hills and mountains, suggest that the most significant environmental predictor of fatality rate is proximity to steep slopes with bare rock and no vegetation. Bare rock is warmed by the sun and radiates heat during the night, which likely facilities insect activity over the rocks (Ancilotto et al. 2014), possibly explaining higher fatality at sites near steep, rocky slopes. Alternatively, rocks on tops of hills and mountains might provide suitable roosts.

Piorkowski and O'Connell (2010) documented the first evidence of fatality of Mexican free-tailed bats at a North American wind facility that could be attributed to the site's proximity (~15 km) to a large maternity colony. In Wisconsin, Grodsky (2010) found no relationship between distances of turbines from a large hibernaculum (Neda Mine), but in this case, hibernating bats did not belong to the species most vulnerable to wind turbine mortality (see above). Georgiakakis et al. (2012) reported that the most frequently killed species at wind facilities in Greece exhibited different spatial patterns of fatality, speculating that this resulted from some turbines being located closer to roosts and/or commuting corridors. It may not be enough to consider the proximity of a facility to a maternity or hibernation site, but rather where it is located relative to feeding grounds or movement corridors (Arnett and Baerwald 2013). We are not aware of other studies demonstrating similar relationships or patterns with large maternity or winter roosts.

11.3.4 Climate and Weather Variables

Arnett (2005) was first to employ daily carcass searches and relate them to weather variables, discovering that most bats were killed on low-wind nights when power production appeared insubstantial. Based on this approach, Arnett et al. (2008) estimated that 82–85 % of bat fatalities at two facilities in the eastern USA occurred on nights with median nightly wind speeds of <6 m/s. Since this pivotal discovery, studies worldwide document that most bat fatalities occur during low-wind periods. In the USA, for example, Jain et al. (2011) found that maximum wind speeds when bat collisions likely occurred ranged from 2.4 to 5.3 m/s. Korner-Nievergelt et al. (2013) found that maximum collision rates of bats occurred at wind speeds between 3.5 and 5.7 m/s. Several other studies from Europe demonstrate a similar pattern (e.g., Amorim et al. 2012). Indeed, this consistency suggesting bat fatality is highest during lower wind speeds greatly assists predicting high-risk periods during which to apply operational mitigation.

Fatalities appear to increase as ambient temperature rises, a relationship observed in North America (e.g., Grodsky 2010; Young et al. 2011) and Europe (e.g., in Portugal; Amorim et al. 2012). Amorim et al. (2012) also found that bat fatalities increased with decreasing relative humidity. The effect of high temperature on fatality rate seems to apply both on the broader regional and climatic scales and according to daily changes in the weather (Dubourg-Savage et al. 2011 and unpublished data). Hence, at least in southern Europe, high fatality rates at wind turbines are most likely in warm and dry geographic areas (Mediterranean and low elevation) and also in warm weather (most common in late summer). In the end, this suggests that fatalities may be correlated with periods of high insect activity, which generally is most likely to occur under warm and dry conditions (Heinrich 1993).

Bat fatalities also have been correlated with other climatic factors that could assist with predicting high-risk periods. Baerwald and Barclay (2011) reported that species–specific fatalities were affected by greater moon illumination. They also observed that falling barometric pressure and the number of deaths were correlated and that whereas fatalities of silver-haired bats increased with increased activity of this species, moon illumination, and south-easterly winds, hoary bat mortality increased most significantly with falling barometric pressure. Interestingly, neither hoary bat activity nor fatality was influenced by any measured variables other than falling barometric pressure (Baerwald and Barclay 2011). Again, this could result from decreasing barometric pressure that triggers insect flight activity and therefore may motivate foraging efforts among bats by indicating a potential increase in food availability (Wellington 2011).

11.4 Offshore Wind Facilities

Potential impacts of offshore wind-energy development on bats are poorly understood, although observations in Europe and anecdotal accounts of bats occurring offshore suggest that impacts may occur. Bats are known to regularly migrate across the Baltic and North Seas and visit offshore facilities (Hutterer et al. 2005; Boshamer and Bekker 2008; Ahlén et al. 2009; Poerink et al. 2013; Rydell et al. 2014). Ahlén et al. (2009) recorded 11 species of bats flying and feeding over the sea up to 14 km from the shore. In spring and late summer, migrating bats are found along coastlines of the Baltic Sea and southeastern North Sea in northern Europe, including all offshore islands where observations have been made (Rydell et al. 2014). This suggests bats, including Nathusius' pipistrelles, soprano pipistrelles, and common noctules, migrate on a broad front across the Baltic Sea and along its coasts, using small islands for stopovers. Researchers in North America also have reported activity of bats in both near and offshore habitats, suggesting impacts are highly probable at facilities located in such places. Cryan and Brown (2007) discovered longitudinal movement by hoary bats from inland summer ranges to coastal regions during autumn and winter and suggested that coastal regions with non-freezing temperatures may be important wintering areas for hoary bats. Off the coast of Maryland, Johnson et al. (2011) recorded five species of bats, including eastern red bats, big brown bats (*Eptesicus fuscus*), hoary bats, tri-colored bats (*Perimyotis subflavus*), and silver-haired bats, on a barrier island and concluded these species used this island during migration, which could have implications for wind energy development near and offshore.

It seems likely that near and offshore wind facilities also will kill bats, but it is difficult or impossible to find bat fatalities at sea and no attempts to assess offshore turbine bat fatality have been made to date. Arnett and Baerwald (2013) suggested that impacts of the first several offshore wind-energy facilities proposed and built in North America, including those on inland waters such as the Great Lakes, be evaluated extensively both for fatalities and displacement effects.

They also suggested that a method for predicting fatalities at existing and planned wind facilities offshore will be required to understand impacts and develop mitigation strategies, because finding and retrieving dead birds and bats from water bodies will be a considerable challenge (Arnett et al. 2007; Arnett 2012).

11.5 Estimating Risk

Kunz et al. (2007b) found a positive correlation between post-construction bat activity and fatality from carcass searches conducted simultaneously. However, Kunz et al. (2007b) warned of several limitations of their analysis and noted that it was unclear whether pre-construction call rates could predict risk and level of post-construction fatality rates. When comparing 5 sites with fatality and activity data, and tall turbines (towers 65 m), Baerwald and Barclay (2009) found a significant positive relationship between post-construction activity and fatality at 5 wind facilities in Alberta. Amorim et al. (2012) and Korner-Nievergelt et al. (2013) also found increasing number of bat fatalities with increasing acoustic bat activity at facilities in Portugal and Germany, respectively. These studies correlating post-construction bat activity with fatality suggest that it may be possible to use indices of pre-construction bat activity to predict future fatality and, thus, risk and need for mitigation. However, while numerous studies have documented pre-construction activity of bats with hopes of inferring risk of collision mortality, these studies have yet to link with post-construction fatality data gathered from carcass searches. Hein et al. (2013) were the first to correlate pre-construction acoustic activity with post-construction fatalities from 12 paired study sites in the USA and found that no statistically significant relationship existed between bat fatalities/MW and bat passes/detector night and only a small portion of the variation in fatalities was explained by activity. Thus, Hein et al. (2013) concluded that prediction of risk prior to construction of a wind facility is highly variable and imprecise and acoustic data may not necessarily predict bat fatality in any reliable way. One explanation as to why correlations between pre-construction measurements of bat activity with similar measurements made post-construction or fatality estimates are weak could be that bats are attracted to the turbines once they are built and sites are used differently by at least some species (open-air bats) afterward (Horn et al. 2008; Kunz et al. 2007b; Arnett et al. 2008; Cryan et al. 2014).

Theoretical estimations of exposure risk of bats to collisions with turbines based on models may also improve our understanding of factors influencing fatality and the context of fatalities. Species distribution models developed in Italy suggest that 41 % of the region offers suitable foraging habitat for 2 species of bats vulnerable to wind turbines, Leisler's bat and the common pipistrelle, and these same areas encompass over 50 % of existing or planned wind farms (Roscioni et al. 2013). The authors believe fatality risk for these species is increased by the common proximity to forest edges, but this contradicts other findings from southern Europe, suggesting the opposite relationship (Dubourg-Savage et al. 2011).

Roscioni et al. (2014) further investigated habitat connectivity as a surrogate for assessing risks of wind facilities to bat migration and commuting in Italy. Using species distribution models, they found that most corridors used by bats were concentrated in an area where existing (54 %) and planned (72 %) wind facilities would interfere with important corridors connecting the western and the eastern parts of the region. In Portugal, mortality risk models indicated wind farms located in humid areas with mild temperatures and within 600 m of steep slopes had higher probabilities of mortality (Santos et al. 2013). They also demonstrated that high mortality risk areas overlapped greatly with the potential distribution of Leisler's bat in Portugal, suggesting that populations of this species may be at high risk to turbine fatalities (Santos et al. 2013). They also found that a large extent of the area predicted to be high risk for mortality overlapped with sites highly suitable for wind farm construction.

11.6 Cumulative Impacts

Estimates of fatalities, and thus any estimate of cumulative fatalities, are conditioned by field methodology for each study (e.g., search interval) and how each study did or did not account for sources of field sampling bias when calculating fatality rate estimates. Arnett and Baerwald (2013) synthesized information from 122 post-construction fatality studies (2000–2011) from 73 regional facilities in the USA and Canada and developed a regional weighted mean estimate of cumulative bat fatalities for the USA and Canada. Assuming fatality rates were (1) representative of all regional sites and (2) consistent from year to year without behavioral modification or mitigation, Arnett and Baerwald (2013) estimated cumulative bat fatalities in the USA and Canada ranged from 0.8 to 1.7 million over a 12-year period from 2000 to 2011. This estimate was projected to increase by 0.2–0.4 million bats in 2012 based on the assumptions and installed wind power capacity. Smallwood (2013) estimated 888,000 bats killed/year at wind facilities in the USA, while Hayes (2013) concluded that over 600,000 bats may have been killed by wind turbines in 2012 alone. However, neither of these estimates used all data available at the time they were published, nor did they weight their estimates by regionally collected data and installed wind energy capacity as Arnett and Baerwald (2013) did; the latter approach likely provides a more conservative and accurate estimate based on the studies and installed capacity from each region.

When controlling for field biases, an estimated 10–12 bats are killed annually at each wind turbine in Germany, if no mitigation measures have been implemented (Brinkmann et al. 2011). Assuming these numbers are representative of all types of wind turbines for all of Germany, it has been suggested that more than 200,000 bats were killed at onshore wind turbines in Germany, assuming no behavioral modification or mitigation measures were practiced (Voigt et al. 2015a). Over the past ten years of wind energy development, it is estimated that more than two million bats may have been killed by wind turbines in Germany, based on the reported large-scale development of wind turbines in that country (Berkhout et al. 2013; Voigt et al. 2015a).

Importantly, the context of wind turbine fatalities remains poorly understood, in part because little population data exist for most species of bats (O'Shea et al. 2003) and this hinders understanding population-level impacts, as well as effectiveness of mitigation measures. Population estimates for most species of bats around the world are lacking, and some bat populations are suspected or known to be in decline (e.g., Frick et al. 2010; Hutson et al. 2001; Ingersoll et al. 2013). Other populations, such as hibernating species in Europe, appear to be increasing (9 of 16 species examined by Van der Meij et al. (2014) increased at their hibernation sites from 1993 to 2011), but these species are not largely affected by wind turbines. In addition to natural and other forms of anthropogenic-induced mortality, wind turbine mortality further compounds population declines for many species of bats and warrants mitigation.

11.7 Mitigating Bat Mortality

As reported previously, most bat fatalities occur during relatively low-wind conditions over a relatively short period of time in late summer (Arnett et al. 2008) and operational adjustments under these conditions and during this time could reduce impacts on bats (Arnett 2005; Arnett et al. 2008; Kunz et al. 2007a). Behr and von Helversen (2006) were the first to examine operational mitigation in Germany, documenting around 50 % fewer bats killed at turbines having their cut-in speed (wind speed at which turbines begin producing electricity into the power grid) raised above the set manufacture's cut-in speed of 4.0 m/s. In the synthesis of operational mitigation studies in the USA and Canada, Arnett et al. (2013a) reported that most studies documented at least a 50 % reduction in bat fatalities when turbine cut-in speed was increased by 1.5 m/s above the manufacturer's cut-in speed, with up to a 93 % reduction in bat fatalities in one study (Arnett et al. 2011). Baerwald et al. (2009) demonstrated beneficial reductions (~60 %) with a low-speed idling approach. Young et al. (2011) discovered that feathering turbine blades (pitched 90° and parallel to the wind) at or below the manufacturer's cut-in speed resulted in up to 72 % fewer bats killed when turbines produced no electricity into the power grid. Arnett et al. (2013a) noted that studies failing to demonstrate statistically significant effects could be explained by lack of treatments being implemented during the study (i.e., winds were either too low or high to enable comparison of treatments). In Portugal, a mitigation study found that estimated mortality at turbine with raised cut-in speed was 0.3 bats/turbine compared to 1.6 bats/turbine at turbines operating normally, which resulted in a 78.5 % reduction in bat fatalities assuming all turbines at the facilities had raised cut-in speed (LEA 2010).

More recently, situation-dependent operation protocols, so-called algorithms, were developed for the operation of wind turbines. These algorithms consider a number of parameters such as ambient temperature, wind speed, season, and time of day as well as recorded bat activities for defining a set of operation rules for wind turbines (Korner-Nievergelt et al. 2013). However, these algorithms have been formulated for a single type of turbine and for a limited number of sites. Thus, the suggested algorithms may be unsuitable for other places with varied geographical and topographic characteristics, bat communities, and turbine types (Voigt et al. 2015a).

Few studies have disclosed actual power loss and economic costs of operational mitigation, but those that have suggest that <1 % of total annual output would be lost if operational mitigation was employed during high-risk periods for bat fatalities. While costs of lost power due to mitigation can be factored into the economics, financing, and power purchase agreements of new projects, altering turbine operations even on a limited-term basis potentially poses difficulties on existing projects. Although curtailment is relatively straightforward to implement on large modern turbines, for older models and for small to medium energy-generating turbines, there often is no way to remotely control or change cut-in speed; some turbines would require a technician to physically change turbine operating systems (which is not feasible). However, raising cut-in speed or altering blade angles to reduce rotor speed (termed “low-speed idling” by Baerwald et al. 2009) where blades are near motionless in low wind speeds remain the only proven solutions to mitigating bat kills at wind facilities. The fact that it may be difficult to apply these mitigation techniques to some old turbines should not compromise its use on contemporary turbines.

Other approaches to mitigating bat fatalities have been suggested, including projecting electromagnetic signals from small, portable radar units (Nicholls and Racey 2009) and ultrasonic broadcasts (Arnett et al. 2013b). However, the former approach has not been tested at large, utility-scale facilities, and none are yet being implemented broadly at wind energy facilities. Future studies of any mitigation approach must demonstrate greater or equal effectiveness to operational adjustments and also be cost-competitive with different operational strategies for mitigation.

11.8 Conservation Policy

In this section, we discuss a few selected issues regarding policy and regulation of wind facilities as they relate to wildlife impacts and successful integration of science, policy, and management to improve siting that minimizes risk to wildlife, including bats. This discussion is by no means exhaustive or comprehensive, but rather offers examples of policy issues from different regions of the world.

In the USA, the federal government’s role in regulating wind power development is limited to projects occurring on federal lands, impacting federal trust species, or projects that have some form of federal involvement (e.g., interconnect with a federal transmission line) or require federal permits. The primary federal regulatory framework for protecting wildlife from impacts from wind power includes three laws—the US Migratory Bird Treaty Act, the Bald and Golden Eagle Protection Act, and the Endangered Species Act (ESA; GAO 2005; NRC 2007). Because wind-energy development has primarily occurred on non-federal land, regulating such facilities is largely the responsibility of state and local governments (GAO 2005). The primary permitting jurisdiction for wind-energy facilities in many instances is a local planning commission, zoning board, city council, or county board of supervisors or commissioners, and typically, these local jurisdictional entities regulate wind projects under zoning ordinances and building codes (GAO 2005), often without the basic knowledge needed to make informed decisions. Additionally, each state may enforce its laws regarding wind energy and wildlife impacts or establish cooperative efforts to address impacts. The US Fish and Wildlife Service has voluntary guidelines designed to help wind energy project developers avoid and minimize impacts of land-based wind projects on wildlife and their habitats (U.S. Fish and Wildlife Service 2012). In the USA, most species of bats, including migratory tree-roosting species killed most frequently by turbines, are not protected under federal, state, or provincial laws (Arnett 2012; Cryan 2011). Documented presence or fatality of species listed as threatened or endangered under the ESA (e.g., Indiana bat) does not necessarily mandate monitoring or mitigation as one might expect; rather, all efforts are voluntary even in cases involving a listed species, although threat of prosecution under the ESA increases when operators fail to collaborate or develop a conservation and mitigation plan.

Until recently, an Environmental Impact Assessment (EIA) in Canada was required under the Canadian Environmental Assessment Act (CEAA) when a Federal Authority initiated a wind project, granted any form of financial assistance or land for the project, and/or performed a regulatory duty in relation to the project, such as issuing a permit or license. Given that the Canadian Federal Government provided financial incentives for wind energy from 2002 to 2011, EIAs of wind energy projects were generally mandatory. However, wind energy projects no longer require federal environmental assessments (Canadian Environmental Assessment Act 2012), but projects may still require an environmental assessment if requested by the province or territory. Bats fall under the jurisdiction of the individual provinces (ten) and territories (three). As such, there are no Canada-wide bat and wind-energy policies or regulations; each province or territory sets their own policy and/or regulation regarding bats and wind energy projects (e.g., Ontario Ministry of Natural Resources 2011; Government of Alberta 2013). The Ontario Ministry of Natural Resources set a mortality threshold of 10 bats/turbine/year, which if exceeded triggers operational mitigation across the wind facility from 15 July to 30 September for the duration of the project (Ontario Ministry of Natural Resources 2011). This mortality threshold was based on fatality rates of bats at wind energy projects in Ontario and across North America. Ontario's guidelines do not explicitly consider cumulative effects (i.e., operational mitigation is only triggered by project-specific fatality rates). In Alberta, the integration of data, including acoustic data, collected during both the pre- and post-construction monitoring, helps guide the mitigation framework (Government of

Alberta 2013). For example, if less than five migratory-bat passes/detector night are recorded during pre-construction acoustic monitoring, then the project is considered to be a potentially acceptable risk, but if greater than ten migratory-bat passes/detector night were recorded, the project is considered to have a potentially high risk of bat fatalities and will likely require operational mitigation (Government of Alberta 2013). Unlike Ontario's guidelines, Alberta's mitigation framework explicitly considers cumulative effects (i.e., the proximity and risk at wind energy projects in the area are considered when determining the need for operational mitigation). Given the wide-ranging movement patterns of migratory tree bats and the tendency for wind energy projects to be clustered, from a conservation perspective, a policy which considers cumulative effects is superior to one that does not (Arnett et al 2013c).

Development of wind facilities in Mexico is regulated by laws and norms that have been enacted to achieve sustainable development. The General Law of Ecological Balance and Environmental Protection (GLEBEP) and its regulations are the main legal instruments the Mexican government has to protect ecosystems (www.semarnat.gob.mx). According to the GLEBEP, for a wind facility to be built, it is necessary to develop an EIA to determine the environmental feasibility of the project. The environmental authority has developed methodological guidelines for productive sectors to perform studies that meet the minimum information necessary for evaluation. In this case, the wind facilities are included in the energy sector, which includes, among others, hydroelectric, thermal, combined cycle plants, transmission lines, dams, and electrical substations. The first wind facility EIA (2000–2004) was completed with evaluations similar to those used for any other infrastructure (e.g., hydroelectric, thermoelectric, etc.) and was therefore not focused on impacts associated with wind facilities; collisions of birds and bats are not considered in the EIA. Thus, mitigation to reduce these impacts was not required by any regulatory authority at the first wind facilities in Mexico. Recently, the Mexican government has begun considering negative impacts on birds and bats and has incorporated measures including an annual monitoring program in these taxa during the entire cycle of wind energy projects. While there is no regulatory framework specifically for protection or conservation of bats in Mexico, there is an official standard that includes listings of flora and fauna found in risk categories similar to the Red List of the International Union for Conservation of Nature. The NOM-059-SEMARNAT-2010 (SEMARNAT 2010) includes the three categories of risk in order from most to least critical: in danger of extinction, threatened, and under special protection. The inclusion of species in each of these three categories is in accordance with technical and scientific criteria (SEMARNAT 2010). The NOM-059-SEMARNAT-2010 includes 38 species of bats, 19 of which warranted special protection. To date, however, only four species included in the NOM-059 have been found killed at wind facilities, and none of the species killed most frequently by turbines in Mexico are included in the NOM-59 given their abundance and wide distribution (Ceballos and Arroyo-Cabrales 2012; Ceballos et al. 2005). Apart from these legal instruments, there are no other legal mechanisms in Mexico to protect Mexican bats per se.

In the European Union, all species of bats, regardless of numbers, are strictly protected by law and it is illegal to deliberately kill or harm bats irrespective of any population effects. “Deliberately” means in this case that the actor is aware that activity may have an effect but still carries out the activity. The EIA Directive 85/337/EEC (amended to Council Directive 97/11/EC in 2011) legally requires an assessment to be carried out for all wind facilities with 5 or more turbines, or which are over 5 MW capacity. In addition, member states must restore or maintain their bat populations in favorable conservation status (Council Directive 92/43/EEC). All members of the EU have translated these directives into their domestic legislation which in theory should provide high levels of protection and a consistent way of handling the issue, based on the EUROBATS guidelines (Rodrigues et al. 2015). However, while bat issues are taken very seriously in some countries, this is not true in others. In the UK and Republic of Ireland, it is an offense to deliberately or recklessly kill or injure a bat or to deliberately disturb bats in a way that would significantly affect their local distribution or abundance, and detailed guidance is in place about the requirements for EIA.

The EUROBATS guidance (Rodrigues et al. 2015) proposes that turbines should not be placed closer than 200 m to woodland, whereas the current recommendations for the UK are that the blade tips should be at least 50 m from woodland or hedgerows. It is argued that a smaller buffer size is acceptable because the activity of bats found in the UK tends to decline rapidly with increasing distance from linear landscape features and woodlands (Natural England 2014). It is officially acknowledged that risk assessments for bats in the UK and Republic of Ireland are hampered by a lack of evidence in crucial areas (Bat Conservation Ireland 2012; Natural England 2014). Not only are collision rates unknown, but population estimates, and therefore inferences about the impact of turbine collisions on population viability, are uncertain. Standardized post-construction monitoring, including acoustic and carcass surveys, is recommended for sites identified as “high risk” (Bat Conservation Ireland 2012; Natural England 2014).

In reality, little post-construction monitoring occurs. This is at least partly because responsibility for requiring and enforcing survey conditions lies with local planning authorities, which are reluctant to impose conditions which may be open to legal challenge. A particular difficulty is that while generic guidance on survey designs is available, there is no standardized methodology and so it is extremely difficult to judge whether a particular level of bat activity would place a site as being in a “high risk” category: This point has already been raised at a legal review. Further, there has been no assessment of the relationship between pre-construction and post-construction acoustic surveys (or collision risk). It is therefore unclear how data collected pre-construction can be used to predict post-construction risk, particularly given evidence from the USA demonstrating a poor relationship between pre-construction activity surveys and bat fatalities (Hein et al. 2013). A final difficulty for Local Authorities is that the legal basis of bat protection relates to the conservation status of local populations (except in Scotland, where recklessly killing a bat is also an offense). Given that local population sizes are very poorly characterized, it is unclear how mitigation (such as raising turbine cut-in speed) could be enforced on the basis of reduced bat activity or bat fatalities.

In Sweden, there were no national guidelines until 2011 (Rydell et al. 2012), and more than ten years after the first turbines were built. Hence, many wind turbines in Sweden were constructed in poor locations with respect to bats, such as along the coast, and with operation permitted without any mitigation measures. After 2011, however, the Swedish Environmental Protection Agency concentrated resources to achieve national acceptance for the guidelines among decision makers, the industry and NGOs, and to implement them on all new project. In 2014, all proposed wind facilities are subject to a pre-construction survey and an evaluation regarding the risk to bats. In the Netherlands, all bats are species of annex II and/or IV of the European Habitats Directive EIA, and risk assessment and evaluation under Flora and Fauna law (research on what species are present) and possibly Nature Conservation law (when EHD annex II species are present) are obligatory. When risk species are present and fatalities cannot be excluded, a permit for construction is needed under FF law and NC law, and information on fatalities needs to be established using protocols and a curtailment may be required (Boonman et al. 2013; Limpens 2013).

Mitigation studies have shown that bat fatalities can be reduced substantially (e.g., Baerwald et al. 2009; Arnett et al. 2011). Although curtailing turbines holds great promise, the problem is that developing thresholds—those values that trigger some action—to mitigate bat kills is difficult, especially when supporting data are limited or imperfect (Arnett et al. 2013c). In Germany, recent models accounting for multiple environmental variables that predict and reduce collision rate and further minimize loss of energy production offer promise for mitigating bat fatalities (Korner-Nievergelt et al. 2013). However, these algorithms and most other operation protocols still tolerate an arbitrary number of bat fatalities (currently two bat fatalities per wind turbine per year where these algorithms are used in Germany) (Voigt et al. 2015a); any such fatality trigger in Europe is seemingly in opposition to current law, given that European legislation does not allow deliberate killing of any bat, regardless of population effects. Additionally, with increasing numbers of wind turbines, fixed annual “per capita” (i.e., per wind turbine) mortality rates may not be acceptable in light of limited bat population sizes, and the acceptance of a reduced fatality rate may not necessarily be consistent with national and EU legislation (Voigt et al 2015a). Regulatory authorities in the US state of Pennsylvania and the Canadian province of Ontario set thresholds for initiating curtailment based on the annual mean number of bats killed per turbine (28 and 10 bat fatalities/turbine, respectively Arnett et al. 2013c). Arnett et al. (2013c) argued that this approach sets a dangerous precedent and has several flaws, none the least of which is the assumption that bat populations are currently stable and remain so. This approach also ignores expanding development of wind turbines that will likely yield increasing bat fatalities per population or region. Policy and management efforts to mitigate bat fatalities and conserve bat populations affected by wind turbines should be proactive and based on science rather than being reactive and arbitrary.

11.9 Future Directions

Population data are generally lacking, and this not only impedes our understanding of actual impacts of wind turbines, but also impedes knowing the effectiveness of mitigation efforts. For example, we do not know whether raising turbine cut-in speed that might result in 50 % fewer bat fatalities will mitigate population-level impacts or simply delay inevitable losses (Arnett and Baerwald 2013). The lack of population data also makes it difficult to set triggers for mitigation (i.e., number of bats killed per turbine or MW that requires mitigation; but see Arnett et al. 2013c). However, population data are not likely to be available for most bat species in the near future, and thus, wind operators should practice the precautionary principle and implement operational mitigation at sites where bat fatalities are high, or are predicted to be high, even in the absence of population data.

Several knowledge gaps remain that must be filled in the immediate future. Most notably, many regions of the world lack any publicly available monitoring information on the impacts of wind energy facilities on bats and other wildlife (e.g., China). We strongly encourage wind energy developers and governments to end this trend and gather needed data to inform siting and operating wind facilities around the world. In addition to population studies and basic monitoring data described above, some key research priorities germane to all regions of the world include:

1. Evaluating effectiveness of pre-construction bat activity surveys in predicting future fatalities at wind facilities.
2. Determining whether approaches such as temperature profiles in relation to weather types and seasons (and different regions) or habitat suitability modeling for bats can effectively predict high-risk sites and be used by planning authorities and industry to help situate wind turbines in areas where the potential for conflict with bats is minimized.
3. Evaluate methods for assessing the risk and minimizing and mitigating impacts posed by offshore wind turbines to bats (including approaches such as radar and collision sensors).
4. Investigate the extent of migratory activity worldwide, particularly offshore, by international collaboration using a range of techniques [stable isotopes (Voigt et al. 2012; Lehnert et al. 2014; Baerwald et al. 2014), population genetics, potentially GPS tracking, etc.]. Although difficult, it may be possible to gather and pool acoustic data of activity patterns established through automated real-time recorders in numerous wind energy facilities to evaluate spatial and temporal patterns.
5. Future operational mitigation experiments should be designed to determine which factors (e.g., habitat, insect occurrence, temperature, wind, humidity, moon illumination) or combination of factors (Weller and Baldwin 2012) will best improve predictability of bat fatalities, while minimizing economic costs. Alternative mitigation approaches to operational adjustments should be proven equally or more effective at reducing bat fatalities at operating wind facilities before being accepted as viable mitigation approaches.

6. Detailed meta-analyses of existing data on cumulative fatality impacts and factors influencing fatalities are needed. It should be noted that data disclosure from many sites by some companies hinders such analyses.

We strongly encourage developers to follow guidelines (e.g., Kunz et al. 2007b; Rodrigues et al. 2015; Strickland et al. 2011; Bat Conservation Ireland 2012) consistently when implementing pre- and post-construction monitoring. Data should be placed into the public domain or preferably published in refereed journals. There are a number of policies, regulatory, and communication challenges we face in protecting bats while developing wind energy responsibly across the globe (Arnett 2012). Unless there is a federal, state, or provincial nexus, most research, siting, and mitigation efforts by wind energy developers and operating companies will be voluntary, likely without regard for cumulative effects. Sites that do trigger a regulatory nexus will usually be driven by endangered species issues (e.g., Indiana bats in the USA). It is apparent most local jurisdictional entities, regardless of country, lack experience in wildlife science, and unless they coordinate with their wildlife or natural resource agency specialists, concerns about bat fatalities may never be addressed in decision making for wind energy development. Another key issue is consistent application of regulations. The authors have encountered many situations where different individuals had varied interpretations of the same law or guidance policy, and this creates untenable situations, considerable uncertainty, consternation, and lack of trust among stakeholders that seems completely unnecessary and easily remedied (Arnett 2012).

We encourage continuing cooperation among all stakeholders, gathering needed information, avoiding construction in high-risk sites, considering cumulative effects, and implementing mitigation where needed even when no regulatory process is triggered (Arnett 2012; Arnett and Baerwald 2013). Wind energy developers should, however, be treated fairly and consistently to ensure proactive measures are implemented. Arnett (2012) noted that when some companies choose to cooperate, while others may not, unnecessary angst is generated and deters resolving wildlife impacts and other issues. Decision making must be based on the best available science. Also, consistent policy, accountability, effective siting and mitigation strategies, and a "level-playing field" for the industry (i.e., consistent requirements and incentives for all companies) are fundamental if we are to successfully develop wind energy that protects bats and other wildlife.

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References

Adams JK (1989) Pteronotus davyii. Mamm Species 346:1–5

Ahlén I, Baagøe HJ, Bach L (2009) Behavior of Scandinavian bats and foraging at sea. J Mammal 90:1318–1323

Amorim F, Rebelo H, Rodrigues L (2012) Factors and mortality at a wind farm in the Mediterranean region. Acta Chirop 14:439–457

Ancilotto L, Rydell J, Nardone V, Russo D (2014) Coastal cliffs on islands as foraging habitat for bats. Acta Chirop 16:103–108

Arnett EB (2005) Relationships between bats in Pennsylvania and West Virginia: an assessment of bat fatality search protocols, patterns of fatality, and behavioral interactions with wind turbines. Bat conservation international, Austin, Texas, USA http://www.batsandwind.org/pdf/postconpatbatfatal.pdf. Accessed 22 Dec 2014

Arnett EB (2012) Impacts of wind energy development on wildlife: challenges and opportunities for integrating science, management. In: Sands JP, DeMaso SJ, Brennan LA, Schnupp MJ (eds) Wildlife science: with management. Taylor and Francis, New York, pp 213–237

Arnett EB, Baerwald EF (2013) Impacts of wind energy development on bats: implications for conservation. In: Adams RA, Peterson SC (eds) Bat evolution, ecology, and conservation. Springer, New York, pp 435–456

Arnett EB, Inkley DB, Larkin RP, Manes S, Manville AM, Mason JR, Morrison ML, Strickland MD, Thresher R (2007) Impacts of wind energy facilities on wildlife and wildlife habitat. Wildl Soc Tech Rev 07-2 (The Wildlife Society, Bethesda, Maryland)

Arnett EB, Brown K, Erickson WP, Fiedler J, Henry TH, Johnson GD, Kerns J, Kolford RR, Nicholson CP, O'Connell T, Piorkowski M, Tankersley R Jr (2008) Patterns of fatality of bats at wind energy facilities in North America. J Wildl Manage 72:61–78

Arnett EB, Huso MMP, Schirmacher MR, Hayes JP (2011) Changing wind turbine reduces at wind facilities. Front Ecol Environ 9:209–214. doi:10.1890/100103

Arnett EB, Johnson GD, Erickson WP, Hein CD (2013a) A synthesis of studies to reduce at wind energy facilities in North America. Bat conservation international, Austin, Texas http://www.batsandwind.org/pdf/Operational%20Mitigation%20Synthesis%20FINAL%20REPORT%20UPDATED.pdf. Accessed 22 Dec 2014

Arnett EB, Hein CD, Schirmacher MR, Huso MMP, Szewczak JM (2013b) Evaluating the effectiveness of an ultrasonic acoustic deterrent for reducing. PLoS ONE 8(6):e65794. doi:10.1371/journal.pone.0065794

Arnett EB, Barclay RMR, Hein CD (2013c) Thresholds for bats killed. Front Ecol Environ 11:171. doi:10.1890/1540-9295-11.4.171

AronsonJB, Thomas AJ, Jordaan SL (2013) Bat fatality at a wind energy facility in the western Cape. Afr Bat Conserv News 31:9–12 (ISSN 1812-1268)

Baerwald EF, Barclay RMR (2009) Geographic variation in activity and fatality bats at wind energy facilities. J Mammal 90:1341–1349

Baerwald EF, Barclay RMR (2011) Patterns of activity and fatality bats at a wind energy facility in Alberta. J Wildl Manage 75:1103–1114

Baerwald EF, D'Amours GH, Klug BJ, Barclay RM (2008) Barotrauma is a significant cause of bat fatalities at wind turbines. Curr Biol 18(16):R695–R696

Baerwald EF, Edworthy J, Holder M, Barclay RMR (2009) A large-scale mitigtion experiment to reduce at wind energy facilities. J Wildl Manage 73:1077–1081

Baerwald EF, Patterson WP, Barclay RMR (2014) Origins patterns of bats killed in southern Alberta: evidence from stable isotopes. Ecosphere 5(article 118):1–17

Barclay RMR, Harder LM (2003) Life histories of bats: life in the slow lane. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 209–259

Bat Conservation Ireland (2012) Wind turbine/wind development bat survey guidelines—version 2.8. Bat conservation Ireland http://www.batconservationireland.org/pubs/reports/BCIreland%20Wind%20Farm%20Turbine%20Survey%20Guidelines%20Version%202%208.pdf. Accessed 20 January 2015

Bateman GC, Vaughan TA (1974) Nightly activities of mormoopid bats. J Mammal 55:45–65

Behr O, von helversen O (2006) Gutachten zur Beein -trächtigung im freien Luftraum jagender und ziehender Fle -dermäuse durch bestehende Windkraftanlagen. Wirkungs -kontrolle zum Windpark “Rosskopf” (Freiburg i Br.) im Jahr 2005. Report to Regiowind GmbH & Co., Freiburg

Bennett E (2012) Hepburn wind farm bird and bat mortality survey interim report 11th July 2011–9th Jan 2012. Elmoby ecology http://hepburnwind.com.au/downloads/Hepburn%20Wind%20interim%20report%20Bird%20&%20Bat%20Monitoring.pdf. Accessed 25 Aug 2014

Berkhout V, Faulstich S, Görg P, Kühn P, Linke K, et al. (2013) Wind energy 2012. Fraunhofer-Institut für Windenergie und Energiesystemtechnik. IWES, Kassel

Bernstein MA, Griffin J, Lempert R (2006) Impacts on energy expenditures of use. Technical report prepared for the energy future coalition, RAND Corporation, Santa Monica, CL

Boonman M, Limpens HJGA, La Haye MJJ, van der Valk M, Hartman JC (2013) Protocollen leermuisonderzoek bij windturbines. Rapport 2013.28, Zoogdiervereniging & Bureau Waardenburg. 29 pp+ 1 bijlage

Boshamer JPC, Bekker JP (2008) Nathusius’ pipistrelles (*Pipistrellus nathusii*) and other species of bats platforms in the Dutch sector of the North Sea. Lutra 51:17–36

Brinkmann R, Behr O, Niermann I, Reich M (2011) Entwicklung von Methoden zur Untersuchung und Reduktion des Kollisionsrisikos von Fledermausen an onshore-Windenergieanlagen. Schriftenreihe Institut fur Umweltplanung. Cuvillier Verlag Gottingen, p 457

Briones-Salas M, Peralta-Pérez My, García-Luis M (2013) Acoustic characterization of new species of bats for the state of Oaxaca. Theyra 4:15–32

Camina A (2012) At wind farms in—lessons to be learned. Acta Chirop 14:205–212

Canadian Environmental Assessment Act (2012) An ACT respecting the environmental assessment of certain activities and the prevention of significant adverse environmental effects. Assented to 29 June 2012, in force 06 July 2012. (Online). Government : Justice Laws http://laws-lois.justice.gc.ca/eng/acts/C-15.21/page-1.html. Accessed 6 Jan 2015

Ceballos G, Arroyo-Cabrales J (2012) Lista actualizada de los mamíferos de México 2012. Rev Mex Mastozoología 1:27–80

Ceballos G, Oliva G, coords. (2005) Los mamíferos silvestres de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Fondo de Cultura Económica, México, DF

Cryan PM (2008) Mating behavior as a possible cause of bat fatalities at wind turbines. J Wildl Manage 72:845–849

Cryan PM (2011) Wind turbines as landscape impediments to connectivity of bats. Environ Law 41:355–370

Cryan PM, Barclay RMR (2009) Causes of bat fatalities at wind turbines: hypotheses and predictions. J Mammal 90:1330–1340

Cryan PM, Brown AC (2007) Migration of bats past a remote island offers clues towards the problem of bat fatalities at wind turbines. Biol Conserv 139(1–2):1–11

Doty AC, Martin AP (2012) Assessment of bat and avian mortality at a pilot wind turbine at Coega, Port Elizabeth, Eastern Cape, South Africa. New Zeal J Zool. doi:10.1080/03014223.2012.741068

Dubourg-Savage M-J, Rodrigues L, Santos H, Georgiakakis P, Papadotou E, Bach L, Rydell J (2011) Patterns of comparing north and south. Poster and abstract. In: Conference on wind energy and environmental impacts, Trondheim, Norway, May 2011

EUROBATS (2014) Report of the intersessional working group on wind turbines and bat populations. http://www.eurobats.org/sites/default/files/documents/pdf/Advisory_Committee/Doc.AC_.20.5.ReportIWGWindTurbines_0.pdf. Accessed 1 Aug 2015

Frick WF, Pollock JF, Hicks AC, Langwig KE, Reynolds DS, Turner GG, Butchkoski CM, Kunz TH (2010) An emerging disease causes regional population collapse of a common North American bat species. Science 329:679–682

Gannon MR, Kurta A, Rodríguez-Durán A, Willig MR (2005) Bats of Puerto Rico: an island focus and a Caribbean perspective. Texas Tech University Press, Lubbock

García-Grajales J, Silva AB (2012) Revisión al conocimiento de los murciélagos del estado de Oaxaca. Therya 3:277–293

Georgiakakis P, Kret E, Cárcamo B, Doutau B, Kafkaletou-Diez A, Vasilakis D, Papadatou E (2012) Bat fatalities at wind farms in north-eastern Greece. Acta Chirop 14:459–468

Cryan PM, Gorresen, PM, Hein CD, Schirmacher MR, Diehl RH, Huso MM, Hayman DTS, Fricker PD, Bonaccorso FJ, Johnson DH, Heist K, Dalton DC (2014) Behavior of bats at wind turbines. Proc Nat Acad Sci. doi:10.1073/pnas.1406672111

Government Accountability Office (GAO) (2005) Wind Power: impacts on wildlife and government responsibilities for regulating development and protecting wildlife. Report to Congressional Requesters, GAO-05-906, U.S. Government Accountability Office, Washington

Government of Alberta (2013) Bat mitigation framework for wind power development. In: Environment and sustainable resource development. Alberta, Canada

Grodsky SM (2010) Aspects of bird and bat mortality at a wind energy facility in southeastern Wisconsin: impacts, relationships, and cause of death. Thesis, University of Wisconsin, Madison

Grodsky SM, Behr MJ, Gendler A, Drake D, Dieterle BD, Rudd RJ, Walrath NL (2011) Investigating the causes of death for wind turbine-associated bat fatalities. J Mammal 92:917–925

Hall LS, Richards GC (1972) Notes on *Tadarida australis* (Chiroptera:Molossidae). Aust Mammal 1:46–47

Hayes MA (2013) Bats killed in large numbers at United States wind energy facilities. Bioscience 63:975–979

Hein CD, Gruver J, Arnett EB (2013) Relating pre-construction bat activity and post-construction bat fatality to predict risk at wind energy facilities: a synthesis. Bat conservation international, Austin, Texas http://www.batsandwind.org/pdf/Pre-%20Post-construction%20Synthesis_FINAL%20REPORT.pdf. Accessed 23 Dec 2014

Heinrich B (1993) The hot-blooded insects. Springer, Berlin

Horn J, Arnett EB, Kunz TH (2008) Behavioral responses of bats to operating wind turbines. J Wildl Manage 72:123–132

Hull CL, Cawthen L (2012) Bat fatalities at two wind farms in Tasmania, Australia: bat characteristics, and spatial and temporal patterns. New Zeal J Zool. doi:10.1080/03014223.2012.731006

Huso MMP (2011) An estimator of wildlife fatality from observed carcasses. Environmetrics 22:318–329. doi:10.1002/env.1052

Huso MMP, Dalthorp D (2013) Accounting for unsearched areas in estimating wind turbine-caused fatality. J Wildl Manage. doi:10.1002/jwmg.663

Hutson AM, Mickleburgh SP, Racey PA (2001) Global status and conservation action plan: microchiropteran bats. IUCN/SSC Chiroptera Specialist Group, Cambridge

Hutterer R, Ivanova T, Meyer-Cords C, Rodrigues L (2005) Bat migrations in Europe: a review of banding data and literature. Naturschutz und Biologische Vielfalt, Bonn 28:1–176

Ingersoll TE, Sewall BJ, Amelon SK (2013) Improved analysis of long-term monitoring data demonstrates marked regional declines of bat populations in the Eastern United States. PLoS ONE 8(6):e65907. doi:10.1371/journal.pone.0065907

Inkley DB, Anderson MG, Blaustein AR, Burkett VR, Felzer B, Griffith B, Price J, Root TL (2004) Global climate change and wildlife in North America. Wildl Soc Tech Rev 04-1 (The Wildlife Society, Bethesda, Maryland)

Jain AA, Koford RR, Hancock AW, Zenner GG (2011) Bat mortality and activity at a northern Iowa wind resource area. Am Mid Nat 165:185–200

Johnson GD (2005) A review of bat mortality at wind-energy developments in the United States. Bat Res News 46:45–49

Johnson GD, Perlik MK, Erickson WP, Strickland MD (2004) Bat activity, composition, and collision mortality at a large wind plant in Minnesota. Wildl Soc Bull 32:1278–1288

Johnson JB, Gates JE, Zegre NP (2011) Monitoring seasonal bat activi ty on a coastal barrier island in Maryland, USA. Environ Monit Assess 173:685–699

Korner-Nievergelt F, Brinkmann R, Niermann I, Behr O (2013) Estimating bat and bird mortality occurring at wind energy turbines from covariates and carcass searches using mixture models. PLoS ONE 8(7):e67997. doi:10.1371/journal.pone.0067997

Kunz TH, Arnett EB, Erickson WP, Hoar AR, Johnson GD, Larkin RP, Strickland MD, Thresher RW, Tuttle MD (2007a) Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Front Ecol Environ 5:315–324

Kunz TH, Arnett EB, Cooper BM, Erickson WP, Larkin RP, Mabee T, Morrison ML, Strickland MD, Szewczak JM (2007b) Methods and metrics for studying impacts of wind energy development on nocturnal birds and bats. J Wildl Manage 71:2449–2486

Ladle RJ, Firmino JVL, Malhado ACM, Rodríguez-Durán A (2012) Unexplored diversity and conservation potential of Neotropical hot caves. Conserv Biol 26:978–982

LEA (2010) Monitorização dos efeitos da Medida de Minimização de Mortalidade do Parque Eólico do Outeiro Relatório final. Laboratório de Ecologia Aplicada da Universidade de Trás-os-Montes e Alto Douro. Vila Real, 78 pp

Lehnert LS, Kramer-Schadt S, Schonborn S, Lindecke O, Niermann I, Voigt CC (2014) Wind farm facilities in Germany kill noctule bats from near and far. PLoS ONE 9(8):e103106. doi:10.1371/journal.pone.0103106

Limpens HJGA, Boonman M, Korner-Nievergelt F, Jansen EA, van der Valk M, La Haye MJJ, Dirksen S, Vreugdenhil SJ (2013) Wind turbines and bats in the Netherlands—measuring and predicting. Report 2013.12, Zoogdiervereniging & Bureau Waardenburg. 77 pp+ 2 appendices

McLeish T (2002) Wind power. Nat N Eng 11:60–65

Miller A (2008) Patterns of avian and bat mortality at a utility-scalewind farm on the southern high plains. Thesis, Texas Tech University, Lubbock

National Research Council [NRC] (2007) Ecological impacts of wind-energy projects. National Academies Press, Washington

Natural England (2014) Natural England technical information note TIN051. Bats and onshore wind turbines, 3rd edn, March 2014 http://publications.naturalengland.org.uk/search?q=Bats+and+onshore+wind+turbines&num=100. Accessed 4 Jan 2015

Nicholls B, Racey PA (2009) The aversive effect of electromagnetic radiation on foraging bats—a possible means of discouraging bats from approaching wind turbines. PLoS ONE 7:e6246. doi:10.1371/journal.pone.0006246

O'Shea TJ, Bogan MA, Ellison LE (2003) Monitoring trends in bat populations of the United States and Territories: status of the science and recommendations for the future. Wild Soc Bull 31:16–29

Ontario Ministry of Natural Resources (2011) Bats and bat habitats: guidelines for wind power projects. Ontario, Canada

Piorkowski MD, O'Connell TJ (2010) Spatial pattern of summer bat mortality from collisions with wind turbines in mixed-grass prairie. Am Mid Nat 164:260–269

Poerink BJ, Lagerveld S, Verdaat H (2013) Bat activity in the Dutch offshore wind farm OWEZ and PAWP. IMARES Report no. C026/13 / tFC report no. 20120402. The Fieldwork Company, Wageningen, Holland http://edepot.wur.nl/248979. Accessed 29 Nov 2014

Rodrigues L, Bach L, Dubourg-Savage MJ, Karapandza B, Kovac D, Kervyn T, Dekker J, Kepel A, Bach P, Collins J, Harbusch C, Park K, Micevski B, Minderman J (2015) Guidelines for consideration of bats in wind farm projects – revision 2014. EUROBATS Publication Series no. 6 (English version). UNEP/EUROBATS Secretariat, Bonn, Germany, UNEP/EUROBATS Secretariat. http://www.eurobats.org/sites/default/files/documents/publications/publication_series/pubseries_no6_english.pdf. Accessed 1 Aug 2015

Rodríguez-Durán A (2009) Bat assemblages in the West Indies: the role of caves. In: Fleming TH, Racey P (eds) Island bats: evolution, ecology, and conservation. University of Chicago Press, Chicago, pp 265–280

Rollins KE, Meyerholz DK, Johnson GD, Capparella AP, Loew SS (2012) A forensic investigation into the etiology of bat mortality at a wind farm: barotrauma or traumatic injury? Vet Pathol 49:362–371

Roscioni F, Russo D, Di Febbraro M, Frate L, Carranza ML, Loy A (2013) Regional-scale modeling of the cumulative impact of wind farms on bats. Biodivers Conserv. doi:10.1007/s10531-013-0515-3

Roscioni F, Rebelo H, Russo D, Carranza ML Di Febbraro M, Loy A (2014) A modeling approach to infer the effects of wind farms on landscape connectivity for bats. Landscape Ecol. doi 10.1007/s10980-014-0030-2

Rydell J, Bach L, Dubourg-Savage M, Green M, Rodrigues L, Hedenstrom A (2010a) Bat mortality at wind turbines in northwestern Europe. Acta Chirop 12:261–274

Rydell J, Bach L, Dubourg-Savage MJ, Green M, Rodrigues L, Hedenström A (2010b) Mortality of bats at wind turbines links to nocturnal insect migration? Euro J Wildl Res 56:823–827

Rydell J, Engström H, Hedenström A, Larsen JK, Pettersson J, Green M (2012) The effect of wind power on birds and bats: a synthesis report. Report 6511, Swedish Environmental Protection Agency, Stockholm, Sweden

Rydell J, Bach L, Bach P, Guia Diaz L, Furmankiewicz J, Hagner-Wahlsten N, Kyheröinen EM, Lilley T, Masing M, Meyer MM, Petersons G, Suba J, Vasko V, Vintulis V, Hedenström A (2014) Phenology of migratory bat activity across the Baltic Sea and the south-eastern North Sea. Acta Chirop 16:139–147

Santos H, Rodrigues L, Jones G, Rebelo H (2013) Using species distribution modelling to predict bat fatality risk at wind farms. Biol Conserv 157:178–186

Schlesinger ME, Mitchell JFB (1987) Climate model simulations of the equilibrium climate response to increased carbon dioxide. Rev Geophys 25:760–798

Smallwood KS (2013) Comparing bird and bat fatality-rate estimates among North American wind-energy projects. Wildl Soc Bull 37:19–33

Steffens R, Zophel U, Brockmann D (2004) 40th anniversary bat marking Centre Dresden—evaluation of methods and overview of results. Sachsisches Landesamt für Umwelt und Geologie, p 132

Strickland MD, Arnett EB, Erickson WP, Johnson DH, Johnson GD, Morrison ML, Shaffer JA, Warren-Hicks W (2011) Comprehensive guide to studying wind energy/wildlife interactions. National Wind Coordinating Collaborative, Washington http://www.batcon.org/pdfs/wind/National%20Wind%20Coordinating%20Collaborative%202011_Comprehensive%20Guide%20to%20Studying%20Wind%20Energy%20and%20Wildlife%20Interactions.pdf. Accessed 4 Jan 2015

U.S. Fish and Wildlife Service (2012) Land-based wind energy guidelines. U.S. fish and wildlife service, Arlington, VA, USA http://www.fws.gov/windenergy/docs/WEG_final.pdf. Accessed 1 February 2015

Van der Meij T, Van Strien AJ, Haysom KA, Dekker J, Russ J, Biala K, Bihar Z, et al. (2014) Return of the bats? A prototype indicator of trends in European bat populations in underground hibernacula. Mammal Biol. doi:10.1016/j.mambio.2014.09.004

Villegas-Patraca R, Macías-Sánchez S, MacGregor-Fors I, Muñoz-Robles C (2012) Scavenger removal: bird and bat carcass persistence in a tropical wind farm. Acta Oecol 43:121–125

Voigt CC, Popa-Lisseanu AG, Niermann I, Kramer-Schadt S (2012) The catchment area of wind farms for European bats: a plea for international regulations. Biol Conserv 153:80–86

Voigt CC, Lehnert LS, Petersons G, Adorf F, Bach L (2015a) Wildlife and renewable energy: German politics cross migratory bats. Eur J Wildl Res (in press)

Voigt CC, Aguirre L, Phelps K, Schoeman C, Vanitharani J, Zubaid A (2016) Bats and buildings: the conservation of synanthropic bats. In: Voight CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp. 427–453

Weller TJ, Baldwin JA (2012) Using echolocation monitoring to model bat occupancy and inform mitigations at wind energy facilities. J Wildl Manage 76:619–631

Wellington WG (2011) The effects of variations in atmospheric pressure upon insects. Can J Res 1946, 24d(2):51–70

Young DP, Bay K, Nomani S, Tidhar WL (2011) Nedpower mount storm wind energy facility post-construction avian and bat monitoring: July–October 2010. Western EcoSystems Technology, Inc, Cheyenne, Wyoming http://www.batsandwind.org/pdf/WV%20-%20Young%20et%20al.%202011%20-%20Mount%20Storm%20Fall%202010%20Report(%202-10-11).pdf. Accessed 4 Jan 2015

Chapter 12
Exploitation of Bats for Bushmeat and Medicine

Tammy Mildenstein, Iroro Tanshi and Paul A. Racey

Abstract Bat hunting for consumption as bushmeat and medicine is widespread and affects at least 167 species of bats (or c. 13 % of the world's bat species), in Africa, Asia, across the islands of Oceania, and to a lesser extent in Central and South America. Hunting is particularly prevalent among the large-bodied fruit bats of the Old World tropics, where half (50 %, 92/183) the extant species in the family Pteropodidae are hunted. Pteropodids that are hunted are six times more likely to be Red Listed as threatened: 66 % of species in IUCN threatened categories (CR, EN, VU, NT), compared to 11 % of species in the 'Least Concern' (LC) category. However, there still appears to be an information gap at the international level. One third of the hunted species on the Red List are not considered threatened by that hunting, and nearly a quarter of the bat species included in this review are not listed as hunted in IUCN Red List species accounts. This review has resulted in a comprehensive list of hunted bats that doubles the number of species known from either the IUCN Red List species accounts or a questionnaire circulated in 2004. More research is needed on the impacts of unregulated hunting, as well as on the sustainability of regulated hunting programs. In the absence of population size and growth data, legislators and managers should be precautionary in their attitude towards

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T. Mildenstein (✉)
Department of Biology, Cornell College, Mt. Vernon, IA, USA
e-mail: TMildenstein@cornellcollege.edu

I. Tanshi
Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA

I. Tanshi
Department of Animal and Environmental Biology, University of Benin, Benin City, Nigeria

P.A. Racey
Centre for Ecology and Conservation, College of Life and Environmental Sciences,
University of Exeter, Penryn Campus, Penryn TR10 9FE, UK

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hunting. Roost site protection should be a priority as it is both logistically simpler than patrolling bat foraging grounds and reduces the comparatively larger scale mortality and stress that hunting at the roost can cause. Education and awareness campaigns within local communities should demonstrate how bats are a limited resource and emphasize characteristics (nocturnal, slow reproducing and colonial) that make them particularly vulnerable to hunting pressure.

12.1 Introduction

Most of the chapters in this book (Voigt and Kingston 2016) consider negative consequences for bats from indirect effects of anthropogenic perturbations. In contrast, this chapter explores the direct exploitation of bats by humans for bushmeat and medicine.

A global review of bats as bushmeat was published in 2009 providing an overview of bat hunting based on published literature and a questionnaire widely distributed among bat biologists in 2004 (Mickleburgh et al. 2009). Here, we summarize what is currently known about the exploitation of bats for consumption and medicinal use, synthesizing the 2009 review with what has been published since and unpublished information the authors have gathered from colleagues. The result is a comprehensive list of hunted bats species that contains nearly twice as many species as known from either the IUCN Red List species accounts or the 2009 review. It is unclear whether the increased concern about hunting is the result of greater actual hunting pressure, or just represents our increased understanding of hunting impacts. What is clear is that reviews now explicitly attribute species declines and extinction risk to hunting pressure.

Most of the chapter discusses conservation needs in light of what is known about bat hunting. We summarize regional patterns in bat hunting and protection efforts and highlight areas of conservation concern. We provide details of current research aimed at learning more about hunting impacts, and we give examples of management activities to strengthen protection efforts against population-level effects of hunting. We end with recommendations for research to better understand the effects of hunting on bat populations as well as strategies for effectively managing hunting to support bat conservation. All common and scientific species names follow Simmons (2005).

12.2 Background

12.2.1 *Overview of Bat Hunting*

Bat hunting is widespread and affects at least 167 species of bats (or c. 13 % of the world's 1331+ bat species, Bat Conservation International 2015), occurring in Africa, Asia, across the islands of Oceania, and in some parts of Central and

South America (compiled from IUCN 2014; Mickleburgh et al. 2009, and personal communications by the authors; Appendix). Hunting is particularly prevalent on the large-bodied fruit bats (family Pteropodidae) in the Old World tropics, where half (50 %, 92/183) of all extant species experience hunting pressure (Mickleburgh et al. 2009; IUCN 2014). A much smaller proportion of insectivorous (<8 %, 75/962 species) are hunted, particularly members of the Emballonuridae, Hipposideridae and Molossidae in Asia and Southeast Asia, Vespertilionidae in North Africa and West and Central Asia, and Phyllostomidae in Brazil, Peru, and Bolivia as well as Rhinolophidae in sub-Saharan Africa, (Mickleburgh et al. 2009; Lizarro et al. 2010; IUCN 2014) (Appendix).

Bats are hunted for a variety of reasons, from their perceived medicinal properties e.g. Nicobar flying fox, *Pteropus faunulus*, Kingston et al. (2008); 'small bats' in Nepal (Tuladhar-Douglas 2008); fat from pteropodid species in Pakistan (Roberts 1997) to their use in ornate decoration such as the teeth of the Makira flying fox (*Pteropus cognatus*) used for necklaces (James et al. 2008). Bats are also hunted for sport by urban residents seeking country pursuits (e.g. large fruit bat hunting at Subic Bay, Philippines, S. Stier, pers. comm.) and tourists seeking exotic eating experiences (e.g. Pacific flying fox, *Pteropus tonganus*, hunting is offered as a recreation option at hotels in Vanuatu; A. Brooke pers. comm. in Hamilton and Helgen 2008). However, the most widespread reason for bat hunting, by far, is for consumption; all 167 species that are hunted are, at least in part, wanted for their meat as a source of protein. Bat meat ranges in value from a highly sought-after delicacy served at special ceremonies and traditional celebrations (e.g. *Pteropus mariannus* in the Mariana Islands) to "finger food" consumed in social drinking settings (e.g. many bat species in Southeast Asia, Mildenstein 2012; and in West Africa, M. Abedi-Lartey pers. comm.). Elsewhere, it provides an alternative source of protein for local people for whom meat is an expensive commodity (Jenkins and Racey 2008) and in extreme cases, bats are consumed as starvation food (Goodman 2006).

The intensity and frequency of bat harvesting varies from year round to periodical depending on the seasonality of the species, hunters' lifestyles, and/or local legislation. On the Islands of São Tomé and Príncipe, bats are hunted opportunistically for food all year round (Carvalho et al. 2014). In Southeast Asia, regular harvest of bats occurs in Indonesia and the Philippines (T. Mildenstein, unpublished data). A migratory species, the African straw-colored fruit bat (*Eidolon helvum*) is hunted whenever it is present in Accra (Fig. 12.1) and Kumasi, Ghana, between November and March (Kamins et al. 2011). Reduced hunting intensity in March is likely due to the northward migration of forest resident bats and/or the shift in hunters' occupation to farming. Similarly, in Madagascar, local legislation specifies two hunting seasons—one for fruit bats, and another for Commerson's leaf-nosed bat (*Hipposideros commersoni*) (Jenkins and Racey 2008), though actual hunting intensity is driven more by local availability (e.g. the lychee season for fruit bats). In some localities in east and western Nigeria, year round harvest of the Egyptian rousette (*Rousettus aegyptiacus*) is known (Fig. 12.1) (I. Tanshi pers. obs.), and *E. helvum* was documented as hunted during peak population periods in the southwest (Funmilayo 1978; Halstead 1977).

Fig. 12.1 Collection and sales of bats in Africa **a** *R. aegyptiacus* collected by a hunter with sticks from a limestone cave in Etapkini near Calabar, Nigeria (*credit* I. Tanshi), **b** Fruit bat kebab on sale in Kumasi, Ghana (*credit* M. Abedi-Lartey), **c** *E. helvum* and *H. monstrosus* on sale in a small market by the River Congo in Kisangani, DRC (*credit* Guy-C. Gembu)

Bushmeat is preferred to domestic livestock in many places because of the taste and perceived higher nutritional alue (Mbete et al. 2011, T. Mildenstein unpublished data). In locations where domestic meats and fish are generally preferred, such as Madagascar (Randrianandrianina et al. 2010), bushmeat becomes more important in periods of food shortage (Jenkins and Racey 2008). Similarly, on the island of Yap (Micronesia), hunting is socio-economically based, and bats are less desirable than seafood. Only people of lower social ranks with no access to the coast hunt fruit bats (Falanruw 1988). Consumption of bushmeat varies indirectly with the availability of other protein sources (e.g. in west Africa: Brashares et al. (2004)). In areas where bats are eaten, they are rarely the only available source of protein. The exception to this is in times of food insecurity, when people turn to bats as a food source, especially following natural disasters (e.g. typhoons: Aldabra flying fox, *Pteropus aldabrensis*, Mickleburgh et al. 2008a; Vanuatu flying fox, *Pteropus anetianus*, Helgen and Hamilton 2008a; Ontong Java flying fox, *Pteropus howensis*, Helgen and Allison 2008; Rodrigues flying fox, *Pteropus rodricensis*, Mickleburgh et al. 2008b; Samoan Flying Fox, *Pteropus samoensis* and *P. tonganus*, Brooke 2001, and *P. mariannus*, Esselstyn et al. 2006, USFWS 2009) and during civil unrest (e.g., Bougainville monkey-faced fruit bat, *Pteralopex anceps antrata*, S. Hamilton, pers. comm.). Similarly, species found in low-lying areas (e.g. *P. aldabrensis* and *P. howensis*) may become increasingly important food to local communities as rising sea-levels destroy other food sources (Mickleburgh et al. 2008a; Helgen and Allison 2008).

Twenty years ago marked the end of a long period of international trade in the Pacific with many pteropodids being imported into Guam and the Northern Mariana Islands. Once local bat populations were depleted, bats were imported from other island groups and mainland Southeast Asia (e.g. Wiles and Payne 1986; Wiles 1992; Stinson et al. 1992). Protracted international effort eventually led in 1987–1989 to the addition of pteropodid species to the Appendices of the Convention on International Trade of Endangered Species (CITES), which has stopped legal trade of bats between nation states, although a black market still occurs (e.g. into Europe, Samuel 2013).

Currently, hunting of bats for trade tends to be locally-based, and not international, but varies widely in intensity. An extensive commercial chain of bat trade exists outside markets in Ghana (Kamins et al. 2011). Other high levels of trade, include that of the large flying fox (*Pteropus vampyrus*) in Kalimantan, Indonesia (Harrison et al. 2011) and of the Malagasy flying fox (*Pteropus rufus*) in Madagascar (Jenkins et al. 2007; Oleksy et al. 2015b). More commonly, bats are traded locally and on a lesser scale, with relatively few individuals sold in markets (e.g. *P. vampyrus* in the Philippines, Sheffers et al. 2012; and in Southeast Asia, Mickleburgh et al. 2009). Prices per bat range from <1 USD in Southeast Asia (Indonesia: Heinrichs 2004; the Philippines: T. Mildenstein unpublished data) to more than 130 USD when acquired through black market trading (e.g. *P. mariannus* on Guam and the Northern Mariana Islands, USFWS 2009).

12.2.2 Hunting Overview by Region

12.2.2.1 Africa

In total, 55 species of bats are hunted in Africa, including mainly abundant large-bodied fruit bats (Mickleburgh et al. 2009) such as *E. helvum*, Franquet's epauletted fruit bat (*Epomops franqueti*), Gambian epauletted fruit bat (*Epomophorus gambianus*), hammer-headed fruit bat (*Hypsignathus monstrosus*), *R. aegyptiacus* and medium-sized species like Angolan soft-furred fruit bat (*Myoncyteris angolensis*) (formerly *Lissonycteris*), Peter's lesser epauletted fruit bat (*Micropteropus pusillus*) and to a lesser degree insectivorous bats such as the large slit-faced bat (*Nycteris grandis*), Maclaud's horseshoe bat (*Rhinolophus maclaudi*), Ruwenzori horseshoe bat (*Rhinolophus ruwenzori*) and *Hipposideros* species. Although insectivorous bats are considered to be less palatable in many regions and may appear to be under low hunting pressure, (Kamins et al. 2011; Dougnon et al. 2012) this is not necessarily the case. Goodman (2006) showed that in addition to fruit bats, mainly the Malagasy straw-colored fruit bat (*Eidolon dupreanum*), *P. rufus,* and the Malagasy rousette (*Rousettus madagascariensis*), insectivorous *H. commersoni* is frequently hunted, especially during periods of food shortages. In addition, while fruit bats are probably the most commonly hunted group, 64 % of the 55 bat species hunted in Africa are animalivores (Appendix).

Hunting bats for food is common in West and Central African states where it can be a major threat to their populations (Funmilayo 1978; Mickleburgh et al. 2009; Kamins et al. 2011). Frequent bat hunting is recorded from Benin Republic, Ghana, Guinea, Liberia and Nigeria (Funmilayo 1978; Anstey 1991; Kamins et al. 2011; Dougnon et al. 2012) (Fig. 12.1), as well as in Cameroon, Congo Republic, Democratic Republic of Congo (DRC), Equatorial Guinea and Gabon. High levels of hunting have also been reported in the past from islands off Africa—the Comoros, Madagascar, Mauritius and Rodrigues and São Tomé and Príncipe as well as Pemba Island, Tanzania (Jenkins and Racey 2008; Carvalho et al. 2014), although conservation efforts have reduced this pressure in some of these islands (Trewhella et al. 2005).

While occasional bat hunting occurs in Mali and Zambia, there is almost no hunting in East Africa, except eastern Uganda, and bat hunting is rare in South Africa (Mickleburgh et al. 2009). Bats are also persecuted because of negative perceptions in Ethiopia (Mickleburgh et al. 2009) but that is not the focus of this chapter.

Although, Halstead (1977) reported the potential for sustainable harvesting of bats at the Ile Ife campus, over-exploitation of *E. helvum* in southwestern Nigeria was also evident (Funmilayo 1978). People in rural areas in southern Nigeria admit to eating bats occasionally, whereas in parts of eastern Nigeria, *R. aegyptiacus* is hunted intensively (Fig. 12.1). Over 3000 individuals of this species have been collected in one night from a cave in Buanchor village by several hunters who hunt more than once a month (I. Tanshi, unpublished).

North Africa and West and Central Asia. Bat hunting is less prevalent in North Africa and West and Central Asia. Of the 98 bat species that occur in this region, five are known to be hunted and these are for medicinal purposes, of the 98 bat species that occur in this region, five (all Vespertilionidae) are known to be hunted: long-fingered Myotis (*Myotis capaccinii*), Geoffroy's myotis (*Myotis emarginatus*), whiskered myotis (*Myotis mystacinus*), Natterer's myotis (*Myotis nattereri*), Maghrebian myotis (*Myotis punicus*) (Table 12.1, Appendix).

12.2.2.2 Asia

In Asia, hunting is known to affect 64 species, which represents the largest absolute number of hunted bat species in a region.

Southeast Asia. The hunting pressure on bats is greatest in Southeast Asia, where 56, or 17 % of the region's bat species are hunted (Table 12.1, Appendix). Bat hunting is widespread in 10 out of the 11 countries (Brunei, Cambodia, Indonesia, East Timor, Laos, Malaysia, Myanmar, Philippines, Thailand, and Vietnam). Only in Singapore are bats not thought to be hunted heavily (Mildenstein 2012; IUCN 2014).

Table 12.1 Proportion of bats hunted by region (Calculated by total number of extant bats species hunted divided by the total number of bat species in the region)

Taxon	Region	Total#	On Red List	Not on list	Total hunted	%hunted
Chiroptera		1146	97	70	167	14.6
	Caribbean islands	106	0	0	0	0.0
	East Asia	130	3	4	7	5.4
	Europe	42	0	0	0	0.0
	Meso America	177	0	0	0	0.0
	North Africa	41	3	1	4	9.8
	North America	49	0	0	0	0.0
	North Asia	43	0	0	0	0.0
	Oceania	173	25	15	40	23.1
	South America	249	0	8	8	3.2
	South and Southeast Asia	365	43	20	63	17.3
	SE	333	36	20	56	16.8
	South	114	8	5	13	11.4
	Sub-Saharan Africa	249	25	26	51	20.5
	West and Central Asia	94	1	0	1	11

High levels of hunting occur in Indonesia, where there is a long history of bat consumption (Fujita 1988) and large numbers of individuals are still sold in markets (e.g. *P. vampyrus*, Harrison et al. 2011; Sulawesi fruit bat, *Acerodon celebensis*, gray flying fox, *Pteropus griseus,* black flying fox, *Pteropus alecto*, Heinrichs 2004). Hunting pressure is also high in the Philippines, with a third (24/75) of its species known to be hunted. Although Philippine bats are protected from hunting by the Philippine Wildlife Act and the Philippine Cave Management Act, these laws are not well enforced, and hunting for personal consumption and local trade is widespread.

In Malaysia, hunting of some species is regulated, which may curb some of the hunting pressure but has not reduced hunting rates to sustainable levels (Epstein et al. 2009). The laws and levels of enforcement are different for the different regions of Malaysia. All bats are legally protected in Sarawak, but this is not the case in Sabah and peninsular Malaysia. Illegal hunting still occurs in orchards and by sport hunters in Sarawak at places where enforcement is lacking. Legal protection for Old World frugivorous bats is reviewed by Abdul-Aziz et al. (2015).

In Buddhist countries (Cambodia, Myanmar, Thailand and Vietnam), most roost sites of large fruit bats are found in the gardens around temples and monasteries because of the protection the monks provide (e.g. Ravon et al. 2014; T. Mildenstein unpublished data). Whether this degree of protection is sufficient to maintain stable populations of these species has yet to be investigated (Table 12.1, Appendix).

South Asia. In Bangladesh, large fruit bats are hunted for food by members of tribal groups (Mickleburgh et al. 2009). In India and Pakistan, bats are classified as vermin and are persecuted, although they are consumed infrequently, and more often killed for medicinal purposes (Noureen 2014). The exception is the Indian flying fox (*Pteropus giganteus*), which is eaten by indigenous forest-dwelling people (Mickleburgh et al. 2009). On the Andaman and Nicobar islands, black-eared flying fox (*Pteropus melanotus*) and *P. faunulus* are hunted and eaten on special occasions (Mickleburgh et al. 2009) (Table 12.1, Appendix).

North Asia. Bats are not specifically protected in China and many species are eaten, especially in southern China, where bats are found regularly in markets (Mickleburgh et al. 2009) (Table 12.1, Appendix). Requests from international agencies following the SARS outbreak, (which resulted in several hundred human deaths) that wildlife legislation be introduced in China prohibiting *inter alia* hunting and sale of bats have been ignored.

12.2.2.3 Pacific (Oceania)

Bats are often the only native mammals on remote Pacific Islands, and there is a long history of bat species being hunted in many of these areas. Bats are eaten on American Samoa, the Cook Islands and Niue, the Federated States of Micronesia, Fiji, Guam and the Northern Mariana Islands, New Caledonia, Palau, the Solomon Islands, and Vanuatu (Chambers and Esrom 1991; Mickleburgh et al. 2009). In total, 40 bat species are affected, 23 % of Oceania's bats, making this the region with the highest proportion of hunted bat species on the planet. The value of bat meat is highly variable in Oceania. It is a sought-after delicacy on Guam and the Mariana Islands, where the bats are strictly protected by the United States' Endangered Species Act (USFWS 2009). In contrast, in the nearby Federated States of Micronesia, the same bat species are rarely eaten (Mickleburgh et al. 2009). In American Samoa, (another United States territory), bats were consumed regularly in the past (Brooke 2001) but are now highly protected. Bat meat is also a delicacy in the Cook Islands, Niue, and Raratonga (Brooke and Tshapka 2002) and is a popular food on Fiji, New Caledonia, and Vanuatu (Mickleburgh et al. 2009).

12.2.2.4 South America

Bat hunting is much less common in South America, occurring in highly localized areas and affecting eight species in the families Phyllostomidae (7 spp.) and Vespertilionidae (1 sp.) (Table 12.1, Appendix).

12.3 Why Bat Hunting is a Conservation Problem

12.3.1 Negative Impacts on Bat Populations and Ecosystems

Bats are particularly vulnerable to the effects of hunting for a number of reasons. They are long-lived for their body size (five species live >30 years, Racey 2015) and reproduce slowly, with generally one young per year. They have a slow rate of fetal growth and long gestation periods (Racey and Entwistle 2000). Females and young bats are thus sensitive to hunting disturbance during a large portion of the year.

Bats are nocturnal, making them susceptible to hunting at their roost sites by day when humans can easily find them. This is especially a concern for the highly sought-after fruit bats in the Old World, which tend to roost conspicuously, aggregating in large numbers in the forest canopy (e.g. Mildenstein et al. 2008). Whether roosting colonies are in caves, cliffs, or trees, hunting at the roost site is likely to affect the entire colony. Hunting disturbance at the roost site causes injury to many bats from the spread of shot gun pellets, large-scale infant mortality when pups fall from fleeing mothers (Mildenstein and Stier unpublished data; R. Ulloa, pers. comm.), and higher stress levels as resting bats are startled and forced to flee from hunters (Van der Aa et al. 2006). In their survey of *P. rufus* in Madagascar, Mackinnon et al. (2003) recorded a high incidence of abandonment of historical roosts, which they attributed, at least in part, to high hunting pressure.

Finally, bat colonies are characterized by high roost site fidelity (e.g. Banack 1996; Brooke et al. 2000; Gumal 2004; Stier and Mildenstein 2005). Hence, bats may be reluctant to leave when hunting starts and may find it difficult to find alternative roost sites after fleeing hunters. Because bats are likely to eventually return to the preferred roost site, they are predictable prey for hunters. The overall effect of hunting at roost sites is reduction of bat population densities to a fraction of local carrying capacity (e.g. Mildenstein 2012).

These population-level impacts may also have negative ecological consequences. Some bat species play prominent roles in insect population control, pollination, seed germination and dispersal, and in many areas, bat species are essential to forest regeneration (e.g. large fruit bats are primary seed dispersers for hemiepiphytic figs, Shanahan 2001; Oleksy et al. 2015a). On isolated islands, where there is little ecological redundancy, bats are often recognized as keystone species due to their unique roles in seed dispersal (Shilton and Whittaker 2009). Mortality due to hunting may, therefore, have cascading effects on ecological communities (e.g. Mildenstein 2012) and ecosystem function (e.g. McConkey and Drake 2006).

12.3.2 Negative Impacts on Humans

The negative impacts of bat hunting extend beyond natural ecosystems to human communities. Bats in their natural ecological roles perform valuable ecosystem services beneficial to humans (e.g. insect suppression: Cleveland et al. 2006, pollination: Bumrungsri et al. 2008b, 2009, seed dispersal maintaining local watersheds: Banack 1998; Stier and Mildenstein 2005), all of which are reduced when bats are hunted. Bat colonies have also proved valuable as eco-tourism attractions supporting local economies (e.g., in Costa Rica, Lao People's Democratic Republic, Madagascar, the Philippines, and North America; examples in Pennisi et al. 2004). However, hunted bats that are wary of human presence often do not maintain colonies in locations easily viewed by people. Hence, reductions in bat populations as a result of hunting could have expensive ramifications on local communities' water supplies, agriculture, and eco-tourism industries.

Finally, the hunting of bats may also expose human communities to potentially zoonotic pathogens (Leroy et al. 2005). In the past decade, considerable attention has been paid to bats as natural reservoirs of emerging infectious diseases (Calisher et al. 2006). Studies that link infectious disease outbreaks to bats demonstrate the spillover potential through contact with bats or exposure to faeces and urine in bat habitats (reviewed by Plowright et al. 2015). Most notable are the Ebola virus outbreaks, which have attracted international attention. Leroy et al. (2009) suggest that the 2007 emergence of Ebola virus in the Occidental Kasai province of DRC could be attributable to the consumption of freshly killed bats. The authors trace the virus spread from a first patient with bat bushmeat contact to an outbreak of the disease in 260 persons resulting in 186 deaths in 2007. The re-emergence of the disease in 2014 may also have arisen from contact with bats (Saéz et al. 2015) and has proven far more deadly.

12.4 Overhunting as a Growing Concern for Conservation

Human communities have long exploited bat populations for consumption. Current hunting pressure, however, is likely to be much greater than historical pressure with increases in human population density, greater accessibility to natural areas, technological advances in bat capture methods and transport options, and relaxed adherence to cultural taboos (Brooke and Tschapka 2002; Millner-Gulland and Bennett 2003). Hence, bat hunting is likely to be unsustainable (Bradshaw et al. 2009), especially when coupled with other anthropogenic stressors (such as those described throughout this book).

Overhunting (commonly also “unregulated” hunting, although not all unregulated hunting is unsustainable, nor regulated hunting sustainable) is a globally-recognized threat to many wild species of animals (Robinson and Bennett 2000; Milner-Gulland and Bennett 2003). For bats, overhunting has been a conservation concern for over three decades (Lemke 1986; Mickleburgh et al. 1992, 2002, 2009; IUCN 2014). However, there has been a substantial lag time in our identification of which species are affected and assessment of the impact of hunting.

Twenty years ago, the conservation status of nearly half (78/160) of the Old World fruit bats was unknown due to lack of data (compiled from Mickleburgh et al. 1992). Today only 11 % (21/183) of the extant Old World fruit bat species on the Red List are considered data deficient (IUCN 2014). (These two reviews may differ slightly in their definitions of data deficient species.) This general increase in knowledge about bats includes a better understanding of the extent of hunting pressure. In the first conservation review, 49 (31 % of the total 160 known) Old World fruit bat species were recognized as hunted (Mickleburgh et al. 1992). Two decades later, nearly twice as many species ($N = 92$) are known to be hunted, representing over half of the 183 recognized species of Old World fruit bats (IUCN 2014) (Table 12.1).

Although there has been relatively little research explicitly focused on quantifying hunting impacts, the general level of concern about hunting effects on bat conservation has increased. Using Old World fruit bats as an example, in the first review, hunting was not considered a threat for most (60 %) of the hunted species (Mickleburgh et al. 1992). Now, all but five of these hunted species (25/30, 83 %) have been moved up to a higher threat status because of perceived pressures that hunting causes (IUCN 2014). Overhunting is a recognized factor in the loss of three (and probably also the little known fourth) of the now extinct fruit bat species (IUCN 2014) and a cause behind local extirpations within species' historic distributions (e.g. Polynesian sheath-tailed bat, *Emballonura semicaudata*, from Vanuatu, Helgen and Flannery 2002). Similarly, the declines of seven of the ten fruit bat species listed as critically endangered are attributed directly to hunting; the remaining three species are still virtually unknown (IUCN 2014) (Table 12.2).

The increased concern about bat hunting may be due to greater hunting pressure, or may just represent our increased awareness of hunting impacts. What is clear is that bat conservation biologists now explicitly attribute species declines and increased extinction risk to hunting. Seven hunted bat species previously assumed to be unaffected by hunting (Mickleburgh et al. 1992) now have hunting listed as a major threat (IUCN 2014). Most (68 %) of the species that are hunted, are listed as threatened by that hunting, while only 15 % of the hunted species are expected not to be affected. However, it should be pointed out that for the remaining 38 % of hunted species, reviews remain ambivalent about whether hunting is a problem. Similarly, in the review of bats as bushmeat carried out in 2004 (Mickleburgh et al. 2009), 59 % of questionnaire respondents said bat hunting

Table 12.2 Comparison of the conservation status of old world fruit bat species across two decades from two sets of species accounts: 1992 IUCN Action Plan (Mickleburgh et al. 1992); 2014 IUCN Red List; and for comparison, the 2009 Bats as Bushmeat review (Mickleburgh et al. 2009)

	IUCN Action Plan 1992	IUCN Red List 2014	Bushmeat Review 2009
# species considered	160	183	138 reports
# species hunted (% total)	49 (31 %)	92 (50 %)	82 (59 %)
# species perceived as threatened by hunting (% total hunted)	20 (40 %)	63 (68 %)	44 (54 %)
# data deficient species (% total species)	78 (49 %)	21 (11 %)	
# hunted species listed as LC (% total hunted)	29 (59 %)	10 (5.3 %)	
# hunted species not listed as hunted on IUCN list (% total hunted)	Unknown	18 (20 %)	

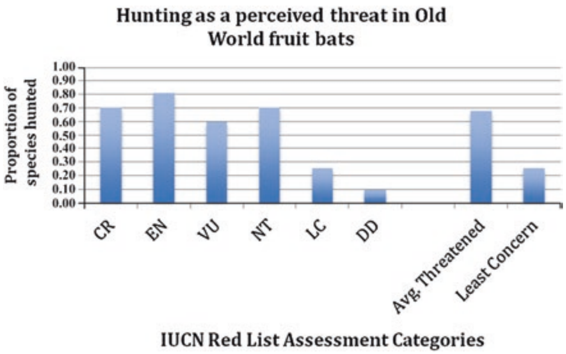

Fig. 12.2 Proportion of pteropodid species in IUCN categories listed as hunted. 69 % of species in threatened categories (*CR*, *EN*, *VU*, *NT*) list hunting as a threat, compared to 25 % of species in the "least concern" (*LC*) category

occurred in their region, and over half (54 %) of those species hunted were perceived to be negatively affected (Table 12.2).

The general consensus among biologists and managers is that hunting is a major conservation threat. Despite lacking measures of hunting impacts, there are many examples of population declines and extirpations of bats that are hunted (e.g. loss of historical bat roosts and reduced population sizes in Madagascar, Mackinnon et al. 2003; and in the Philippines, Heideman and Heaney 1992). Biologists studying Old World fruit bats currently rank hunting as the top conservation concern for this taxon (Mildenstein 2012). The IUCN Red List also reflects this concern. Fruit bat species that are known by the IUCN to be hunted are almost three times more likely to be listed as threatened ($N = 58$ spp. in IUCN categories: CR, EN, VU, NT compared to 21 species in the "LC" category) (Fig. 12.2). However, there still appears to be an information gap at the international level. Nearly 42 % (70/167) of the hunted species listed in this review are not listed by the IUCN Red List as threatened by hunting. Half of these (35 spp.) may be for lack of awareness, as they are not known to be hunted at all by the IUCN. The other half are described as hunted by the IUCN but not considered to be threatened by that hunting. In other words, these 35 species are described as hunted in their Red List species accounts, but then hunting is not included in the list of threats (compiled from IUCN 2014).

12.5 How Hunting Affects Bats

The least known area of bat biology is population dynamics, so it is difficult to extrapolate from hunting mortality rates to a quantitative assessment of hunting impacts on bat populations. Hence, one of the main conservation recommendations for protecting hunted species is the direct study of the population–level impacts of hunting (IUCN 2014).

Hunting does not necessarily lead to population declines in wild species. There are some examples of hunted bats that appear to have stable population sizes or where the effects of hunting are minimal. In these cases, hunting pressure is small relative to the bat population size due to effective law enforcement (e.g. *P. mariannus* on Rota, Mariana Islands, Mildenstein and Mills 2013), due to cultural/religious taboos (e.g. related to Muslim beliefs: *R. obliviosus* and *P. seychellensis* in the Comoros Islands, Sewall et al. 2003, 2007; *P. vampyrus* in the southern Philippines, Mildenstein 2012), and/or for the reasons given for the 35 species on the Red List that are hunted but not considered threatened by that hunting (see Appendix).

To evaluate the impacts of hunting on a bat population, research must compare the direct and indirect mortality rates of hunting with that population's capacity for growth. Falling short of these data-intensive lines of evidence, biologists have found other ways to provide inferences of hunting impacts, e.g., expert opinion, models of hunting and population growth, indices to measure population growth and/or hunting mortality, and by comparing hunted to non-hunted populations. Below, we describe the research that has contributed to knowledge of the impacts of hunting on bat populations to date.

12.5.1 Expert Opinion

Expert opinion surveys can be an efficient means of gathering information on conservation priorities when research is lacking. Because of the paucity of data on hunting impacts, much of the current concern about bat hunting is based largely on expert opinion derived from anecdotal evidence and observations of bat hunting impacts on local scales. Red List risk assessments for lesser known bats are often the result of consensus among biologists who have worked on the species. Conservation recommendations for most bat species that are hunted are based on perceived relationships between apparent bat population declines and levels of hunting that appear to be unsustainable (e.g. *Pteropus flanneryi*, Helgen et al. 2008a).

Surveys of bat biologists have been used to provide overviews of bats that are hunted and where. Most recently, Mickleburgh et al. (2009) conducted a literature review and global survey of bat biologists in 2004 to collate what is known about bat hunting. From 109 questionnaire respondents, there were 138 reports of bat consumption from which the authors provided a synthesis of bat hunting, identifying West Africa and Asia as the principal regions of conservation concern.

Expert opinion surveys have also shed light on hunting as the main threat and priority for conservation management to address. Mildenstein (2012) conducted surveys through questionnaires at two Southeast Asia regional bat conferences to learn about threats to fruit bat species. According to the 78 participants representing all Southeast Asian countries except East Timor, hunting is the main direct threat to fruit bats across this region.

Caveats. While expert opinion is a readily available source of information to identify conservation priorities in lieu of data, it does not replace systematically-acquired knowledge. There are many examples of subsequent research leading to recommendations that differ from expert opinion, especially when species-specific ecological distinctions are concerned (e.g. how to conserve co-occurring specialist and generalist species, Mildenstein 2012). It is incumbent upon conservation biologists to conduct research to verify priorities identified through expert opinion to focus conservation resources and efforts on the most urgent issues.

12.5.2 Determining Hunting Impacts on Bat Populations

To directly study the impacts of hunting, research must measure and compare hunting mortality rates to a bat populations' size and capacity for growth. To date, there are only a few studies that have tried to evaluate the sustainability of bat hunting. The first was Halstead's (1977) on the Ile-Ife campus of the University in Nigeria, which was unfortunately cut short by his return to the UK. Brooke and Tschapka (2002) modeled what would be "sustainable take" on Niue, based on the current bat population size and estimated reproductive rates. Comparing their modeled sustainable take to the numbers of bats hunted on Niue, they determined current hunting rates were unsustainable. Epstein et al. (2009) estimated potential harvest rates of *P. vampyrus* in Malaysia as a function of the number of hunting licenses issued. Incorporating these hunting mortality rates into their estimated bat population growth matrix, they projected declines in the Malaysian bat population using even the most conservative measures of hunting pressure. On Madagascar, Goodman (2006) extrapolated total hunting pressure on hipposiderids from a single hunter he interviewed. Comparing this estimated mortality rate to the local bat population surveyed, he then inferred hunting levels were detrimental, because take exceeded the breeding potential of the local bat populations.

Caveats. Rarely will information be available on harvest levels, population sizes, and reproductive rates for the same bat species. The studies described here work around missing information by using indices of bat harvest levels (e.g. licenses), estimates of reproduction rates from better known congenerics, and models of sustainable take based on rules of thumb from other harvested species (e.g. "RR" production method, named after its authors, Robinson and Redford 1991).

When indices, estimates, and models based on other species are used, there are caveats to consider. Researchers should be sure that the relationship between the index and the measure of interest is known and does not vary. Estimates based on similar species may differ from the species of interest. With population growth rates in particular, ignoring density-dependent factors could lead to inaccurate estimates of reproduction and population growth capability. Finally, models for determining sustainable hunting rates, such as the RR method used by Brooke and Tschapka (2002), predict a sustainable take rate of 40 % of the annual growth for species with life spans the length of fruit bats. However, this rate is based on similar species with potentially different life histories and may not take into account the other stressors that bats face today.

12.5.3 Measuring Hunting Mortality Rates

Surveys from local markets, hunters, and consumers can be used to gain insights into hunting rates and trends. Studies use a variety of methods to estimate hunting pressure on bats. In the Mariana Islands, Esselstyn et al. (2006) interviewed hunters of *P. mariannus* and found a 34 % increase in hunting pressure after a recent typhoon. In Madagascar, Goodman (2006) used his interview of a single bat hunter as a sample to extrapolate local hunting pressure on hipposiderids. In Niue, Brooke and Tschapka (2002) used government permit records to identify households with guns potentially used for hunting, and then interviewed a third of these potential hunters about their bi-monthly harvest rates. The authors used their results from this sample to extrapolate to hunting pressure over all hunters during the two month hunting season on the island. Kamins et al. (2011) interviewed a total of 551 Ghanians including hunters, vendors and consumers, demonstrating a high off-take of >128,000 *E. helvum* per year. A recent study on the same population used annulus markers in teeth to age bats and develop a static life table to determine age structured survival rates (Hayman et al. 2012). Markets were surveyed in Sulawesi to determine bat consumption rates of local people and number of bats exported to neighboring provinces for trade (Sheherazade and Tsang 2015). A questionnaire survey in 13 villages in Madagascar resulted in an estimate of 6500 bats taken each year (Razakarivony 2003) and staff at a roadside restaurant in western Madagascar reported serving about 30 *P. rufus* each day, which extrapolates to 10,000 a year (Racey et al. 2009). The largest roost counted during surveys at that time consisted of 5000 individuals (Mackinnon et al. 2003) which cast doubt on the reported rate of bat consumption. Nevertheless about 30 live *P. rufus* were present in panniers in the food storage area of the restaurant during a casual visit (Racey et al. 2009). Also in Madagascar, Oleksy et al. 2015b) interviewed hunters to learn about bat numbers taken as well as the location, time of night, and season in which the hunting occurred, to measure harvest rates.

Caveats. When using surveys of people’s knowledge and opinions to collect information for conservation, it is important to remember the limitations of this source of information. Hunters can provide insight into numbers of bats killed, but not all of these are sold. So, when the study question involves bat trade, researchers must extend surveys to the end consumers of bats. To address this problem, the surveys by both Kamins et al. (2011) and Harrison et al. (2011) employed questionnaire approaches where all actors at different stages of the commodity chain were interviewed instead of restricting data collection only to market surveys.

There is a potential for market surveys to underrepresent the extent of fruit bat hunting, especially when many bats are not sold in regular or bushmeat markets (Kamins et al. 2011). Mbete et al. (2011) interviewed householders in Brazzaville and assembled a long list of bushmeat species consumed together with details of the markets from which they were purchased. Bats were conspicuous by their absence and enquiries (by PA Racey) revealed that they were ‘marketed differently’.

In addition, hunter interviews have received conflicting reports on the accuracy of information gathered. For example, some studies report that hunters overestimate what they take, as has been shown for geese in the United States where goose hunting is legal (Andersen et al. 1996). Similarly, hunters who are being interviewed for their unique traditional knowledge may want to please or impress their interviewers, which could lead to overestimated harvest rates (e.g. indigenous Aeta people in the Philippines, T. Mildenstein and S. Stier, unpublished reports). However, in places where the species hunted is of perceived conservation concern, hunters may underestimate their take levels to avoid scrutiny, especially if hunting is illegal (e.g. for Mariana fruit bats, *P. mariannus*, in the Mariana Islands, T. Mildenstein unpublished reports).

To address the potential for inaccurate reports by hunters, some studies provide methods for hunters to report take anonymously. The study of typhoon impacts on hunting levels in the Mariana Islands, used a local hunter to collect data from other hunters (Esselstyn et al. 2006). In Madagascar, Oleksy et al. (2015b) provided a subpopulation of hunters with notebooks and monetary incentives to keep track of hunting off-take over time and return the information anonymously at the end of the study.

12.5.4 Estimating Hunting Impact from Population Declines

In cases where hunting mortality rates are unknown and/or difficult to measure, study of population trends in hunted areas can provide an indication of hunting impacts. Hunting is often assumed to be the cause behind measured population declines. For example, biologists interviewed local people at more than 30 bat roosting sites in Pakistan where bats were hunted, and the consensus of local knowledge suggested there were large-scale declines in bat populations in areas where hunting was common (Venkatesan 2007). The inference power of this type of study is stronger, however, if a comparison can be made to areas free from hunting. In comparisons of areas with and without hunting, bat population densities were 5–10 times larger when roost sites were protected (in the Philippines, Mildenstein 2012) and up 100 times larger when their entire habitat was protected (in the Mariana Islands, Mildenstein and Mills 2013).

Other studies have used indices of bat population size that are directly linked to hunted bats for measuring trends. Harrison et al. (2011) used questionnaires to survey hunters and market vendors across 12 key population centers in Kalimantan, Indonesia to gain insight into hunting intensity, seasonality, and market dynamics. They used capture rates by hunters and sales rates in markets as indices of the population size of bats in the wild. From reductions in the numbers of bats captured and the decreasing number of bats brought to market for sale, they inferred that the bat population in the wild was declining.

Caveats. Again, caution is warranted when inferences are based on surveys of people's opinions and care should be taken in planning surveys and interviews especially when researchers lack sociological training (St. John et al. 2013; see also Nuno and St. John 2014 for a review of survey techniques). Similarly, it is important to remember that population reductions in areas with hunting are the net result of many stressors, natural and human-caused (e.g. chapters of this book), and may not correlate directly with hunting pressure.

12.6 Conservation Management to Mitigate Hunting Impacts

12.6.1 Enforcement of Hunting Prohibition

For threatened populations, the elimination of hunting as a threat can produce population-level results within decades (see also roost site protection). For areas that have been not hunted, bat population sizes can be large, with densities (individuals/hectare of habitat) that are hundreds of times that of the same species in similar areas with hunting pressure (e.g. Mariana Islands, Mildenstein and Mills 2013; Tacio 2015). Similarly, eliminating hunting allows bat populations to recover. In American Samoa, typhoons and overhunting sent populations of *P. samoensis* and *P. tonganus* into a sharp decline, eventually triggering a hunting ban in 1992 (Craig et al. 1994a, b). Two decades later, the population sizes of these bats is much larger and considered stable (Brooke and Wiles 2008, A. Miles pers. comm.).

12.6.2 Regulated Hunting

Theoretically, hunting can be sustainable if regulated tightly to ensure population declines due to harvest do not exceed what bat populations can naturally replace given the range of environmental variability to which they are subjected (methods in Mills 2012). Although several countries permit hunting, bat hunting has generally proved difficult to regulate for sustainability for a number of reasons. In some places, hunting laws are hard to understand and therefore not followed by hunters. In Madagascar for example, bats can be hunted legally between May and August or February to May, depending on the species (Jenkins and Racey 2008). In addition, according to the regulations, hunting is allowed only during the day, and game species cannot be hunted at their roost. Hence bat hunting is technically impossible, but hunters harvest bats despite the rules (Racey et al. 2009).

In other countries, hunting regulations are poorly designed from a conservation perspective. In peninsular Malaysia, bat hunting is legal and numbers harvested are said to be regulated. However, while limits on the number killed are issued by the provincial government where the hunter resides, the license owners are allowed to hunt in multiple provinces which creates a potential for seasonal take that far exceeds the bat populations' capacities for regeneration (Epstein et al.

2009). In Niue, bat hunting is allowed for two months per year. Hunting levels are not regulated because of the assumption that the bat supply is unlimited. However, bats roost in sacred forest grounds that are taboo for humans to enter, making it impossible to obtain a count of the population size. Based on models of similar species, harvest rates exceed what is expected to be sustainable (Brooke and Tschapka 2002).

In other countries, harvest laws are not enforced or followed. For example, the main threat to the ornate flying fox (*Pteropus ornatus*) in New Caledonia is local hunting for food (Brescia 2007). There is a short legal fruit bat hunting season, which includes only the weekends of April with a quota of five bats/hunter. However, based on reports, there is widespread and substantial illegal hunting, including the commercial harvesting of these fruit bats (Brescia 2007).

Finally, there are a few countries where hunting is legal and unregulated. In Pakistan and India, bats are considered "vermin" or "pests" and hunting is actually encouraged by the government without concern for long-term sustainability or conservation (Noureen 2014).

Whenever hunting regulation is being considered, managers should be aware that sustainable off-take will have to be much lower than projected recruitment for a number of reasons. Current bat population sizes, distribution, and number of populations are a fraction of historical numbers. For example, mixed colonies of *P. vampyrus* and golden-crowned flying fox (*Acerodon jubatus*) in the Philippines are thought to once have been present on every major island in populations numbering in the hundreds of thousands (Heideman and Heaney 1992). Now, these bats have been extirpated from most islands. Fewer than 15 mixed colonies remain, often with less than 2000 individuals and dangerously small numbers of the endangered *A. jubatus.* (Mildenstein 2012). In addition to already being at historically low population sizes, other human-caused stressors (persecution, habitat fragmentation, global climate change and other perturbations described in this book) continue to act on bat populations, exacerbating detrimental effects of harvest. Hence, it is prudent for managers to be conservative when establishing regulated harvest limits, and to carefully monitor populations and adapt regulatory management as needed to meet sustainable goals.

12.6.3 Control of Guns, Ammunition, and Other Bat Hunting Tools

Gun control is expected to have a positive effect on bats. In those countries where private gun ownership is not allowed, *Pteropus* often benefits. After a coup d'état in the Seychelles in 1977, all guns were confiscated and the numbers of Seychelles flying fox (*Pteropus seychellensis*) rose having previously been of some conservation concern (Racey 1979; Nicoll and Racey 1981). A similar story occurred in Palau following the death of the President by gunshot wounds (A. Brooke, pers. comm.).

In Myanmar, private gun ownership is a crime with reportedly severe penalties. Perhaps as a result, bat populations are large and easily approached. Bats are still harvested. For example, *Pteropus* are catapulted to provide medicine for asthma, *Rousettus* is often netted at cave entrances and sold in a market close to Mandalay, and insectivorous bats are also caught at cave entrances, fried and sold as beer snacks (U Khin Maung Gyi, pers. comm.). However, the harvest rates and overall disturbance to bats in Myanmar are thought to be much lower without guns.

Bat hunting may also be regulated through control of capturing equipment. For example, in Sarawak, as in many countries, it is illegal to sell or buy mist nets without a permit. This method of protecting bats, however, is only effective if hunters use commercially-manufactured nets. Many bat hunters avoid the high cost and regulation of mist nets and make their own nets or hook and line traps from monofilament line and other inexpensive fishing materials (e.g. in the Philippines, Mildenstein 2012).

12.6.4 Roost Site Protection

Bats are most vulnerable at their day roosting sites. So, it is not surprising that bat populations settle in areas where they are most protected. In Buddhist countries like Cambodia, Myanmar, Thailand, and Vietnam, large fruit bats are commonly found in the gardens surrounding temples and monasteries (T. Mildenstein, unpublished data). The presence of monks and religious activities turn these areas into de facto sanctuaries for bats that would otherwise experience hunting pressure. In nearby non-Buddhist countries, such as Indonesia and the Philippines, the same fruit bat species colonize other “safe” spots such as privately protected lands and parks, especially in the forest interior, using topographical features that afford protection from people (e.g. along rivers, within mangrove islands, and on cliff edges, Mildenstein 2012). Active protection of roost sites alone (i.e. hunting still occurs away from the roost) has been shown to result in as much as ten times the number of roosting fruit bats for the same amount of forest habitat, and is especially important for sensitive species such as ecological specialists (Mildenstein 2012). Because of this, and the fact that roost sites are geographically predictable, conservation management by local government units and non-government organizations often target roost site protection.

Case Studies. Conservation efforts for the Pemba flying fox (*Pteropus voeltzkowi*) included roost protection through the setting up of community conservation clubs (Robinson et al. 2010). The recovery following these conservation programs led to the downgrading of the species’ Red List threat assessment from Critically Endangered to Vulnerable.

Until recently, permanent nets were a regular method of hunting in the roost at Analalava, Madagascar by the people of Ambatondrazaka. The national NGO, Madagasikara Voakajy, initiated community-based protection of the fruit bat roost by incorporating payment for local rangers in a local peanut cooperative it funded.

Currently, hunting at the roost has ceased and the colony has increased from 200 to nearly 2000 individuals (Razafimanahaka 2013).

In Malaysia, the Wildlife Conservation Society has worked with local communities and the government in Sarawak to establish protected roosting areas of *P. vampyrus*. (M. Gumal, pers. comm. 2015). Four out of the five maternity roosting sites identified by Gumal (2004) are now protected for *P. vampyrus,* including: Loagan Bunut National Park, Sedilu National Park, Limbang Mangroves National Park, and Bruit National Park. A fifth maternity roost site at Bukit Sarang is in the preliminary proclamation stage for a National Park (M. Gumal pers. comm.).

In the Philippines, the Filipinos for Flying Foxes project is building on the successes of Bat Count-Philippines by developing bat roost site sanctuaries with local governments. The collaborating organizations (Philippine Biodiversity Conservation Foundation and Mabuwaya Foundation) are establishing community-managed roost site sanctuaries across the distribution of the endemic and endangered *A. jubatus* and studying bat population size increases and roost site fidelity in these newly protected roost sites (SOS 2012).

12.6.5 Education and Awareness Raising

One of the first steps toward conservation management of hunted bats is educating local communities. Bats are important to human communities in a number of ways, particularly for the valuable ecosystem services they provide, but local communities are often unaware of these. Because hunting, like other human-caused stressors, is tied directly to population declines in bats, it is important that human communities are aware of the trade-offs between temporary gains from bat exploitation and the risk of losing bats entirely from the region. Following a knowledge/attitude/behavior approach to understanding responsible environmental behavior (Hines et al. 1987), communities may come to appreciate bats and support bat conservation only after understanding their role in the environment (see Kingston 2016).

12.6.5.1 Knowledge

People are generally aware of bats present near their local communities. Bats are not cryptic animals, especially fruit bats that aggregate in large numbers by day using conspicuous roosting sites, and they often forage at night in fruiting and flowering trees on farms and in residential areas. Hence, local people's knowledge of bats often surpasses that of outside biologists, especially with respect to bat roosting locations, foraging habits, seasonal behaviors, and even threats (e.g. local community members' awareness of subtle seasonal changes in fruit bat diet of *P. mariannus,* Mildenstein and Mills 2013). It is, therefore, surprising how little is known about bat conservation status in these same areas. Population size and growth trends tend to be unknown by biologists and managers, much less by the non-scientific members of the local community. So, even though local people are aware of the disturbance they may be causing, they often have no idea of the severity of population-level consequences. Because bats appear to be numerous, popular belief is that humans can have only minimal impact on their populations. For example, the greater short-nosed fruit bat (*Cynopterus sphinx*) is believed by experts to be threatened by hunting in parts of its range, but in other parts, <1 % of local people surveyed believe the species could be threatened by their hunting (Johnson et al. 2003). Similarly, throughout the Philippines, bats are eaten regularly with little understanding of the impacts that harvest is causing. Hunters who join biologists on bat population counts commonly overestimate the population size by three orders of magnitude prior to the count and then are shocked when the counted population is in the hundreds or low thousands (Mildenstein et al. 2007; Mildenstein 2012).

Education and awareness programs. One of the most hunted bats in sub-Saharan Africa, *E. helvum* is the focus of members of the Eidolon Monitoring Network (EMN) who conduct education activities in areas near bat colonies (J. Fahr, pers. comm.). In Kenya and Nigeria, scientists and volunteers of the EMN carry out education programs in schools (Fig. 12.3) and among the general public (Tanshi et al. 2013). Education on islands around Africa has proven effective in drawing local attention to bat protection. Examples include the recovery program

Fig. 12.3 Conservation education and bat population monitoring by volunteers in Eidolon Monitoring Network in Benin City, Nigeria, school students engage in conservation outreach event, **a** volunteers prepare conservation outreach materials, **b** volunteers counting straw-coloured fruit bats *Eidolon helvum* at King square, Ring Road, Benin City, **c** undergraduate student volunteers Eidolon Population Monitoring team from University of Benin, Benin City, Nigeria

for the *P. voeltzkowi* in Pemba Tanzania, for *P. rufus* in Madagascar, *P. rodricensis* in Rodrigues and the Comoro flying fox (*Pteropus livingstonii*) in the Comoros (Wilson and Graham 1992; Trewhella et al. 2005; O'Connor et al. 2006; Robinson et al. 2010; H. Doulton, pers. comm.).

12.6.5.2 Behavior—Local Commitment to Conservation of Bats and Bat Habitat

Finally, once communities that value bats become aware of the threats bats face, the may start to change their behaviors to support bat conservation (but see Kingston 2016). A multi-faceted education and awareness program in the Comoros Islands is a good example of how outreach can lead to changes in attitude and behavior that support conservation. Local citizens became involved in monitoring bat populations and directing conservation management (Trewhella et al. 2005).

12.6.5.3 Capacity Building of Local Rangers/PA Managers

Many programs include training and capacity building in their bat conservation efforts. Bat Count—Philippines held a national workshop in 2004 to train protected area managers in bat identification and monitoring techniques (Mildenstein et al. 2007; Mildenstein 2011). The project, Filipinos for Flying Foxes, is now working with local communities to establish sustainable management practices for bats (SOS 2012). The project trains local rangers and management staff to monitor their bat populations and encourages them to self-regulate their hunting pressure. In Dalaguete, Cebu, rangers have continued forest protection despite the inconsistencies in availability of their modest stipends provided by the local government (SOS 2012). In Divilacan, Northern Sierra Madre, Luzon, rangers receiving bat conservation training have elevated bat roost protection to the top priority in their regular monitoring activities (SOS 2012).

12.6.6 Stakeholder Engagement and Citizen Science

Collaborative conservation is more likely to be sustainable. In community-based conservation management, stakeholders from a variety of factions within the community are required to work together to implement effective conservation practices. This often creates unlikely partnerships that bridge normal political, socioeconomic and religious divides. For example, former rebels work with local government officials to monitor bats in southern Mindanao, Philippines, a region known for often violent stand-offs between the Philippine government and Islamic separatists (LM Paguntalan pers. comm., SOS 2012). Uniting stakeholders toward the common goal of bat conservation, however, creates collaborative programs that prove to be robust to the changes that commonly lead to the demise of wildlife conservation programs (e.g. change in political administrations).

Validity of data. A frequent concern when working with citizen scientists, is that data gathered by untrained biologists may be less accurate and obscure the signal that is being studied (reviewed in Johnson 2008). However, community-based bat counts are perhaps a best case scenario for the use of citizen science. The data gathered are the number of bats observed, requiring just the ability to count and no other special training or equipment. Because bats, especially fruit bats, tend to aggregate, the population being counted is all in one place, by-passing many sources of error arising from sampling approaches to abundance assessment. Finally, the goal of community-based counts is detection of population trends across time, so that local communities can track impacts that hunting may be causing. Studies of count error in untrained observers show that while training and experience has a positive effect on count accuracy, counts made by untrained observers are as likely to detect population trend direction as those made by experienced biologists (Mildenstein 2012; Mildenstein and Mills 2013; Barlow et al. 2015).

Case studies. Population monitoring and roost protection for *P. rufus* in Madagascar provides a good example of the effectiveness of citizen science and participatory conservation efforts. Following the decline in populations of *P. rufus* in Madagascar from overhunting and habitat loss, the NGO Madagasikara Voakajy engaged local communities at four roost sites for the protection of the species. With the help of the local government, roost sites were designated for protection and firebreaks with bare ground areas constructed around roost sites. Local volunteers where trained to monitor the roosts of *P. rufus* using binoculars and hand tally counters and have continued to do so. In addition, the engagement of local people led to an interesting partnership where habitat restoration through tree planting is ongoing, while local farmers receive support through a crop seed loan system. Similarly, the local community is enforcing sustainable land use within the protected roost areas. The project organizers ascribe the success of the project to environmental education and outreach efforts, highlighting the benefits of local community engagement through citizen science and partnerships that improve local economies (Mahefatiana Ralisata pers. comm.).

In Asia, Filipinos for Flying Foxes also trains local bat stakeholders as citizen scientists. By providing these community members with the skills and experience to monitor their bat populations, the project is encouraging local stakeholders to conduct regular counts and to self-regulate their hunting pressure. So far, the project has visited more than 35 communities near to fruit bat roosts, and trained more than 200 local stakeholders in surveying and monitoring techniques. It is encouraging that after training, monitoring has continued by the local communities. Twelve communities have counted bats subsequent to training, and five of these have regularly conducted annual counts for 10 years after their training (Mildenstein 2011).

On Guam in the Mariana Islands, *P. mariannus* is a threatened species that must be monitored regularly by the US government under the US Endangered Species Act. Guam's last colony of *P. mariannus* has declined precipitously since the establishment of the invasive brown treesnake (*Boigia irregularis*, USFWS 2009). In the past 10 years the bats have no longer been aggregating in the historical colony location but rather are seemingly scattered in the forest, making population abundance assessments using traditional roost counting methods impossible. Given limited human resources and adherence to historical practices, biologists contracting with the US government have conducted fruit bat surveys sequentially using one or two observers from single observation sites in the forest on a survey morning. These surveys yield occasional bat sightings and location information but provide no basis on which to estimate the population size of the bats, which is essential to generate funding and motivate protective management of this formally-recognized USA national endangered species. In 2014, a different approach to surveying was initiated. Using 85 trained citizen scientists placed at observation stations throughout the forest, simultaneous observation permitted a survey of about 10 % of the forest habitat on Andersen Air Force Base. This collaborative project between the University of Guam and the U.S. Navy resulted in the first population size estimate for the threatened *P. mariannus* since the early 2000s. The survey also brought together local stakeholders representing 25 government and non-government organizations (including schools, environmental clubs, hunters, and local media) toward the common goal of supporting the conservation of a local endangered species (Fig. 12.4; Mildenstein et al. 2014).

Fig. 12.4 Citizen science support enabled the first population count of Mariana fruit bats on Andersen Air Force, Guam in nearly a decade. (Survey participants are showing the number of bats they counted on their raised fingers) (*credit* SSgt. M. White)

12.7 Recommendations for Conservation of Hunted Bats

12.7.1 *More Research is Needed to Understand Hunting Impacts*

One of the major challenges to bat conservation is lack of knowledge of how hunting affects bats, their population size, and distribution. Collecting these data requires trained biologists, sociologists, statisticians, and well-planned survey techniques and questionnaires that can address sensitive questions. For many regions and species, there is little or no population information on bats, so that population trends are unknown. Managers are therefore encouraged to start monitoring programs by which hunting impacts on population size can be tracked over time. Some bat conservation initiatives provide useful models for population size assessment and monitoring (e.g. Southeast Asian Bat Conservation Research Unit, Filipinos for Flying Foxes, WCS Malaysia, United States Department of Defense in the Mariana Islands, FFI Cambodia). Using the population size estimation and monitoring described, more studies are also needed that investigate the direct and indirect impacts of hunting on bat populations. For example, long term monitoring projects of both people and bats, could show trends in the correlations between number of hunted bats and bat population responses.

Finally, more needs to be learned about the people hunting bats and the conditions that lead to increased hunting (Cawthorn and Hoff 2015). If it is understood why people hunt (e.g. for protein? for livelihoods? to vary their diet? for

Fig. 12.5 Members of the women's peanut cooperative in Madagascar, which grows peanuts to supplement local protein supplies and uses a portion of the proceeds to pay rangers to protect fruit bat roosts (Razafimanahaka 2013)

tradition?) and what are the patterns in hunting intensity (e.g. seasonal, food insecurity), conservation managers can find creative solutions for mitigating hunting impacts (e.g. Razafimanahaka 2013; Fig. 12.5).

12.7.2 Research to Understand How to Protect Bats

There is a need to evaluate methods employed in bat protection programs. For example, roost site protection has been correlated with greater bat density (Mildenstein 2012). It is important to follow this up with research that demonstrates the effectiveness of this strategy and advises managers how to proceed. Important questions are: what is the bats' fidelity to protected roost sites? How quickly do bat populations increase with roost site protection? How quickly do bats become habituated to human presence?

Protection of habitat outside the roost area is also important, although much more difficult to enforce. Studies of the relationship between foraging habitat and bat population sizes would guide managers in their habitat-based conservation strategies.

Equally important is to understand where protection efforts are failing. There are many examples of regulated bat hunting leading to population declines. It is important to understand where laws and implementation are falling short and why.

12.7.3 Education/Outreach

Education and outreach in local communities is essential to successful hunting management campaigns. Many hunters do not perceive bats as a limited resource and are unaware of the effect they may be having on bat species' extinction risks. An obvious first step to bat conservation in hunted areas is therefore the dissemination of information on the bat population size, basic biology, and monitoring techniques, so that hunters can assess the impacts they are having.

Local communities should understand the benefits of bats and the valuable ecological services they provide, including their contribution to forest regeneration through seed dispersal. Communities that appreciate bats may be more likely to pursue conservation management. If people understand the array of risks of ignoring declining populations, they will be more inclined to exert effort to protect bats.

Local communities should also understand the human health risks of bat hunting and consumption. Bat handling, trade, preparation, and consumption by humans create a direct transmission route for disease spillover into human communities and warrants consideration in bat protection programs. Education about these risks is needed, as only a small percentage of participants in bat hunting and trade are aware of their risk of exposure to disease in Asia (Harrison et al. 2011) and Africa (Subramanian 2012). Finding a balance between the needs for bat conservation, sustainable harvesting and public health management is an important approach in the regions where regulated bat hunting is a goal (Halstead 1977).

Change in perceptions and attitudes towards conservation and wildlife in general require an effective outreach approach. Thus, education and public awareness projects should be designed to engage the audience as has been demonstrated to be effective in Madagascar (Racey 2013) and Latin America (Navarro 2013). The involvement of all stakeholders and policy makers in conservation outreach projects is crucial to the effectiveness of education programs by facilitating the enactment and enforcement of protective legislation (Robinson et al. 2010).

12.7.4 Protect Colony Locations at the Roost

Bat conservation through roost protection by local communities has been demonstrated to be effective for the recovery of previously declining populations (Mildenstein 2012; Fig. 12.6). The adoption of such roost protection programs in other countries could hold the key to sustaining populations. This is especially true for areas where fruit bat hunting is intense. If successful roost site protection programs could be demonstrated and published, these could be used as models for other areas (e.g. *P. rufus* populations in Madagascar—M. Ralisata pers. comm.; *P. vampyrus* in Malaysia, M. Gumal, pers. comm.; *P. vampyrus* and *A. jubatus* populations in the Philippines, SOS 2012).

Fig. 12.6 Tourists viewing formerly hunted fruit bats at their protected roost site in Mambukal Resort, Negros Occidental, Philippines (*credit* LM Paguntalan)

12.7.5 Regulated Hunting

In many areas where hunted bats are threatened, hunters do not want to extirpate bat populations, but they also do not want to lose the ability to hunt bats (Mildenstein 2012; Cawthorn and Hoffman 2015). In fact, some roost site protection campaigns are successful, because hunting outside the roost site is not discussed or prohibited, making it easier for hunters to respect roost site sanctuaries (T. Mildenstein pers. obs.; SOS 2012). Once communities understand that human disturbance has population-level impacts and that conservation management must balance negative impacts with the bats' innate ability to add to their population, community-level planning of a sustainable hunting program can ensue. Targets must be established for minimum population sizes and numbers of viable populations before hunting can be allowed. After thresholds are reached, sustainable harvest levels must be determined using adaptations of the well-developed harvest management practices for other species.

Finally, an effective enforcement and harvest regulation program must be designed that starts out conservatively, carefully tracking impacts of hunting on bat populations and making adjustments to hunting allowances as needed. Halstead (1977) described how regulated hunting of *E. helvum* at the University of Ile Ife in south western Nigeria can be mutually beneficial to the bat population, local community livelihoods, and managers of property where roosts are present. In places where hunting laws are in place but not respected or enforced, education and outreach are instrumental in garnering public support (as Madagasikara Voakajy has done for roosts of *P. rufus* in Madagascar).

12.7.6 Encourage Local Researchers and NGO's

A key to effective and sustainable conservation is to develop the capacity of local people, including local researchers and the establishment of local NGOs (Racey 2013). Few detailed studies report reliable estimates of bat hunting impacts on bat populations. Some studies may indeed have been conducted but remain as Masters or PhD theses or published as grey literature or in local journals, thereby limiting the distribution of such information. Because valuable results are not often published or accessible, current efforts to revise species account entries in the IUCN Red List have had to rely heavily on experts gathering unpublished information to determine conservation priorities for hunted species (T. Mildenstein, unpublished data). It is important that biologists are encouraged to publish their findings, even in lesser developed countries where there are few if any personal incentives for doing so (Milner-Gulland et al. 2010).

Finally, the establishment of local non-profit organizations creates a network for stakeholders and a bridge between local interests and conservation management. Such organizations play a critical role in ensuring the sustainability of conservation projects across political administration changes by engaging the local stakeholders and coordinating conservation activities in harmony with local needs (e.g. Figs. 12.5 and 12.6).

12.8 Conclusion

Conservation biologists' understanding of the role hunting plays in bat population declines has changed over the last three decades. Conservation concerns were originally focused on large scale hunting operations and especially international commercial trade (e.g. *Pteropus* spp. in the Pacific and Southeast Asia). After international trade was largely shut down in the late 1980s, conservation managers turned their attention to hunting within countries, still focusing on commercially hunted species as a highest priority (e.g. Mickleburgh et al. 1992).

Although commercially harvested species are still a high priority today, conservationists' concerns are no longer limited to species found in markets. With more research and experience, conservation managers have become increasingly aware of the negative impacts caused by hunting even on small scales, i.e. for personal use and/or local trade. Especially detrimental is hunting at roost sites, which can lead to a tenfold increase in population declines (Mildenstein 2012). This is probably because hunting disturbance at roosts also affects non-target individuals, including mothers and babies which are especially sensitive to disturbance. For hunted bat taxa (e.g. Old World fruit bats), hunting now ranks as a top threat among bat conservation biologists.

Research that quantifies the relationship between hunting rates and bat population declines is still lacking, but general awareness about the breadth of bat hunting effects has increased. The number of bat species known to be hunted is larger than in earlier reviews. Similarly, biologists now recognize that hunting is usually a threat to bats; the number of species documented as threatened by hunting is much larger now and includes many species that are not commercially hunted. However, for 28 % of the species known to be hunted according to IUCN Red List species accounts, hunting was either not considered to be a threat or not evaluated at all. Finally, information about a quarter (38/167) of the species listed as hunted by this review has come from sources other than the IUCN Red List, where there is no mention of hunting for those species. More research on population sizes and trends, hunting impacts, and effective management tools will provide very important information for bat conservation.

Research should also address the role of bat meat in local people's diets. Studies that focus on seasonal patterns in bat consumption and the dependency on bats as a source of protein would provide managers with information that would guide policy and conservation actions complementary to the dietary needs of local communities. Similarly, research on the use of bats for medicinal purposes should investigate patterns of bat use and ailments that bat consumption is said to cure. Study of the effects of bat use on ailing consumers in situ as well as in randomized trials could play a significant role in conservation by helping tease out whether the medicinal properties of bats have a real effect or are a myth. These investigations should begin with asthma and other chest complaints since anecdotes about the curative effects of bats for such conditions are widespread across the Old World tropics.

Along with conservation-focused research, public education and capacity building of local managers must also be encouraged to counter what is clearly a major threat to bat populations in the Old World tropics. Greater awareness about bats' reproductive characteristics of one young a year together with the ecological services bats provide will strengthen local communities' commitment to supporting conservation management. Hunters, in particular, begin to cooperate, even tracking their harvest rates as a community, when they realize that bats are a limited resource and that populations may be extirpated altogether if hunting pressure is not halted or highly regulated (Mildenstein 2011). Local managers can be empowered to track bat conservation and hunting with training in the simple and inexpensive field techniques needed to monitor bat population abundance, and these local stakeholders are key to creating sustainable monitoring programs.

Hunting has already led to the loss of four bat species in the last few decades. Without research, public education and awareness, and bolstering local managers' capacity to protect bats, unregulated hunting may well claim more many species.

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Appendix. List of Hunted Bat Species Showing Primary Use (Food or Medicine), Summarized by Region and Country. We Followed IUCN Regional Classification

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
East Asia	China	*Cynopterus sphinx*	*LC*		x	Bates et al. (2008d), Mickleburgh et al. (2009)
	China	*Eonycteris spelaea*	*LC*	x		Francis et al. (2008c), Stebbings (1987)
	China	*Hipposideros pomona*	*LC*	x	x	Bates et al. (2008a)
	China	*Pteropus giganteus*	*LC*	x	x	Molur et al. (2008a), Mickleburgh et al. (2009)
	China	*Rousettus leschenaultii*	*LC*	x	x	Molur et al. (2002), Bates and Helgen (2008), Mickleburgh et al. (2009)
	Japan	*Pteropus pselaphon*	*CR*	x		Ishii and Maeda (2008)
	Taiwan	*Pteropus dasymallus*	*NT*	x		Heaney et al. (2008d)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
North Africa	Algeria, Morocco, Tunisia, Libya	*Myotis punicus*	*NT*		x	Aulagnier et al. (2008)
	Algeria, North Africa	*Myotis emarginatus*	*LC*		x	Hutson et al. (2008h)
	North Africa	*Myotis capaccinii*	*VU*		x	Hutson et al. (2008g)
	North Africa	*Myotis nattereri*	*LC*		x	Hutson et al. (2008a)
Oceania	American Samoa, Cook Islands and Niue, Fiji, New Caledonia, Vanuatu	*Pteropus tonganus*	*VU*	x		Hamilton and Helgen (2008),
	American Samoa, Fiji, Samoa	*Pteropus samoensis*	*NT*	x		Brooke and Wiles (2008)
	Fiji	*Mirimiri acrodonta/ Pteralopex acrodonta*	*CR*			Flannery (1995b)
	Fiji, Vanuatu	*Chaerephon bregullae/ Tadarida bregullae*	*EN*	x		Flannery (1995b), Palmeirim (2014)
	Fiji, Vanuatu	*Notopteris macdonaldi*	*VU*	x		Flannery (1995b), Palmeirim et al. (2007), Palmeirim (2008)
		Pteropus ualanus	*VU*	x		Wiles et al. (2008)
	Indonesia, Papua New Guinea	*Dobsonia moluccensis*	*LC*	x		Hutson et al. (2008j)
	Micronesia, Federated States of	*Pteropus yapensis*	*VU*	x		Wiles et al. (2008b)
	Micronesia, Federated States of; Caroline Islands	*Pteropus insularis/ Pteropus phaeocephalus*	*CR*	x		Helgen and Wiles (2010)
	Micronesia	*Pteropus molossinus*	*VU*	x		Buden et al. (2008)
	Micronesia, Guam and Commonweatlh of Northern Mariana Islands	*Pteropus mariannus*	*EN*	x		Falanruw and Manmaw (1992), Allison et al. (2008), Lemke (1992)
	New Caledonia	*Notopteris neocaledonica*	*VU*	x		Brescia (2008a), Boissenin and Brescia (2007)
	New Caledonia	*Pteropus ornatus*	*VU*	x		Brescia (2008b)
	New Caledonia	*Pteropus vetulus*	*VU*	x	x?	Brescia (2008c), Flannery (1995b)
	Palau	*Pteropus pelewensis*	*NT*	x		Wiles (2008), Wiles et al. (1997)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
	Papau New Guinea	*Pteropus hypomelanus*	*LC*	x		Francis et al. (2008a), Fujita and Tuttle (1991), Fujita (1988)
	Papau New Guinea	*Aproteles bulmerae*	*CR*	x		Flannery (1995b), Hutson et al. (2008m)
	Papau New Guinea	*Miniopterus magnater*	*LC*	x		Bonaccorso and Reardon (2008b), Cuthbert (2003a, b)
	Papau New Guinea	*Nyctimene aello*	*LC*	x		Bonaccorso and Helgen (2008), Cuthbert (2003a, b)
	Papau New Guinea	*Nyctimene cyclotis*	*DD*	x		Cuthbert (2003a)
	Papau New Guinea	*Pteralopex flanneryi*	*CR*	x		Helgen et al. (2008a)
	Papau New Guinea	*Pteropus neohibernicus*	*LC*	x		Salas et al. (2008)
	Papau New Guinea	*Rousettus amplexicaudatus*	*LC*	x		Csorba et al. (2008g), Utzurrum (1992)
	Papau New Guinea	*Syconycteris australis*	*LC*	x		Cuthbert (2003a)
	Papau New Guinea, possibly Cambodia and Vietnam	*Miniopterus pusillus*	*LC*	x		Cuthbert (2003a, b)
	Papau New Guinea, Solomon Islands	*Pteralopex anceps*	*EN*	x		Helgen et al. (2008c)
	Papau New Guinea, Vanuatu	*Miniopterus macrocneme*	*DD*	x		Bonaccorso and Reardon (2008a)
	Solomon Islands	*Pteralopex atrata*	*EN*	x		Helgen and Hamilton (2008b)
	Solomon Islands	*Pteralopex taki*	*EN*	x		Hamilton et al. (2008a)
	Solomon Islands	*Pteropus cognatus*	*EN*	x		James et al. (2008)
	Solomon Islands	*Pteropus nitendiensis*	*EN*	x		Leary et al. (2008a)
	Solomon Islands	*Pteropus rennelli*	*VU*	x		Hamilton et al. (2008b)
	Solomon Islands	*Pteropus tuberculatus*	*CR*	x		Leary et al. (2008b)
	Solomon Islands, Papau New Guinea	*Pteropus rayneri*	*NT*	x		Hamilton and Leary (2008), Bowen et al. (1997)
	Vanuatu	*Emballonura semicaudata*	*EN*	x		Bonaccorso et al. (2008), Chambers and Esrom (1991)
	Vanuatu	*Miniopterus tristis*	*LC*	x		Chambers and Esrom (1991)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
	Vanuatu	*Pteropus anetianus*	*VU*	x		Mickleburgh et al. (1992), Helgen and Hamilton (2008a), Chambers and Esrom (1991)
	Vanuatu	*Pteropus fundatus*	*EN*	x		Helgen and Hamilton (2008c), Chambers and Esrom (1991)
	Vanuatu, others?	*Aselliscus tricuspidatus*	*LC*	x		Bonaccorso et al. (2008), Chambers and Esrom (1991)
	Vanuatu, Papua New Guinea	*Miniopterus australis*	*LC*	x		Chambers and Esrom (1991)
South America	Bolivia	*Artibeus sp.*	*LC*			Lizarro et al. (2010)
	Bolivia	*Carollia perspicillata*	*LC*	x		Lizarro et al. (2010)
	Bolivia	*Desmodus rotundus*	*LC*			Lizarro et al. (2010)
	Bolivia	*Myotis sp.*	?			Lizarro et al. (2010)
	Brazil	*Glossophaga sp.*	*LC or DD*	x		Mickleburgh et al. (2009)
	Brazil	*sp. 1*		x		Lévi-Strauss (1979), Setz and Sazima (1987), Setz (1991)
	Brazil	*sp. 2*		x		Lévi-Strauss (1979), Setz and Sazima (1987), Setz (1991)
	Brazil	*sp. 3*		x		Lévi-Strauss (1979), Setz and Sazima (1987), Setz (1991)
South Asia	Bangladesh	*Pteropus giganteus*	*LC*	x	x	Mickleburgh et al. (2009), Molur et al. (2008a)
	India	*Hipposideros speoris*	*LC*		x	Molur et al. (2008b)
	India	*Latidens salimalii*	*EN*	x		Molur and Vanitharani (2008)
	India	*Megaderma lyra*	*LC*	x	x	Csorba et al. (2008a)
	India	*Megaderma spasma*	*LC*	x	x	Csorba (2008e)
	India	*Nyctalus montanus*	*LC*		x	Molur and Srinivasulu (2008)
	India	*Pteropus faunulus*	*VU*		x	Kingston et al. (2008); Singaravelan et al. (2009)
	India	*Pteropus melanotus*	*VU*	x		Hutson et al. (2008d), Mickleburgh et al. (2009)
	India	*Taphozous melanopogon*	*LC*	x		Csorba et al. (2008f), Molur et al. (2002)
	India	*Taphozous theobaldi*	*LC*	x	x	Bates et al. (2008e), Molur et al. (2002)
	India, Sri Lanka	*Hipposideros lankadiva*	*LC*	x	x	Molur et al. (2008c)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
	South Asia wide	*Rousettus leschenaultii*	*LC*		x	Molur et al. (2002), Bates and Helgen (2008), Mickleburgh et al. (2009)
	South Asia wide	*Cynopterus sphinx*	*LC*	x		Bates et al. (2008d), Molur et al. (2002)
South East Asia	Brunei (Borneo), Cambodia, Lao PDR, Malaysia, Thailand, Vietnam	*Chaerephon plicatus/ Tadarida plicata*	*LC*	x		Csorba et al. (2014)
	Brunei, Indonesia, Malaysia, Philippines, Thailand	*Pteropus vampyrus*	*NT*	x		Bates et al. (2008f), Clayton and Milner-Gulland (2000)
	Cambodia, Indonesia, Lao PDR, Philippines, Thailand, Vietnam	*Cynopterus brachyotis*	*LC*	x		Lacerna and Widmann (1999)
	Cambodia, Indonesia, Lao PDR, Thailand, Vietnam	*Cynopterus sphinx*	*LC*	x	x	Bates et al. (2008d), Johnson et al. (2003)
	Cambodia, Philippines, Thailand, Vietnam	*Eonycteris spelaea*	*LC*	x		Mickleburgh et al. (2009)
	Cambodia, Thailand	*Pteropus lylei*	*VU*	x		Bumrungsri et al. (2008b); Mickleburgh et al. (2009)
	Indonesia	*Acerodon celebensis*	*LC*	x		Hutson et al. (2008c), Clayton and Milner-Gulland (2000)
	Indonesia	*Acerodon humilis*	*EN*	x		Hutson et al. (2008b), Clayton and Milner-Gulland (2000)
	Indonesia	*Acerodon mackloti*	*VU*	x		Hutson et al. (2008i)
	Indonesia	*Cheiromeles parvidens*	*LC*	x		Csorba et al. (2008b)
	Indonesia	*Harpyionycteris celebensis*	*VU*	x		Hutson et al. (2008l)
	Indonesia	*Neopteryx frosti*	*EN*	x		Hutson et al. (2008k)
	Indonesia	*Pteropus alecto*	*LC*	x		Bergmans and Rozendaal (1988), Hutson et al. (2008n)
	Indonesia	*Pteropus caniceps*	*NT*	x		Hutson and Helgen (2008a)
	Indonesia	*Pteropus chrysoproctus*	*NT*	x		Hutson and Helgen (2008b)
	Indonesia	*Pteropus griseus*	*DD*	x		Heinrichs and Zahnke (1997)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
	Indonesia	*Pteropus lombocensis*	*DD*	x		Clayton and Milner-Gulland (2000), Helgen and Salas (2008a)
	Indonesia	*Pteropus melanopogon*	*EN*	x		Helgen and Salas (2008b)
	Indonesia	*Pteropus ocularis*	*VU*	x		Helgen and Salas (2008c)
	Indonesia	*Pteropus pohlei*	*EN*	x		Helgen and Bonaccorso (2008a)
	Indonesia	*Pteropus temminckii*	*VU*	x		Helgen and Bonaccorso (2008b)
	Indonesia	*Rousettus bidens*	*VU*	x		Helgen et al. (2008d)
	Indonesia	*Rousettus celebensis*	*LC*	x		Ruedas et al. (2008b)
	Indonesia	*Styloctenium wallacei*	*NT*	x		Ruedas et al. (2010), Mickleburgh et al. (2009)
	Indonesia	*Thoopterus nigrescens*	*LC*	x		Ruedas et al. (2008a), Mickleburgh et al. (2009)
	Indonesia, Thailand	*Rousettus leschenaultii*	*LC*	x	x	Mickleburgh et al. (2009)
	Lao PDR	*Hipposideros scutinares*	*VU*	x		Francis and Bates (2008)
	Lao PDR	*Tadarida latouchei*	*DD*	x		Francis and Maeda (2008)
	Lao PDR, Philippines, Thailand	*Taphozous melanopogon*	*LC*	x		Csorba (2008f), Magnus (2001)
	Lao PDR, Thailand, Vietnam	*Hipposideros armiger*	*LC*	x		Bates et al. (2008b)
	Malaysia	*Cheiromeles torquatus*	*LC*	x		Csorba et al. (2008c)
	Malaysia, Philippines, Thailand	*Pteropus hypomelanus*	*LC*	x		Francis et al. (2008a), Fujita and Tuttle (1991), Fujita (1988)
	Myanmar	*Hipposideros pomona*	*LC*	x	x	Bates et al. (2008a)
	Myanmar	*Rhinolophus marshalli*	*LC*	x		Bates (2003)
	Myanmar, Thailand	*Craseonycteris thonglongyai*	*VU*	x		Bates (2003)
	Philippines	*Acerodon jubatus*	*EN*	x		Mildenstein et al. (2008), Heaney and Heideman (1987)
	Philippines	*Acerodon leucotis*	*VU*	x		Ong et al. (2008b)
	Philippines	*Dobsonia chapmani*	*CR*	x		Heaney et al. (2008b), Heaney and Heideman (1987)
	Philippines	*Eonycteris robusta*	*NT*	x		Ong et al. (2008e)
	Philippines	*Harpyionycteris whiteheadi*	*LC*	x		Ong et al. (2008d), Mickleburgh et al. (2009)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
	Philippines	*Hipposideros coronatus*	*DD*	x		Gomez et al. (2008)
	Philippines	*Hipposideros pygmaeus*	*LC*	x		Heaney et al. (2008a)
	Philippines	*Macroglossus minimus*	*LC*	x		Mickleburgh et al. 2009, Francis et al. (2008b)
	Philippines	*Nyctimene rabori*	*EN*	x		Mickleburgh et al. (2009)
	Philippines	*Ptenochirus jagori*	*LC*	x		Heaney and Heideman (1987)
	Philippines	*Pteropus dasymallus*	*NT*	x		Heaney et al. (2008d)
	Philippines	*Pteropus leucopterus/ Desmalopex leucopterus*	*LC*	x		Ong et al. (2008a)
	Philippines	*Pteropus pumilus*	*NT*	x		Heaney et al. (2008c), Mickleburgh et al. (2009)
	Philippines	*Pteropus speciosus*	*DD*	x		Rosell-Ambal et al. (2008)
	Philippines	*Rhinolophus rufus*	*NT*	x		Ong et al. (2008c)
	Philippines	*Styloctenium mindorensis*	*DD*	x		Esselstyn (2008)
	Philippines, Thailand	*Hipposideros lekaguli*	*NT*	x		Csorba (2008d)
	Philippines, Thailand	*Rousettus amplexicaudatus*	*LC*	x		Csorba (2008g), Utzurrum (1992)
	SE Asia	*Megaderma spasma*	*LC*	x	x	Csorba (2008e)
	Thailand	*Hipposideros halophyllus*	*EN*	x		Bates et al. (2008b)
	Vietnam, Cambodia	*Megaderma lyra*	*LC*	x	x	Csorba et al. (2008a)
Sub Saharan Africa	Unspecified	*Epomophorus labiatus*	*LC*	x		Mickleburgh et al. (2008b)
	Unspecified	*Hipposideros gigas*	*LC*	x		Mickleburgh et al. (2008p)
	Unspecified	*Hipposideros jonesi*	*NT*	x		Mickleburgh et al. (2008g)
	Unspecified	*Hipposideros marisae*	*VU*	x		Mickleburgh et al. (2008h)
	Unspecified	*Hipposideros ruber*	*LC*	x		Mickleburgh et al. (2008i)
	Unspecified	*Hipposideros vittatus*	*NT*	x		Mickleburgh et al. (2008f)
	Unspecified	*Mops midas/Tadarida midas*	*LC*	x		Jenkins et al. (2014)
	Unspecified	*Myotis morrisi*	*DD*	x		Jacobs et al. (2008a)
	Unspecified	*Rhinolophus alcyone*	*LC*	x		Jacobs et al. (2008b)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
	Unspecified	*Rhinolophus guineensis*	*VU*	x		Fahr (2008a)
	Unspecified	*Rhinolophus hillorum*	*NT*	x		Jacobs et al. (2010)
	Unspecified	*Rhinolophus silvestris*	*DD*	x		Cotterill (2008)
	Unspecified	*Rhinolophus ziama*	*EN*	x		Fahr (2008d)
	Unspecified	*Rousettus lanosus*	*LC*	x		Mickleburgh et al. (2008n)
	Unspecified	*Taphozous mauritianus*	*LC*			Hutson et al. (2008e)
	Benin	*Epomophorus gambianus*	*LC*	x		Mickleburgh et al. (2008r)
	Benin, Cameroon, Congo Rep., Cote d'Ivoire, DRC, Equatorial Guinea, Ghana, Liberia, Nigeria, Tanzania, Uganda, Zambia	*Eidolon helvum*	*NT*	x	x	Halstead (1977), Kamins et al. (2011), Mickleburgh et al. (2008l)
	Benin, The Democratic Republic of the Congo, Equatorial Guinea, Nigeria	*Epomops franqueti*	*LC*	x		Colyn et al. (1987), Fa et al. (1995), Juste et al. (1995), Bennett Hennessey (1995)
	Comoros Islands	*Pteropus livingstonii*	*EN*	x		Trewhella et al. (1995)
	Congo Republic	*Lissonycteris angolensis*	*LC*	x		Wilson and Wilson (1991), Mickleburgh et al. (2008c)
	Congo Republic	*Nycteris grandis*	*LC*	x		Mickleburgh et al. (2008k), Bennett Hennessey (1995)
	Côte d'Ivoire	*Chaerephon ansorgei/ Tadarida ansorgei*	*LC*	x		Mickleburgh et al. (2008e)
	Equatorial Guinea	*Micropteropus pusillus*	*LC*	x		Juste et al. (1995), Fa (2000)
	Equatorial Guinea, Nigeria	*Rousettus aegyptiacus*	*LC*	x		Fa et al. (1995), Fa (2000), Benda et al. (2008)
	Guinea	*Hipposideros lamottei*	*CR*	x		Mickleburgh et al. (2008q)
	Guinea	*Rhinolophus maclaudi*	*EN*	x		Fahr (2008b), Fahr et al. (2002), Fahr and Ebigbo (2003)
	Guinea	*Rhinolophus ruwenzorii*	*VU*	x		Fahr et al. (2002), Fahr and Ebigbo (2003), Fahr (2008c)
	Madagascar	*Chaerephon jobimena/ Tadarida jobimena*	*LC*	x		Andriafidison et al. (2014a)

IUCN region	Country in which hunted	Species	Status	Food	Medicine	Source
	Madagascar	*Eidolon dupreanum*	*VU*	x		Andriafidison et al. (2008a), Jenkins and Racey (2008)
	Madagascar	*Emballonura atrata*	*LC*	x		Jenkins et al. (2008b)
	Madagascar	*Hipposideros commersoni*	*NT*	x		Goodman (2006), Jenkins and Racey (2008)
	Madagascar	*Miniopterus gleni*	*LC*	x		Andriafidison et al. (2008b), Goodman (2006), Goodman et al. (2008)
	Madagascar	*Miniopterus majori*	*LC*	x		Jenkins and Rakotoarivelo (2008)
	Madagascar	*Miniopterus manavi*	*LC*	x		Andriafidison et al. (2008c), Golden (2005)
	Madagascar	*Mops leucostigma*	*LC*	x		Andriafidison et al. (2014b)
	Madagascar	*Mormopterus jugularis*	*LC*	x		Andriafidison et al. (2008d)
	Madagascar	*Myzopoda aurita*	*LC*	x		Jenkins et al. (2008a)
	Madagascar	*Pteropus rufus*	*VU*	x		Andriafidison et al. (2008e), Jenkins and Racey (2008)
	Madagascar	*Rousettus madagascariensis*	*NT*	x		Andriafidison et al. (2008f), Jenkins and Racey (2008)
	Madagascar	*Scotophilus robustus*	*LC*	x		Andriafidison et al. (2008g)
	Madagascar	*Triaenops furculus*	*LC*	x		J. Razafimanahaka pers. comm
	Madagascar	*Triaenops rufus*	*LC*	x		Goodman (2006), Andriafidison et al. (2008h)
	Mauritius	*Pteropus niger*	*VU*	x		Hutson and Racey (2013), Mickleburgh et al. (2009)
	Mauritius	*Pteropus rodricensis*	*CR*	x		Mickleburgh et al. (2008d), Mickleburgh et al. (2009)
	Rwanda	*Rhinolophus hilli*	*CR*	x		Fahr (2010)
	São Tomé and Príncipe	*Chaerephon tomensis*	*EN*	x		Carvalho et al. (2014)
	São Tomé and Príncipe	*Miniopterus newtoni*	*DD*	x		Carvalho et al. (2014)
	São Tomé and Príncipe	*Myonycteris brachycephala*	*EN*	x		Carvalho et al. (2014)
	Seychelles	*Pteropus seychellensis*	*LC*	x		Carvalho et al. (2014)
	Tanzania (Pemba)	*Pteropus voeltzkowi*	*VU*	x		Mickleburgh et al. (2008m)
	The Democratic Republic of the Congo, Nigeria	*Hypsignathus monstrosus*	*LC*	x		Mickleburgh et al. (2008j), Mickleburgh et al. (2009)
	Unspecified	*Myotis mystacinus*	*LC*		x	Hutson et al. (2008f)

References

Abdul Aziz S, Olival KJ, Bumrungsri S, Richards GC, Racey PA (2016) The conflict between fruit bats and fruit growers: species, legislation and mitigation. In: Voigt CC, Kingston T (eds), Bats in the Anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp. 377–420

Allison A, Bonaccorso F, Helgen K, James R (2008) *Pteropus mariannus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Andersen WL, Thornberg DD, Whitton RM (1996) Estimating goods harvest in southern Illinois quota zones. Wildl Soc Bull 24:233–237

Andriafidison D, Cardiff SG, Goodman SM et al () *Eidolon dupreanum*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2008b) *Miniopterus gleni*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2008c) *Miniopterus manavi*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2008d) *Mormopterus jugularis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2008e) *Pteropus rufus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2008f) *Rousettus madagascariensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2008g) *Scotophilus robustus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2008h) *Triaenops rufus*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 18 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2014a) *Chaerephon jobimena*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Andriafidison D, Cardiff SG, Goodman SM et al (2014b) *Mops leucostigma*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Anstey S (1991) Wildlife utilisation in liberia. The findings of a national survey 1989–1990. Report for WWF-UK, Godalming, UK

Aulagnier S, Juste J, Karataş A et al. (2008) *Myotis punicus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Banack SA (1996) Flying foxes, genus *Pteropus*, in the Samoan Islands: interactions with forest communities. Dissertation. University of California, California

Banack SA (1998) Diet selection and resource use by flying foxes (genus Pteropus). Ecol 79:1949–1967

Barlow KE, Briggs PA, Haysom KA et al (2015) Citizen science reveals trends in bat populations: the national bat monitoring programme in Great Britain. Biol Conserv 182:14–26

Bat Conservation International (2015) 1331 and counting. Bats magazine. Winter 2015. P 16

Bates PJJ (2003) Conservation Status of the Bat and Bird Fauna of the Limestone Karst Areas of Mon and Kayin States, Myanmar (Burma). Unpublished Report for Fauna and Flora International 100 % Fund, Fauna and Flora International, Cambridge, UK

Bates P, Helgen K (2008) *Rousettus leschenaultii*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Bates P, Bumrungsri S, Csorba G et al (2008a) *Hipposideros pomona*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 21 Mar 2015

Bates P, Bumrungsri S, Francis C, Csorba G (2008b) *Hipposideros armiger*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Bates P, Bumrungsri S, Francis C et al (2008c) *Hipposideros halophyllus*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Bates P, Bumrungsri S, Molur S, Srinivasulu C (2008d) *Cynopterus sphinx*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Bates P, Bumrungsri S, Walston J et al. (2008e) *Taphozous theobaldi*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Bates P, Francis C, Gumal M et al. (2008f) *Pteropus vampyrus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Benda P, Aulagnier S, Hutson AM et al (2008) *Rousettus aegyptiacus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Bennett Hennessey A (1995) A study of the meat trade in Ouesso, Republic of Congo. Wildlife Conservation Society, New York

Bergmans W, Rozendaal FG (1988) Notes on collections of fruit bats from Sulawesi and some off-lying islands (Mammalia, Megachiroptera). Verh Leiden 248:5–74

Boissenin M, Brescia F (2007) Inventaire des colonies de mégachiroptère en Province nord de la Nouvelle-Calédonie. Institut Agronomique néo-Calédonien (IAC), Unpublished report

Bonaccorso F, Allison A (2008) *Emballonura semicaudata*. The IUCN Red List of Threatened Species 2008: Version 2014.3. http://www.iucnredlist.org. Downloaded on 18 May 2015

Bonaccorso F, Helgen K (2008) *Nyctimene aello*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Bonaccorso F, Reardon T (2008a) *Miniopterus macrocneme*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Bonaccorso F, Reardon T (2008b) *Miniopterus magnater*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Bonaccorso F, Leary T, Hamilton (2008) *Aselliscus tricuspidatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Bowen-Jones E, Abrutut D, Markham B, Bowe S (1997) Flying foxes on Choiseul (Solomon Islands)-the need for conservation action. Oryx 31:209–217

Bradshaw CJA, Sodhi NS, Brook BW (2009) Tropical turmoil: a biodiversity tragedy in progress. Front Ecol Environ 7:79–87

Brashares JS, Arcese P, Sam MK et al (2004) Bushmeat hunting, wildlife declines, and fish supply in west Africa. Science 306:1180–1183

Brescia F (2007) Amélioration des connaissances et recommandations pour la sauvegarde des populations de mégachiroptères (roussettes) en Province Nord de la Nouvelle-Calédonie. Institut Agronomique néo-Calédonien, Unpublished report

Brescia F () *Notopteris neocaledonica*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Brescia F (2008b) *Pteropus ornatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Brescia F (2008c) *Pteropus vetulus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Brooke AP (2001) Population status and behaviours of the Samoa flying fox, *Pteropus samoensis*, on Tutuila Island, American Samoa. J Zool 254:309–319

Brooke AP, Tschapka M (2002) Threats to overhunting of the flying fox *Pteropus tonganus* (Chiroptera: Pteropodidae) on Niue Island, South Pacific Ocean. Biol Conserv 103:343–348

Brooke A, Wiles G (2008) *Pteropus samoensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Brooke AP, Solek C, Tualaulelei A (2000) Roosting behavior of colonial and solitary flying foxes in American Samoa (Chiroptera: Pteropodidae). Biotropica 32(2):338–350

Buden D, Wiles G, Helgen K et al (2008) *Pteropus molossinus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Bumrungsri S, Harbit A, Benzie C, Carmouche K, Sridith K, Racey PA () The pollination ecology of two species of *Parkia* (Mimosaceae) in southern Thailand. J. Tropl Ecol 24:467–475

Bumrungsri S, Suyanto A, Francis C (2008b) *Pteropus lylei*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Bumrungsri S, Spraoiaya E, Chongsiri I, Sridith K, Racey PA (2009) Does no bat mean no durian—the pollination ecology of semi-wild durian (*Durio zibethinus* L.) in Southern Thailand. J Trop Ecol 25:85–92

Calisher CH, Childs JE, Field H E, Holmes KV, Schountz T (2006). Bats: important reservoir hosts of emerging viruses. Clinical microbiology reviews, 19(3):531–545

Carvalho M, Palmeirim JM, Rego FC et al (2014) What motivates hunters to target exotic or endemic species on the island of São Tomé, Gulf of Guinea? Oryx 1–9

Cawthorn DM, Hoffman LC (2015) The bushmeat and food security nexus: a global account of the contributions, conundrums and ethical collisions. In press at Food Security International, 20 pp

Chambers MR, Esrom D (1991) The fruit bats of Vanuatu. Bat News 20:4–5

Clayton L, Milner-Gulland EJ (2000) The trade in wildlife in north Sulawesi, Indonesia. In: Robinson JG, Bennett E (eds) Hunting for sustainability in tropical forests. Columbia University Press, New York, pp 473–496

Cleveland CJ, Betke M, Federico P et al (2006) Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. Front Ecol Environ 4:238–243

Colyn M, Dudu A, Mbaelele M (1987) Exploitation du petit et moyen gibier des forests ombrophiles du Zaire. Nat et Faune 3:22–39

Cotterill FPD (2008) *Rhinolophus silvestris*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Craig P, Morrell TE, So'Oto K (1994a) Subsistence harvest of birds, fruit bats and other game in American Samoa, 1990–1991. Pac Sci 48:344–352

Craig P, Trail P, Morrell TE (1994b) The decline of fruit bats in American Samoa due to hurricanes and overhunting. Biol Conserv 69:261–266

Craig P, Syron W (1992) Fruit bats in American Samoa: their status and future. In: Wilson DE, Graham GL (eds) Pacific Island Flying Foxes: Proceedings of an International Conservation Conference pp. 145–149

Csorba G, Bates P, Molur S, Srinivasulu C (2008a) *Megaderma lyra*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Csorba G, Bumrungsri S, Francis C et al (2008b) *Cheiromeles parvidens*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Csorba G, Bumrungsri S, Francis C et al (2008c) *Cheiromeles torquatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Csorba G, Bumrungsri S, Francis C et al (2008d) *Hipposideros lekaguli*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Csorba G, Bumrungsri S, Francis C et al (2014). *Chaerephon plicatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Csorba G, Bumrungsri S, Helgen K et al (2008e) *Megaderma spasma*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Csorba G, Bumrungsri S, Helgen K et al (2008f) *Taphozous melanopogon*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 21 Mar 2015

Csorba G, Rosell-Ambal G, Ingle N (2008g) *Rousettus amplexicaudatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Cuthbert R (2003a) The impact of hunting on wildlife populations in Papua New Guinea: report 2. Unpublished Report for Fauna and Flora International 100 % Fund, Fauna and Flora International, Cambridge, UK

Cuthbert R (2003b) The sustainability of hunting in Papua New Guinea: a preliminary analysis. Unpublished Report for Fauna and Flora International 100 % Fund, Fauna and Flora International Cambridge, UK

Dougnon TJ, Djossa BA, Youssao I et al (2012) Bats as bushmeat in Benin: yield in carcass and meat quality of the fruit bats *Eidolon helvum* (Kerr, 1792) and *Epomophorus gambianus* (Ogilby, 1835). Int J Sci Adv Technol 2:81–90

Epstein JH, Olival KJ, Pulliam JRC et al (2009) *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. J App Ecol 46:991–1002

Esselstyn J (2008) *Styloctenium mindorensis*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Esselstyn JA, Amar A, Janeke D (2006) Impact of post-typhoon hunting on Mariana fruit bats (*Pteropus mariannus*). Pac Sci 60:531–539

Fa JE (2000) Hunted animals in Bioko Island, West Africa: sustainability and future. In: Robinson JG, Bennett E (eds) Hunting for sustainability in tropical forests. Columbia University Press, New York, pp 168–198

Fa JE, Juste J, Perez De Val J, Castroviejo J (1995) Impact of market hunting on mammal species in Equatorial Guinea. Conserv Biol 9:1107–1115

Fahr J () *Rhinolophus guineensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Fahr J (2008b) *Rhinolophus maclaudi*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Fahr J (2008c) *Rhinolophus ruwenzorii*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Fahr J (2008d) *Rhinolophus ziama*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Fahr J (2010) *Rhinolophus hilli*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Fahr J, Ebigbo NM (2003) A conservation assessment of the bats of the Simandou Range, Guinea, with the first record of Myotis welwitschii (Gray 1866) from West Africa. Acta Chiropterol 5:125–141

Fahr J, Vierhaus H, Hutterer R, Kock D (2002) A revision of the *Rhinolophus maclaudi* species group with the description of a new species from West Africa (Chiroptera: Rhinolophidae). Myotis 40:95–126

Falanruw M (1988) On the status, reproductive biology, and management of fruit bats in Yap. Micronesica 21:39–51

Falanruw MC, Manmaw CJ (1992) Protection of flying foxes on Yap Islands. In: DE Wilson, GL Graham (eds), Proceedings of an international conservation conference on pacific island flying foxes, US Fish and Wildlife Service Biological Report 90(23). US Department of the Interior, Fish and Wildlife Service, Washington, DC, pp 150–154

Flannery T (1995a) Mammals of New Guinea (Revised and Updated Edition). Reed Books, Chatswood,

Flannery TF (1995b) Mammals of the South-West Pacific, Moluccan Islands. Reed Books, Chatswood, Australia and Cornell University Press, Ithaca, USA

Francis C, Bates P (2008) *Hipposideros scutinares*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Francis C, Maeda K (2008) *Tadarida latouchei*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Francis C, Rosell-Ambal G, Bonaccorso F et al. (2008a) *Pteropus hypomelanus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Francis C, Rosell-Ambal G, Sedlock J et al. (2008b) *Macroglossus minimus*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Francis C, Rosell-Ambal G, Tabaranza B et al. (2008c) *Eonycteris spelaea*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Fujita M (1988) Flying foxes and economics. BATS 6:4–9

Fujita MS, Tuttle MD (1991) Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. Conserv Biol 5:455–463

Funmilayo O (1978) Fruit bats for meat: are too many taken? Oryx 14:377–378

Golden CD (2005) Eaten to endangerment: mammal hunting and the bushmeat trade in Madagascar's Makira Forest. Undergraduate Thesis, Harvard University

Gomez R, Ong P, Rosell-Ambal G et al (2008) *Hipposideros coronatus*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Goodman SM (2006) Hunting of microchiroptera in southwestern Madagascar. Oryx 40:225–228

Goodman SG, Ratrimomanarivo FH, Ranivo J, Cardiff S (2008) The hunting of microchiropteran bats in different portions of Madagascar. Afri Bat Conserv News 16:4–7

Gumal MT (2004) Diurnal home range and roosting trees of a maternity colony of *Pteropus vampyrus natunae* (Chiroptera: Pteropodidae) in Sedilu, Sarawak. J Trop Ecol 20:247–258

Halstead LB (1977) Fruit bats—an example of wildlife management. Nigerian Field 42:50–56

Hamilton S, Helgen K (2008) *Pteropus tonganus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Hamilton S, Leary T (2008) *Pteropus rayneri*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hamilton S, Helgen K, James R et al. (2008a) *Pteralopex taki*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hamilton S, Helgen K, Pilgrim J (2008b) *Pteropus rennelli*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Harrison ME, Cheyne SM, Darma F et al (2011) Hunting of flying foxes and perception of disease risk in Indonesian Borneo. Biol Conserv 144:2441–2449

Hayman DTS, McCrea R, Restif O et al (2012) Demography of straw-colored fruit bats in Ghana. J Mammal 93(5):1393–1404. doi:10.1644/11-MAMM-A-270.1

Heaney LR, Heideman PD (1987) Philippine fruit bats: endangered and extinct. BATS 5:3–5

Heaney L, Balete D, Ong P et al (2008a) *Hipposideros pygmaeus*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Heaney L, Ong P, Tabaranza B et al. (2008b) *Dobsonia chapmani*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Heaney L, Rosell-Ambal G, Tabaranza B et al (2008c) *Pteropus pumilus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Heaney L, Rosell-Ambal G, Tabaranza B, Izawa M (2008d) *Pteropus dasymallus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Heideman PD, Heaney LR (1992) Acerodon jubatus species account. In: Mickleburgh SP, Hutson AM, Racey PA (eds) Old world fruit bats: an action plan for their conservation. IUCN/SSC Chiroptera Specialist Group, Switzerland, pp 37–38

Heinrichs S (2004) Sulawesi fruit bat conservation and education campaign. Unpublished report for the Fauna and Flora International 100 % Fund, Fauna and Flora International, Cambridge, UK

Heinrichs S, Zahnke K (1997) The fruit bats of Sulawesi. BATS 15:11–15

Helgen K, Allison A (2008) *Pteropus howensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Nov 2014

Helgen K, Bonaccorso F (2008a) *Pteropus pohlei*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen K, Bonaccorso F (2008b) *Pteropus temminckii*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen KM, Flannery TF (2002) Distribution of the endangered Pacific sheathtail bat *Emballonura semicaudata*. Aust Mammal 24:209–212

Helgen K, Hamilton S (2008a) *Pteropus anetianus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen K, Hamilton S (2008b) *Pteralopex atrata*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen K, Hamilton S (2008c) *Pteropus fundatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Helgen K, Salas L (2008a) *Pteropus lombocensis*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Helgen K, Salas L (2008b) *Pteropus melanopogon*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen K, Salas L (2008c) *Pteropus ocularis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen K, Wiles G (2010) *Pteropus insularis*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Helgen K, Hamilton S, Leary T (2008a) *Pteralopex flanneryi.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen K, Hamilton S, Leary T, Bonaccorso F (2008b) *Pteralopex anceps*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Helgen K, Kingston T, Ruedas L, Maharadatunkamsi D (2008c) *Rousettus bidens.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hines JM, Hungerford HR, Tomera AN (1987) Analysis and synthesis of research on responsible environmental behavior: a meta-analysis. J Environ Educ 18:1–8

Hutson AM, Helgen K (2008a) *Pteropus caniceps*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Helgen K (2008b) *Pteropus chrysoproctus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Racey PA (2013) *Pteropus niger*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Aulagnier S, Spitzenberger F (2008a) *Myotis nattereri.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 March 2015

Hutson AM, Kingston T, Helgen K (2008b) *Acerodon humilis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Hutson AM, Kingston T, Helgen K, Sinaga U (2008c) *Acerodon celebensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Hutson AM, Kingston T, James D et al (2008d) *Pteropus melanotus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Racey P, Ravino J et al (2008e) *Taphozous mauritianus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Spitzenberger F, Aulagnier S, Coroiu I (2008f) *Myotis mystacinus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Spitzenberger F, Aulagnier S et al (2008g) *Myotis capaccinii*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Spitzenberger F, Aulagnier S, Nagy Z (2008h) *Myotis emarginatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Suyanto A, Helgen K (2008i) *Acerodon mackloti.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Hutson AM, Suyanto A, Helgen K et al (2008j) *Dobsonia moluccensis.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Hutson AM, Suyanto A, Helgen K (2008k) *Neopteryx frosti*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson AM, Suyanto A, Kingston T, Helgen K (2008l) *Harpyionycteris celebensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Hutson T, Helgen K, Flannery T, Wright D (2008m) *Aproteles bulmerae*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Hutson T, Suyanto A, Helgen K et al (2008n) *Pteropus alecto*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 March 2015

Ishii N, Maeda K (2008) *Pteropus pselaphon*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

IUCN (2014) The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 24 Apr 2015

Jacobs D, Cotterill FPD, Taylor PJ (2008a) *Myotis morrisi*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 21 Mar 2015

Jacobs D, Cotterill FPD, Taylor PJ (2008b) *Rhinolophus alcyone*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Jacobs D, Cotterill FPD, Taylor PJ (2010) *Rhinolophus hillorum*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

James R, Hamilton S, Helgen K (2008) *Pteropus cognatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Jenkins RK, Racey PA (2008) Bats as bushmeat in Madagascar. Madagascar Conserv Dev 3(1):22–30

Jenkins RKB, Rakotoarivelo AR (2008) *Miniopterus majori.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Jenkins RK, Racey PA, Andriafidison D, Razafindrakoto N, Razafimahatratra E, Rabearivelo A, Razafimanahaka HJ (2007) Not rare, but threatened: the endemic Madagascar flying fox *Pteropus rufus* in a fragmented landscape. Oryx 41(2):263–271

Jenkins RKB, Rakotoarivelo AR, Ratrimomanarivo FH, Cardiff SG (2008a) *Myzopoda aurita*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Jenkins RKB, Rakotoarivelo AR, Ratrimomanarivo FH, Cardiff SG (2008b) *Emballonura atrata.* The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Jenkins RKB, Racey PA, Ranivo J et al (2014) *Mops midas*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Johnson DH (2008) In defense of indices: the case of bird surveys. J Wildl Manag 72:857–868

Johnson A, Singh S, Dongdala M, Vongsa O (2003) Wildlife hunting and use in the nam ha protected area: implications for rural livelihoods, biodiversity conservation. Wildlife Conservation Society, Vientiane, Lao PDR

Juste J, Fa JE, Perezdel Val J, Castroviejo J (1995) Market dynamics of bushmeat species in Equatorial Guinea. J Appl Ecol 32:454–467

Kamins AO, Restif O, Ntiamoa-Baidu Y et al (2011) Uncovering the fruit bat bushmeat commodity chain and the true extent of fruit bat hunting in Ghana, West Africa. Biol Conserv 144:3000–3008

Kingston T (2016) Cute, creepy or crispy—how values, attitudes and norms shape human behavior toward bats. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp. 571–588

Kingston T, Molur S, Srinivasulu C (2008) *Pteropus faunulus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Lacerna ID, Widmann P (1999) Biodiversity utilisation in a Tagbanua community, southern Palawan, Philippines. In: Goeltenboth F, Milan P, Asio VB (eds), Procedures of the international conference on applied tropical ecology, 8–10 Sept 1998. Visayas State College of Agriculture, BayBay, Leyte, Philippines, pp 52–64

Leary T, Hamilton S, James R (2008a) *Pteropus nitendiensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Leary T, Hamilton S, James R (2008b) *Pteropus tuberculatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Lemke TO (1986) Marianas fruit bats near extinction. BATS 3:1

Lemke TO (1992) Status of the Marianas fruit bat (*Pteropus mariannus*) in the Northern Mariana Islands north of Saipan. In: Proceedings of an international conservation conference on pacific island flying foxes. US Fish and Wildlife Service Biological Report. 90(23)

Leroy EM, Kumulungui B, Pourrut X, Rouquet P, Hassanin A, Yaba P, Swanepoel R (2005) Fruit bats as reservoirs of Ebola virus. Nature 438(7068):575–576

Leroy EM, Epelboin A, Mondonge V, Pourrut X, Gonzalez JP, Muyembe-Tamfum J, Formenty P (2009) Human Ebola outbreak resulting from direct exposure to fruit bats in Luebo, Democratic Republic of Congo, 2007. Vector-Borne Zoonotic Dis 9(6):723–728

Lévi-Strauss C (1979) Tristes Tropicoes. Edicoes 90, Lisbon, Portugal

Lizarro D, Galarza MI, Aguirre LF (2010) Traffic and trade of Bolivian bats. Rev Bol Ecol y Cons Amb 27:63–75

Mackinnon JL, Hawkins CE, Racey PA (2003) Pteropodidae, in Goodman SP, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1299–1302

Magnus N (2001) Bushmeat utilisation in Phu Kheio Wildlife Sanctuary, Northeast Thailand. MSc thesis, University of Alberta, Edmonton, Canada

Mbete RA, Banga-Mboko H, Racey PA et al (2011) Household bushmeat consumption in Brazzaville. Trop Conserv Sci 4:187–202

McConkey KR, Drake DR (2006) Flying foxes cease to function as seed dispersers long before they become rare. Ecol 87:271–276

Mickleburgh SP, Hutson AM, Racey PA (1992) Old world fruit-bats—an action plan for their conservation. IUCN, Gland

Mickleburgh SP, Hutson AM, Racey PA (2002) A review of the global conservation status of bats. Oryx 36:18–34

Mickleburgh SP, Hutson AM, Bergmans W et al. (2008a) *Pteropus aldabrensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Nov 2014

Mickleburgh S, Hutson AM, Bergmans W (2008b) *Epomophorus labiatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W (2008c) *Lissonycteris angolensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W (2008d) *Pteropus rodricensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Cotterill FPD (2008e) *Chaerephon ansorgei*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Cotterill FPD (2008f) *Hipposideros vittatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Fahr J (2008g) *Hipposideros jonesi*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 21 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Fahr J (2008h) *Hipposideros marisae*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 21 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Fahr J (2008i) *Hipposideros ruber*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Fahr J (2008j) *Hypsignathus monstrosus.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Fahr J (2008k) *Nycteris grandis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Fahr J, Racey PA (2008l) *Eidolon helvum*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Howell K (2008m) *Pteropus voeltzkowi*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W, Howell K (2008n) *Rousettus lanosus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W et al (2008o) *Pteropus seychellensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh S, Hutson AM, Bergmans W (2008p) *Hipposideros gigas*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Mickleburgh S, Hutson AM, Bergmans W, Fahr J (2008q) *Hipposideros lamottei*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Mickelburgh S, Hutson AM, Bergmans W (2008r) *Epomophorus gambianus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Mickleburgh SP, Waylen K, Racey PA (2009) Bats as bushmeat: a global review. Oryx 43:217–234

Mildenstein TL (2011) Bat count Philippines, final report to the conservation leadership program. Available on-line at http://www.conservationleadershipprogramme.org/media/2014/11/001706F_Philippines_FinalReport_Bat-Count-Philippines_21stJune2011.pdf

Mildenstein TL (2012) Conservation of endangered flying foxes in the Philippines: effects of anthropogenic disturbance and research methods for community-based conservation. Ph.D. thesis, University of Montana, United States

Mildenstein TL, Mills LS (2013) Mariana fruit bat conservation through research and local capacity building. Final Report for Cooperative Agreement Number: N40192-11-2-8005, prepared for NAVFAC Marianas

Mildenstein TL, Cariño AB, Stier SC (2007) Bat count 2003, final report to conservation leadership programme. Available on-line http://www.conservationleadershipprogramme.org/media/2014/11/001003_2003_Philippines_FR_-Bat-Count-2003.pdf

Mildenstein T, Cariño A, Paul S et al (2008) *Acerodon jubatus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Mildenstein TL, Alexander IR, Miller R (2014) Mariana fruit bat monitoring on Andersen Air Force Base. Final Report for Cooperative Agreement Number: N40192-13-2-8007, prepared for NAVFAC Marianas and U.S. Air Force Base

Mills LS (2012) Conservation of wildlife populations: demography, genetics, and management, 2nd edn. Blackwell Publishing, Oxford

Milner-Gulland EJ, Bennett EL (2003) Wild meat: the bigger picture. Tren Ecol Evol 18:351–357

Milner-Gulland EJ, Fisher M, Browne S, Redford KH, Spencer M, Sutherland WJ et al (2010) Do we need to develop a more relevant conservation literature? Oryx 44:1–2

Molur S, Srinivasulu C (2008) *Nyctalus montanus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Molur S, Vanitharani J (2008) *Latidens salimalii*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Molur S, Marimuthu G, Srinivasulu C et al. (2002) Status of South Asian Chiroptera: Conservation Assessment and Management Plan (C.A.M.P.) Workshop Report. Zoo Outreach Organization/CBSG-South Asia, India

Molur S, Srinivasulu C, Bates P, Francis C (2008a) *Pteropus giganteus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Molur S, Yapa W, Srinivasulu C (2008b) *Hipposideros speoris*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Molur S, Yapa W, Srinivasulu C (2008c) *Hipposideros lankadiva*. The IUCN Red List of threatened species. Version 2015.2. www.iucnredlist.org. Downloaded on 27 July 2015

Navarro L (2013) Communication and education about bats: a powerful tool for changing misconceptions. Under the 43rd international bat research conference. San José, Costa Rica

Nicoll ME, Racey PA (1981) The Seychelles fruit bat *Pteropus seychellensis*. Afr J Ecol 19:361–364

Noureen S (2014) Ecology, roosting habits and reproduction in the Megachiroptera bats of pothwar region, Pakistan. Ph.D. Dissertation, Arid Agriculture University Rawalpindi, 240 pp

Nuno A, St. John FAV (2014) How to ask sensitive questions in conservation: a review of specialized questioning techniques. Biol Conserv 89:5–15

O'Connor T, Riger P, Jenkins RKB (2006) Promoting fruit bat conservation through education in Madagascar. J Int Zoo Educ Assess 42:26–33

Oleksy R, Racey PA, Jones G (2015a) High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. Glob Ecol Cons 3:678–692

Oleksy R, Randrianandrianina F, Jenkins RKB (2015b) Commercial hunting of foraging fruit bats in Western Madagascar. Afr Bat Conserv News 37:3–5

Ong P, Rosell-Ambal G, Tabaranza B et al (2008a) *Pteropus leucopterus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Ong P, Rosell-Ambal G, Tabaranza B et al (2008b) *Acerodon leucotis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 17 Mar 2015

Ong P, Rosell-Ambal G, Tabaranza B, Heaney L (2008c) *Rhinolophus rufus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Ong P, Rosell-Ambal G, Tabaranza B et al (2008d) *Harpyionycteris whiteheadi*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Ong P, Rosell-Ambal G, Tabaranza B et al (2008e) *Eonycteris robusta*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Palmeirim J (2008) *Notopteris macdonaldi*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 March 2015

Palmeirim J (2014) *Chaerephon bregullae*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 15 Mar 2015

Palmeirim JM, Champion A, Naikatini A et al (2007) Distribution, status and conservation of the bats of the Fiji Islands. Oryx 41(4):509–519

Pennisi LA, Holland SM, Stein TV (2004) Achieving bat conservation through tourism. J Ecot 3:195–207

Plowright RK, Eby P, Hudson PJ et al (2015) Ecological dynamics of emerging bat virus spillover. Proc Biol Sci 282:2014–2124

Racey PA (1979) Two bats in the Seychelles. Oryx 15:148–152

Racey PA (2013) Bat conservation: past, present and future. In: Adams RA, Pedersen SC (eds) Bat evolution, ecology, and conservation. Springer, Berlin, pp 517–532

Racey PA (2015) The uniqueness of bats. In: Wang L, Cowled C (eds) Bats and viruses. Wiley, New York

Racey PA, Entwistle AC (2000) Life history and reproductive strategies in bats. In: Crighton E, Krutzsch PH (eds) Reproductive biology of bats. Academic Press, NY, pp 363–414

Racey PA, Goodman SM, Jenkins RKB (2009) The ecology and conservation of malagasy bats. In: Fleming TH, Racey PA (eds) Island bats—ecology, evolution and conservation. Chicago University Press, p 369–404

Randrianandrianina FH, Racey PA, Jenkins RKB (2010) Hunting and consumption of mammals and birds by people in urban areas of western Madagascar. Oryx 44:411–415

Ravon S, Furey NM, Hul V, Capelle J (2014) A rapid assessment of flying fox (*Pteropus* spp.) colonies in Cambodia. Camb J Nat Hist 2014:14–18

Razafimanahaka J (2013) When peanuts help to conserve fruit bats. Madagasikara Voakajy Newsletter on-line. http://www.madagasikara-voakajy.org/index.php?option=com_content&view=article&id=161:when-peanuts-help-to-conserve-fruit-bats&catid=19:livelihoods&Itemid=4

Razakarivony HV (2003) Etude d'impact de la prédation humaine sur la rousette *Pteropus rufus* (Tiedemann, 1808) dans la région de Morondava. Memoire DEA, Départment de Biologie Animale, Université d'Antananarivo

Roberts TJ (1997) The mammals of Pakistan, 2nd edn. Oxford University Press, Pakistan

Robinson JG, Bennett EL (2000) Carrying capacity limits to sustainable hunting in tropical forests. In: Robinson JG, Bennett EL (eds) Hunting for sustainability in tropical forests. Columbia University Press, New York, pp 13–30

Robinson JG, Redford KH (1991) Sustainable harvest of neotropical forest mammals. In: Robinson JG, Redford KH (eds) Neotropical wildlife use and conservation. University of Chicago Press, Chicago, pp 415–429

Robinson JE, Bell DJ, Saleh FM et al (2010) Recovery of the Vulnerable Pemba flying fox *Pteropus voeltzkowi*: population and conservation status. Oryx 44:416–423

Rosell-Ambal G, Heaney L, Helgen K (2008) *Pteropus speciosus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Ruedas L, Kingston T, Helgen K, Sinaga J (2008a) *Thoopterus nigrescens*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Ruedas L, Kingston T, Sinanga U, Maharadatunamsi D (2008b) *Rousettus celebensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Ruedas L, Kingston T, Sinanga U (2010) *Styloctenium wallacei*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Saéz AM, Weiss S, Nowak K et al (2015) Investigating the zoonotic origin of the West African Ebola epidemic. EMBO Mol Med 7:17–23

Salas L, Helgen K, Hamilton S (2008) *Pteropus neohibernicus*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Samuel H (2013) Frozen porcupines and bats confiscated in Paris exotic food raid. The Telegraph, World News, 6 Dec 2013. Accessed on-line http://www.telegraph.co.uk/news/worldnews/europe/france/10500982/Frozen-porcupines-and-bats-confiscated-in-Paris-exotic-food-raid.html

Setz EZF (1991) Animals in the Nambiquara diet: methods of collection and processing. J Ethnobiol 11:1–22

Setz EZ, Sazima I (1987) Bats eaten by Nambiquara Indians in Western Brazil. Biotropica 19:190

Sewall BJ, Granek EF, Trewhella WJ (2003) The endemic Comoros Islands fruit bat *Rousettus obliviosus*: ecology, conservation, and red list status. Oryx 37(3):344–352

Sewall BJ, Granek EF, Moutui MFE, Trewhella WJ, Reason PF, Rodrìguez-Clark KM, Säid I, Caroll JB, Masefield W, Toilibou N, Vély M, Faissoili BM, Feistner TC, Wells S (2007) Conservation action plan for livingstone's flying fox: a strategy for an endangered species, a diverse forest and the Comorian people, 52 pp

Shanahan M, So S, Gompton SG, Gorlett R (2001) Fig-eating by vertebrate frugivores: a global review. Biol Rev 76: 529–572

Sheffers BR, Corlett RT, Diesmos A, Laurance WF (2012) Local demand drives a bushmeat industry in a Philippine forest preserve. Trop Conserv Sci 5(2):133–141

Sheherazade J, Tsang SM (2015) Quantifying the bat bushmeat trade in North Sulawesi, Indonesia, with suggestions for conservation action. Glob Ecol Cons 3:324–330

Shilton LA, Whittaker RJ (2009) The role of pteropodid bats in reestablishing tropical forests on Krakatau. In: Fleming TH, Racey PA (eds) Island bats. Chicago University Press, Chicago, pp 176–215

Simmons N (2005) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammal species of the world: a taxonomic and geographic guide. John Hopkins University Press, Baltimore, pp 312–529

Sinavaiana C, Enright J (1992) The cultural significance of the flying foxes in Samoa: a legendary view. In: Wilson DE, Graham GL (eds) Proceeding of an international conservation conference on Pacific Island flying foxes. US Fish and Wildlife Service Biological Report, vol 90, pp 36–38

Singaravelan N, Marimuthu G, Racey PA (2009) Do fruit bats deserve to be listed as vermin in the Indian Wildlife (Protection), Amended Acts? A critical review. Oryx 43(04):608–613

SOS (2012) Filipinos for flying foxes project page. International Union for Conservation of Nature (IUCN) Save Our Species Fund. http://www.sospecies.org/sos_projects/mammals/filipinos_for_flying_foxes/

Stebbings B (1987) Bats, tequila and the King of Siam. BBC Wildlife, Jan 1987, 4–8

Stier SC, Mildenstein TL (2005) Dietary habits of the world's largest bats. J Mammal 86:719–728

Stinson DW, Glass PO, Taisacan EM (1992) Declines and trade in fruit bats on Saipan, Tinian, Aguijan, and Rota. In: Wilson DE, Graham GL (eds) Pacific island flying foxes: proceedings of an international conservation conference, vol 90. US Fish and Wildlife Service Biological Report No 23, pp 61–67

St. John FAV, Keane AM, Milner-Gulland EJ (2013) Effective conservation depends upon understanding human behaviour. In: MacDonald DW, Willis KJ (eds) Key topics in conservation biology. Wiley, New York

Subramanian (2012) Zoonotic disease risk and the bushmeat trade: assessing awareness among hunters and traders in Sierra Leone. Ecohealth 4:471–482

Tacio HD (2015) To the batcave: a visit to Samal Island's world record-holding bat colony. GMA News Online, Phillipines. http://www.gmanetwork.com/news/story/269418/lifestyle/travel/to-the-batcave-a-visit-to-samal-island-s-world-record-holding-bat-colony

Tanshi I, Labiran AJ, Chukwuyem SF et al (2013) Bat conservation in Nigeria: volunteer contribution to bat population survey and public awareness. In: Olajuyigbe SE, Coker OM, Olaleru F (eds) Proceedings of the 4th annual biodiversity conference. Lagos, Nigeria

Trewhella WJ, Reason PF, Bullock RJ et al (1995) Conservation of *Pteropus livingstonii*: catching fruit bats in the Comores. Myotis 32–33:297–305

Trewhella WJ, Rodriguez-Clark KM, Corp N et al (2005) Environmental education as a component of multidisciplinary conservation programmes: lessons from conservation initiatives for critically endangered fruit bats in the Western Indian Ocean. Conserv Biol 19:75–85

Tuladhar-Douglas W (2008) The use of bats as medicine among the Newars. J Ethno 28:69–91

USFWS (2009) Draft revised recovery plan for the Mariana fruit bat or fanihi (*Pteropus mariannus mariannus*), pp 1–83

Van der Aa PJH, Lorica MRP, Komdeur J (2006) The hormonal and behavioral response to the presence and activities of humans in three co-roosting flying fox species (*Acerodon jubatus, Pteropus vampyrus* and *P. hypomelanus*) in Boracay and Mambukal in the Philippines. Acta Zool Sini 52:827–837

Venkatesan A (2007) Status of Indian flying fox *Pteropus giganteus* in Bengaluru. Bat Net News 8:13–15

Voigt CC, Kingston T (2016) Bats in the Anthropocene: conservation of bats in a changing world. Springer International AG, Cham

Wiles GJ (1992) Recent trends in the fruit bat trade on Guam. In: Wilson DE, Graham GL (eds) Pacific island flying foxes: proceedings of an international conservation conference, vol 90. U.S. Fish and Wildlife Service Biological Report No 23, pp 52–60

Wiles G (2008) *Pteropus pelewensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Wiles GJ, Payne NH (1986) The trade in fruit bats *Pteropus* spp. on Guam and other Pacific islands. Biol Conserv 38:143–161

Wiles GJ, Engbring J, Otobed D (1997) Abundance, biology and human exploitation in the Palau Islands. J of Zool Lond 241:203–227

Wiles G, Helgen K, Allison A (2008a) *Pteropus ualanus.* The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Wiles G, Helgen K, Allison A (2008b) *Pteropus yapensis*. The IUCN Red List of threatened species. Version 2014.3. www.iucnredlist.org. Downloaded on 18 Mar 2015

Wilson DE, Graham GL (eds) (1992) Pacific Island flying foxes: proceedings of an international conservation conference, vol 90. US Fish and Wildlife Biological Report 23. U.S. Department of the Interior, United States

Wilson VJ, Wilson BLP (1991) La chasse traditionnelle et commerciale dans le sud-ouest du Congo. Tauraco Res Rep 4:279–289

Chapter 13
The Conflict Between Pteropodid Bats and Fruit Growers: Species, Legislation and Mitigation

Sheema Abdul Aziz, Kevin J. Olival, Sara Bumrungsri, Greg C. Richards and Paul A. Racey

Abstract Pteropodid bats damage a wide range of fruit crops, exacerbated by continuing loss of their natural food as forests are cleared. In some countries where such damage occurs, bats are not legally protected. In others, as a result of pressure from fruit growers, legal protection is either not implemented or overridden by legislation specifically allowing the killing of bats. Lethal control is generally ineffective and often carried out with shotguns making it an animal welfare issue, as many more animals are injured or orphaned than are killed. Here, we review the literature and current state of the conflict between fruit growers and pteropodids and describe a wide range of potential mitigation techniques. We compile an extensive list of bats and the fruit crops on which they feed where this has resulted in conflicts, or could lead to conflict, with fruit growers. We also discuss the legal status of bats in some countries where such conflicts occur. We found the most effective means of preventing bat damage to crops is the use of fixed nets (that generally prevent entanglement) covering a whole orchard. Netting individual trees, or fruit panicles, using small net bags, is also effective. Management methods that assist netting include pruning to maintain low stature of trees. These

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S.A. Aziz (✉)
Rimba, Muséum National d'Histoire Naturelle, Paris, France
e-mail: sheema.abdulaziz@gmail.com

K.J. Olival
EcoHealth Alliance, New York, USA
e-mail: olival@ecohealthalliance.org

S. Bumrungsri
Department of Biology, Prince of Songkla University, Songkhla, Thailand
e-mail: sarabumrungsri@gmail.com

G.C. Richards
Bat Fauna Consultant, Canberra, Australia
e-mail: batman3812@bigpond.com

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exclusion techniques are the best management options considering both conservation and public health issues. Although lights, sonic and ultrasonic noises, noxious smells and tastes have been used to deter bats from eating fruit, there have been no large-scale systematic trials of their effectiveness. Nevertheless, broadcasting the sound of discharging shotguns followed by the sound of wounded bats has proved effective in Australia. The use of decoy fruit trees is the least investigated method of mitigation and requires detailed knowledge of the natural diet of the bat species involved. The few studies of dietary preferences undertaken to date suggest that bats prefer non-commercial fruit when it is available, and we highlight this as an area for future research.

13.1 Introduction

The Old World bat family Pteropodidae is distributed throughout the tropics and subtropics of Australasia, Africa and Oceania (Marshall 1983; Mickleburgh et al. 1992). It comprises 196 species (Simmons 2005) that feed primarily on fruit, flowers (nectar, pollen, petals and bracts) and leaves of at least 188 plant genera from 64 families (Lobova et al. 2009; Fleming and Kress 2011), although some species have also been recorded eating insects (e.g. Clulow and Blundell 2011; Scanlon et al. 2013). Fujita (1988) and Fujita and Tuttle (1991) used the term 'flying foxes' to refer to all bats in the family Pteropodidae, but we restrict this term to the 70 species in the genera *Pteropus* and *Acerodon* (IUCN 2014), following the definition outlined by Kingston (2010), and use the term 'fruit bats' for the remainder.

Although bat–plant interactions were first recorded in 1772, it is now known that coevolution has shaped these complex interrelationships over millennia, producing bat-flower and bat-fruit syndromes (Marshall 1983; Fleming et al. 2009). This phytophagous diet results in valuable ecosystem services of pollination and seed dispersal (Kunz et al. 2011). Pteropodid bats are responsible for propagating at least 289 species of plants, of which 186 provide economically important resources and products including fruits, drinks, foods, ornamental plants, timbers, fibres, tannins, dyes, medicines, and animal fodder (Fujita and Tuttle 1991; Lobova et al. 2009). In addition, large populations of flying foxes are necessary to maintain the health of Old World tropical forests (Fujita and Tuttle 1991; Nyhagen et al. 2005; McConkey and Drake 2006). Such healthy functioning ecosystems ultimately provide humans with additional benefits such as climate regulation, nutrient cycling, water filtration, and erosion control (Kunz et al. 2011).

P.A. Racey
Centre for Ecology and Conservation, University of Exeter, Cornwall Campus,
Penryn, Cornwall, UK
e-mail: p.a.racey@exeter.ac.uk

S.A. Aziz
University of Nottingham Malaysia Campus, Semenyih, Malaysia

Dependence on plant materials has also led to a long history of interactions between these bats and humans, particularly at shared food resources. Flying foxes with striped faces are depicted in aboriginal cave paintings in Kimberley, Australia, attributed to the Bradshaw people, between 17,000 and 60,000 years ago. Whether they brought such stripe-faced bats to the area or idolised the bat pollinator of a favoured tree, the baobab, in their drawings, is unknown. Genetic studies showed that baobab seeds were brought on their journey from Ethiopia to Australia, as an important provider of food, nutrients and building materials. This ancient rock art may be the first human recognition of the ecosystem services of pteropodids (Richards et al. 2012).

Despite the documented benefits of bats, negative attitudes towards them persist among the general public (Marshall 1983; Fujita and Tuttle 1991; Kunz et al. 2011). Pteropodid bats, in particular flying foxes, are frequently shot, persecuted and even legally culled as agricultural pests (Bumrungsri et al. 2009; Epstein et al. 2009). In Thailand, for example, farmers of durian (*Durio zibethinus*) set nets to catch the dawn bat (*Eonycteris spelaea*) visiting their trees when in flower and leave the bats to die, because they see that flowers fall after bat visits and conclude that bats have destroyed them (S. Bumrungsri, unpublished). In fact, the flowers fall naturally after the bats have pollinated them, but unhelpful misconceptions such as this exacerbate the conflict between bats and humans. In addition, pteropodid bats are hunted intensively for food and medicinal uses (including commercial trade), leading to severe declines throughout their range (Epstein et al. 2009; Mickleburgh et al. 2009; Harrison et al. 2011). Estimates based on current deforestation rates in Southeast Asia project that many pteropodids may become globally extinct by the end of this century (Lane et al. 2006), with flying foxes being of particular concern in Southeast Asia due to intense hunting pressure (Struebig et al. 2007; Meyer et al. in press). The Old World Fruit Bat Action Plan (Mickleburgh et al. 1992) helped stimulate research on pteropodids but is now out of date and is being revised. The conservation status of these bats has worsened since the plan was published, and a quarter of all species are now endangered (IUCN 2014).

Here, we review the current state of knowledge regarding human–pteropodid interactions by geographic region, legal policies affecting pteropodid bats, and methods of mitigating the damage they cause to fruit crops.

13.2 The Extent of Feeding by Bats on Fruit Crops and Its Implications

The fruit crops which bats have been reported to damage are listed in Table 13.1.

13.2.1 The Mediterranean

Madkour (1977), writing about the Egyptian fruit bat (*Rousettus aegyptiacus*) in Egypt, stated that it was ‘a highly dangerous fruit pest’ and that ‘its control is

Table 13.1 Bat species recorded foraging on fruit crops, by country. Fruit species, common name, bat species and countries where conflict/potential conflict has been recorded, and sources of information

Fruit species	Common name	Bat species	Countries	References
Agave sislana	Sisal (flowers only)	*Pteropus rufus*	Madagascar	Oleksy et al. (2015)
Anacardium occidentale	Cashew	*Pteropus hypomelanus*	Malaysia	S.A. Aziz, unpublished
		Pteropus lylei	Thailand	Weber et al. (2015)
		Pteropus voeltzkowi	Tanzania (Pemba)	Entwistle and Corp (1997)^b
		Unknown	Guinea	Van Mele et al. (2009)
Ananas comosus	Pineapple	*Cynopterus sphinx*	Sri Lanka	Yapa et al. (1999)
		Pteropus dasymallus	Japan (Ryukyu)	Vincenot et al. (2015)
		Pteropus giganteus	Sri Lanka	Yapa et al. (1999)
		Rousettus leschenaultii		
Annona sp.	Custard Apple/Soursop	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
Areca catechu	Areca Palm	*Cynopterus sphinx*	India	Chakravarthy and Girish (2003)
		Pteropus giganteus	Myanmar	Win and Mya (2015)
Arecaceae spp.	Palms	*Cynopterus sphinx*	Sri Lanka	Phillips (1980)
		Pteropus giganteus		
		Rousettus leschenaultii		
Artocarpus altilis	Breadfruit	*Pteropus voeltzkowi*	Tanzania (Pemba)	Entwistle and Corp (1997)^b
Artocarpus heterophyllus	Jackfruit	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
Artocarpus lacucha	Monkey Jack	*Pteropus lylei*	Thailand	Weber et al. (2015)^b
Azadirachta indica	Neem	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
Cajanus cajan	Pigeon Pea	*Pteropus giganteus*	Myanmar	Win and Mya (2015)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Carica papaya	Papaya	*Cynopterus sphinx*	Sri Lanka	Yapa et al. (1999)
		Pteropus giganteus	Myanmar	Win and Mya (2015)
		Pteropus lylei	Thailand	Weber et al. (2015)[b]
		Rousettus leschenaultii	Sri Lanka	Yapa et al. (1999)
		Pteropus voeltzkowi	Tanzania (Pemba)	Entwistle and Corp (1997)[b]
		Pteropus spp.	Australia	Ratcliffe (1931)
Ceiba pentandra	Kapok	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
Ceratonia siliqua	Carob	*Rousettus aegyptiacus*	Cyprus	Del Vaglio et al. (2011)[b]
			Israel	Galil et al. (1976)
				Moran and Keider (1993)
				Izhaki et al. (1995)
			Lebanon	Lewis and Harrison (1962)[b]
Citrus paradisi	Grapefruit	*Rousettus aegyptiacus*	Israel	Galil et al. (1976)
				Moran and Keider (1993)
		Pteropus alecto	Australia	Ratcliffe (1931)[a]
		Pteropus conspicillatus		Waples (2002)
		Pteropus poliocephalus		
		Rousettus aegyptiacus	Israel	Galil et al. (1976)
				Moran and Keider (1993)
		Pteropus alecto	Australia	Ratcliffe (1931)[a]
		Pteropus conspicillatus		
Citrus reticulata	Mandarin	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
		Pteropus poliocephalus	Australia	Rogers (2002)
Citrus sinensis	Orange	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
Citrus sp.	Citrus	*Rousettus aegyptiacus*	Cyprus	Del Vaglio et al. (2011)[a]

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Citrus spp.	Citrus fruits	*Rousettus aegyptiacus*	Turkey	Albayrak et al. (2008)
		Pteropus dasymallus	Japan (Ryukyu)	Vincenot et al. (2015)
		Pteropus spp.	Australia	Ratcliffe (1931)[a]
Coccinia grandis	Ivy Gourd	*Pteropus lylei*	Thailand	Weber et al. (2015)
Coffea spp.	Coffee	*Cynopterus* spp.	Indonesia	Huang et al. (2014)
		Pteropus poliocephalus	Australia	Waples (2002)
Dimocarpus longan	Longan	*Pteropus niger*	Mauritius	V. Dooblad, pers. comm.
Diospyros kaki	Persimmon	*Pteropus poliocephalus*	Australia	Rogers (2002)
		Rousettus aegyptiacus	Israel	Korine et al. (1999)
			Turkey	Albayrak et al. (2008)
Diospyros malabarica	Gaub tree	*Pteropus lylei*	Thailand	Weber et al. (2015)[b]
Diospyros rhodocalyx	Tako Naa	*Pteropus lylei*	Thailand	Weber et al. (2015)[b]
Durio zibethinus	Durian (flowers only)	*Eonycteris spelaea*	Thailand	S. Bumrungsri, unpublished
		Pteropus hypomelanus	Malaysia	S.A. Aziz, unpublished
Eriobotrya japonica	Loquat	*Pteropus dasymallus*	Japan (Ryukyu)	Vincenot et al. (2015)
		Rousettus aegyptiacus	Cyprus	Del Vaglio et al. (2011)
			Israel	Izhaki et al. (1995)
				Korine et al. (1999)
			Turkey	Albayrak et al. (2008)
Eucalyptus deglupta	Eucalyptus	*Pteropus vampyrus*	Malaysia	Fujita and Tuttle (1991)
Eugenia aromatica	Clove	*Pteropus voeltzkowi*	Tanzania (Pemba)	Entwistle and Corp (1997)
Euphoria malaiense	Mata Kucing	*Pteropus hypomelanus*	Malaysia	S.A. Aziz, unpublished
Ficus carica	Common Fig	*Rousettus aegyptiacus*	Israel	Korine et al. (1999)
			Turkey	Albayrak et al. (2008)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Ficus rumphii	Rumpf's Fig	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
		Pteropus lylei	Thailand	Weber et al. (2015)[b]
Ficus sp.	Fig	*Rousettus aegyptiacus*	Cyprus	Del Vaglio et al. (2011)[a]
Ficus spp.	Figs	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
			Lebanon	Lewis and Harrison (1962)
		Pteropus spp.	Australia	Ratcliffe (1931)
Fragaria sp.	Strawberry	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
Lansium parasiticum	Langsat	*Cynopterus brachyotis*	Malaysia	Fujita (1988)
		Pteropus spp.		
		Pteropus hypomelanus		S.A. Aziz, unpublished
Litchi chinensis	Lychee/Litchi	*Pteropus niger*	Mauritius	V. Dooblad, pers. comm.
		Pteropus poliocephalus	Australia	Rogers (2002)
				Waples (2002)
		Pteropus rodricensis	Mauritius (Rodrigues)	Price (2013)
		Rousettus aegyptiacus	Israel	Galil et al. (1976)
				Moran and Keider (1993)
Malphigia emarginata	Acerola	*Pteropus lylei*	Thailand	Weber et al. (2015)[b]
Malus domestica	Apple	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
			Israel	Galil et al. (1976)
				Moran and Keider (1993)
Malus sp.	Apple	*Rousettus aegyptiacus*	Turkey	Albayrak et al. (2008)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Mangifera indica	Mango	*Cynopterus sphinx*	Guinea	Van Mele et al. (2009)
			Sri Lanka	Phillips (1980)
				Yapa et al. (1999)
		Pteropus giganteus	Maldives	Dolbeer et al. (1988)
			Myanmar	Win and Mya (2015)
			Sri Lanka	Phillips (1980)
				Yapa et al. (1999)
		Pteropus hypomelanus	Malaysia	S.A. Aziz, unpublished
		Pteropus lylei	Thailand	Weber et al. (2015)
				S. Bumrungsri, unpublished
		Pteropus niger	Mauritius	Dooblad, unpublished
		Pteropus poliocephalus	Australia	Waples (2002)
		Pteropus spp.		Ratcliffe (1931)[a]
		Pteropus rodricensis	Mauritius (Rodrigues)	Price (2013)
		Pteropus voeltzkowi	Tanzania (Pemba)	Entwistle and Corp (1997)[b]
		Rousettus aegyptiacus	Egypt	Madkour (1977)
			Israel	Izhaki et al. (1995)
		Rousettus leschenaultii	Sri Lanka	Phillips (1980)
				Yapa et al. (1999)
		Unknown	India	Singaravelan (2002)
Manilkara zapota	Sapota/Sapodilla	*Pteropus giganteus*	India	Chakravarthy and Girish (2003)
		Pteropus lylei	Thailand	Weber et al. (2015)[b]
Morinda angustifolia	Ye-yo	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
Morus alba	White Mulberry	*Rousettus aegyptiacus*	Egypt	Madkour (1977)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Morus nigra	Black Mulberry/ Blackberry	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
Morus sp.	Mulberry	*Rousettus aegyptiacus*	Cyprus	Del Vaglio et al. (2011)
			Turkey	Albayrak et al. (2008)
Musa paradisiaca	Banana	*Cynopterus sphinx*	Sri Lanka	Yapa et al. (1999)
		Pteropus giganteus		
		Rousettus leschenaultii		
Musa sapientum	Banana	*Pteropus voeltzkowi*	Tanzania (Pemba)	Entwistle and Corp (1997)[b]
Musa sp.	Banana	*Pteropus lylei*	Thailand	Weber et al. (2015)[b]
Musa spp.	Bananas	*Pteropus dasymallus*	Japan (Ryukyu)	Vincenot et al. (2015)
		Pteropus lylei	Thailand	Weber et al. (2015)
				S. Bumrungsri, unpublished
		Pteropus poliocephalus	Australia	Rogers (2002)
		Pteropus spp.		Waples (2002)
				Ratcliffe (1931)[a]
		Rousettus aegyptiacus	Egypt	Madkour (1977)
			Israel	Izhaki et al. (1995)
Nephelium lappaceum	Rambutan	*Cynopterus brachyotis*	Malaysia	Fujita (1988)
		Cynopterus sphinx	Sri Lanka	Yapa et al. (1999)
		Pteropus giganteus		
		Pteropus hypomelanus	Malaysia	S.A. Aziz, unpublished
		Pteropus vampyrus		Fujita (1988)
				K.J. Olival, unpublished
		Rousettus leschenaultii	Sri Lanka	Yapa et al. (1999)
Oroxylum indicum	Midnight Horror	*Pteropus giganteus*	Myanmar	Win and Mya (2015)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Persea americana	Avocado	*Pteropus rufus*	Madagascar	Oleksy et al. (2015)
Phoenix dactylifera	Date Palm	*Rousettus aegyptiacus*	Israel	Izhaki et al. (1995)
				Korine et al. (1999)
			Turkey	Albayrak et al. (2008)
Phoenix sylvestris	Sugar/Silver Date Palm	*Cynopterus sphinx*	Bangladesh	Khan et al. (2011)
		Pteropus giganteus		
		Rousettus leschenaultii		
Phoenix spp.	Dates	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
			Lebanon	Lewis and Harrison (1962)
Prunus dulcis	Almond	*Pteropus giganteus*	Maldives	Dolbeer et al. (1988)
Prunus persica	Nectarine	*Pteropus poliocephalus*	Australia	Comensoli (2002)
	Peach	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
			Turkey	Albayrak et al. (2008)
Prunus sp.	Apricot	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
			Turkey	Albayrak et al. (2008)
Prunus sp.	Cherry	*Rousettus aegyptiacus*	Turkey	Albayrak et al. (2008)
Prunus sp.	Plum	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
			Turkey	Albayrak et al. (2008)
Prunus spp.	Stone fruit: a fruit with flesh or pulp enclosing a stone, such as a peach, nectarine, plum, or cherry.	*Pteropus poliocephalus*	Australia	Ratcliffe (1931)
				Rogers (2002)
				Waples (2002)
		Pteropus scapulatus		Ratcliffe (1931)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Psidium guajava	Guava	*Cynopterus sphinx*	India	Singaravelan (2002)
			Sri Lanka	Yapa et al. (1999)
		Rousettus leschenaultii	Sri Lanka	Yapa et al. (1999)
		Pteropus dasymallus	Japan (Ryukyu)	Vincenot et al. (2015)
		Pteropus giganteus	India	Chakravarthy and Girish (2003)
			Maldives	Dolbeer et al. (1988)
			Myanmar	Win and Mya (2015)
			Sri Lanka	Yapa et al. (1999)
		Pteropus lylei	Thailand	Weber et al. (2015)[b]
		Pteropus poliocephalus	Australia	Waples (2002)
		Pteropus voeltzkowi	Pemba (Tanzania)	Entwistle and Corp (1997)[b]
Punica granatum	Pomegranate	*Rousettus aegyptiacus*	Egypt	Madkour (1977)
			Israel	Galil et al. (1976)
				Moran and Keider (1993)
			Turkey	Albayrak et al. (2008)
		Pteropus giganteus	Myanmar	Win and Mya (2015)
Pyrus communis	Pear	*Rousettus aegyptiacus*	Israel	Galil et al. (1976)
				Moran and Keider (1993)
Pyrus sp.	Pear	*Rousettus aegyptiacus*	Cyprus	Del Vaglio et al. (2011)[a]
			Egypt	Madkour (1977)
Rosaceae	Pome fruit: a fleshy fruit, such as an apple or pear with several seed chambers and an outer fleshy part	*Pteropus poliocephalus*	Australia	Ratcliffe (1931)
				Waples (2002)
		Pteropus scapulatus		Waples (2002)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Saccharum officinarum	Sugar Cane	*Pteropus dasymallus*	Japan (Ryukyu)	Vincenot et al. (2015)
Sandoricum kotejape	Santol	*Pteropus lylei*	Thailand	Weber et al. (2015)[b]
				S. Bumrungsri, unpublished
Sesbania grandiflora	Agate/Hummingbird Tree (flowers only)	*Pteropus* spp.	Thailand	S. Bumrungsri, unpublished[b]
Syzygium aqueum	Water Apple	*Cynopterus brachyotis*	Malaysia	Fujita (1988)
		Pteropus spp.		
Syzygium cumini	Jambul/Jamun	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
			Pakistan	Roberts (1997)
		Pteropus lylei	Thailand	Weber et al. (2015)[b]
		Pteropus voeltzkowi (flowers only)	Tanzania (Pemba)	Entwistle and Corp (1997)[b]
Syzygium jambos	Rose Apple	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
		Pteropus lylei	Thailand	Weber et al. (2015)[b]
Syzygium javanicum	Java Apple	*Pteropus lylei*	Thailand	S. Bumrungsri, unpublished
Syzygium samarangense	Java Apple	*Pteropus lylei*	Thailand	Weber et al. (2015)[b]
Syzygium spp.	Jambu	*Pteropus hypomelanus*	Malaysia	S.A. Aziz, unpublished
Tamarindus indica	Tamarind	*Pteropus giganteus*	Myanmar	Win and Mya (2015)
		Pteropus lylei	Thailand	Weber et al. (2015)
		Pteropus rufus	Madagascar	Oleksy et al. (2015)

(continued)

Table 13.1 (continued)

Fruit species	Common name	Bat species	Countries	References
Theobroma cacao	Cocoa	Unknown	Papua New Guinea	Hicks (1967)
Vitis vinifera	Grape	*Cynopterus sphinx*	India	Verghese (1998)
				Srinivasulu and Srinivasulu (2002)
		Pteropus spp.	Australia	Ratcliffe (1931)[a]
		Rousettus aegyptiacus	Turkey	Albayrak et al. (2008)
Ziziphus jujuba	Jujube	*Pteropus giganteus*	Myanmar	Win and Mya (2015)

[a] Feeding impact was reported to be small enough to be negligible

[b] Although the fruit species may not have been grown commercially, there may still be conflict with bats eating garden fruit of local people

of great economic importance'. He reported that there were records of the species attacking cultivated fruit trees, and during the course of his study, they were recorded feeding on apple (*Malus domestica*), apricot (*Prunus* sp.), banana (*Musa* sp.), custard apple (*Annona* sp.), date (*Phoenix* sp.), mandarin (*Citrus reticulata*), mango (*Mangifera indica*), mulberry (black *Morus nigra* and white *M. alba*), orange (*Citrus sinensis*), peach (*Prunus persica*), pear (*Pyrus* sp.), plum (*Prunus* sp.), pomegranate (*Punica granatum*) and strawberry (*Fragaria* sp.). However, there was no mention of whether this was recorded from in situ observations or feeding trials in captivity.

Korine et al. (1999) showed that *R. aegyptiacus* in Israel ate mainly non-commercial fruits and also to a lesser extent leaves and pollen, challenging the assumption that this species is a major agricultural pest. Out of 14 identified plant species comprising its diet, only four are grown commercially in Israel: persimmon (*Diospyros kaki*), loquat (*Eriobotrya japonica*), fig (*Ficus carica*) and date (*Phoenix dactylifera*), with the largest component consisting of figs (*Ficus* spp.). The perception of *R. aegyptiacus* as a pest (Harrison 1964; Moran and Keidar 1993) led to conflict with farmers, resulting in extermination programs that reduced its population in the country (Korine et al. 1999; Hadjisterkotis 2006). As these control measures involved widespread fumigation of caves by the authorities, using the chlorinated hydrocarbon lindane, many populations of cave-dwelling insectivorous bats were also drastically reduced (Makin and Mendelssohn 1987). Other reports from Israel detail bats consuming commercial fruits such as apples, bananas, carobs (*Ceratonia siliqua*), dates, grapefruits (*Citrus paradisi*), lychees (litchi; *Litchi sinensis*), mandarins, pears and pomegranates (Galil et al. 1976; Moran and Keider 1993; Izhaki et al. 1995). However, the overall extent of actual damage to fruit crops is unknown and requires further detailed investigation.

In Lebanon, *R. aegyptiacus* was observed feeding on carobs, dates and figs. Its preference for dates and figs in particular, which are also cultivated for human consumption, caused it to be the only bat species considered to be of economic importance there. Farmers used shotguns to kill bats, and even though fruit such as dates could be protected by cloth bags or nets before ripening, this was seldom done. Some farmers were even known to starve populations of bats in caves by placing nets over the roost entrance (Lewis and Harrison 1962).

Qumsiyeh (1980) initially stated that the population of *R. aegyptiacus* in Jordan was increasing. However, more than a decade later, Qumsiyeh et al. (1992) concluded that the species was already under threat due to destruction of its roost sites, even though the issue of fruit crop damage had yet to be investigated in the country.

Albayrak et al. (2008) reported that in the Mediterranean region of Turkey, *R. aegyptiacus* fed on both wild and commercially grown fruits. Their study identified 15 different species, of which 13 were marketed: plum, loquat, apple (*Malus* sp.), fig (*F. carica*), pomegranate, grape (*Vitis vinifera*), persimmon, date, mulberry (*Morus* sp.), cherry (*Prunus* sp.), peach, apricot and citrus (*Citrus* sp.). Wild fruits were consumed only during the winter. They concluded that fruit bats could have a considerable impact on fruit crops, with farmers in Hatay Province claiming that bats consumed 10–15 % of their loquat harvest. Fruit bats were thus considered to be serious pests and were subsequently killed regularly. According to Spitzenberger (1979), in the past, this involved fumigating roost caves or walling up their entrances. Harrison and Bates (1991) reported that farmers caged their commercial fruit trees in order to protect them from *R. aegyptiacus*. However, a more recent study in 2012 found that local people in Turkey did not consider bats to be as much of a problem as birds (E. Coraman, pers. comm.).

In Cyprus, only anecdotal reports were previously available for the diet of *R. aegyptiacus.* A preliminary assessment of its diet was carried out by Del Vaglio et al. (2011) from droppings, in order to determine the bats' real impact on crops. The diet consisted mostly of fruits, several species of which were the same as those reported by Korine et al. (1999) for Israel and Albayrak et al. (2008) for Turkey. The species is an opportunistic forager, with non-native plants forming an important component of its diet, yet Del Vaglio et al. (2011) concluded that its damage to economically important plants in Cyprus is negligible. Their study found that the bat fed mainly on wild fruits and escaped ornamental plants and that only five out of the 11 plant species it consumed—citrus, fig, loquat, mulberry and plum—were grown as commercial fruit crops in Cyprus.

13.2.2 Africa and the Indian Ocean

In Guinea, mango and cashew (*Anacardium occidentale*) farmers listed fruit bats among the mammals (together with monkeys, squirrels and other rodents) that cause damage to their harvest. The bats target ripening mangoes and cause significant damage, identified by a visible seed protruding from the eaten lower part of the fruit. However, only 4 % of farmers identified fruit bats as pests, compared to 92 % who identified fruit flies as the most significant pest. Overall, according to the farmers, five species of insects, followed by squirrels, caused greater damage than bats. The majority of farmers did not carry out any pest management (Van Mele et al. 2009).

Entwistle and Corp (1997) examined the diet of *Pteropus voeltzkowi*), which is endemic to the island of Pemba, off the coast of Tanzania. They found that it consisted of a high proportion of cultivated fruit grown on 'shamba' plots, in particular mangoes which formed a key component of the diet during the duration of the study. Breadfruit (*Artocarpus altilis*) was also consumed. In addition, interview surveys with villagers and students yielded additional cultivated fruit species among the food plants of this bat species (Table 13.1).

In the Indian Ocean, Dolbeer et al. (1988) described the Indian flying fox (*Pteropus giganteus*) as a major cause of damage to almonds (*Prunus dulcis*), guavas (*Psidium guajava*) and mangoes in the Maldives, although losses were not quantified. In Mauritius, the Agricultural Research and Extension Unit of the Food and Agricultural Research Council estimated an overall average of 10 % of orchard lychee fruit was damaged by the Mauritian flying fox (*Pteropus* *niger*). Ten trees were studied in each of three orchards and damage to individual fruit averaged 2, 7, and 17 %. In contrast, a smaller study of four longan trees (*Dimocarpus longan*) recorded damage to all fruit panicles. Mangoes were also damaged at a rate of 10–30 % (V. Dooblad, pers. comm.). In contrast, a recent study by Ramlugun (2013) in a lychee orchard found that high winds and introduced birds, but not bats, resulted in fruit losses of 30 and 9.5 %, respectively. On Rodrigues (an autonomous island of the Republic of Mauritius), losses to backyard mango and lychee production were estimated at about 36 %, much of which was perceived to be to the Rodrigues flying fox (*Pteropus rodricensis*) (Price 2013).

Oleksy et al. (2015) carried out GPS tracking of the Madagascan flying fox (*Pteropus rufus*) to determine its foraging movements and habitat selection in south-eastern Madagascar. The study revealed that this species has a strong preference for feeding on the nectar and pollen of sisal (*Agave sislana*) in overgrown plantations. These bats also feed on the fruits of avocado (*Persea americana*), lychee, mango and tamarind (*Tamarindus indica*). However, it was not mentioned whether this causes any conflict issues.

13.2.3 Indian Subcontinent

Bats are causing increasing economic loss in the Indian grape industry due to a decline in wild fruits and flowers, coupled with the increase of grape-growing areas. Verghese (1998) first drew attention to the damage caused by the greater short-nosed fruit bat (*Cynopterus sphinx*) to grapes in Bangalore where the vines are trained to grow on overhead trellises. They entered the vineyard through canopy gaps in the bower, not from the sides, and consumed only the juice of the fruit, while the pulp, seed and skin were discarded. Signs of bat damage included these remnants littered at the base of the grape vine, as well as grape bunches with bare stalks. The damage was greater in parts of the vineyard adjacent to open spaces, suggesting that growing non-commercial trees around the entire vineyard might deter bat foraging. Damage was lower in vines situated closer to an adjacent mango orchard.

Similarly in Andhra Pradesh State, Srinivasulu and Srinivasulu (2002) showed that the magnitude of damage caused by *C. sphinx* to grapes varied with the distance of the vines from the periphery of the vineyard. Damage was extensive (90 %) at the periphery, but none was recorded in the centre, where the higher density of the vines made approach flights difficult. In contrast, in Tamil Nadu State, *C. sphinx* was not known to damage grape crops; rather, eight bird species were the primary crop pests. There were also no records of this bat species damaging sapota (*Manilkara zapota*) in that state; however, considerable damage was reported to mango and guava crops (Singaravelan 2002).

In the State of Karnataka, Chakravarthy and Girish (2003) recorded losses of 18 % of areca nuts (*Areca catechu*) caused by a population of 3500–4000 *P.*

giganteus and 2–28 *C. sphinx*. Bats also damaged 13–22 % of sapota fruits, although higher levels of damage were inflicted by birds. Up to 28 % of guava fruits were also damaged by bats. *C. sphinx* has also been recorded as damaging mango and guava in Tamil Nadu State but did not damage sapota (Singaravelan 2002).

In Bangladesh, *P. giganteus* feeds on date palm sap (*Phoenix sylvestris*), widely harvested in the country as a beverage in the winter months (December–March) (Luby et al. 2006). Infrared camera traps have recorded *P. giganteus* and other pteropodid species (*Cynopterus* spp. and *Rousettus leschenaultii*) drinking from clay pots used to collect the sap at night (Khan et al. 2011), although the magnitude of the loss has not been investigated. This bat–plant sap interaction is a route for the transmission of zoonotic disease (see 13.3).

In Pakistan, *P. giganteus* is also labelled as vermin due to a perception that it raids fruit crops in orchards (Mahmood-Ul-Hassan et al. 2010). Apart from areca nuts, sapota and guava, it is also blamed for heavy economic losses of crops of mango and jamun (*Syzygium cumini*) (Roberts 1997; Chakravarthy and Girish 2003). However, a dietary study conducted by Mahmood-Ul-Hassan et al. (2010) in Lahore found that *P. giganteus* feeds primarily on wild figs rather than commercial crops. The study concluded that the perception of *P. giganteus* as a pest is a misconception, and its economic value as a pollinator is far greater for the fruit industry.

In Sri Lanka, according to Yapa et al. (1999), fruit farmers claimed that pteropodid bats (*C. sphinx, R. leschenaultii* and *P. giganteus*) damage fruit trees in plantations and home gardens. Fruits that were specifically identified as suffering heavy damage by *C. sphinx* were mango and rambutan (*Nephelium lappaceum)*, with mango thought to be particularly vulnerable in monoculture plantations. Bananas (*Musa paradisiaca*), papayas (paw-paws; *Carica papaya*) and even pineapples (*Ananas comosus*) were apparently also targeted. Their study concluded that *C. sphinx* was 'capable of causing heavy damage' and could thus potentially be a 'major fruit pest'. Earlier, casual records collected by Phillips (1980) also reported guava, mango, soursop and several palm species being consumed by pteropodids in Sri Lanka.

13.2.4 Southeast Asia

Although there are 95 species of pteropodids, including 31 flying foxes (IUCN 2014) in Southeast Asia, there is little published information on fruit crop damage caused by bats. Perception of damage is however widespread and has implications for conservation. For example, it may explain the Malaysian government's reluctance to provide full protection for the nation's flying foxes (large flying fox *Pteropus vampyrus* and island flying fox *P. hypomelanus*) by halting licensing which has led to unsustainable hunting (Epstein et al. 2009). So far, little attempt has been made to investigate the issue of conflict or quantify the economic loss.

Fujita (1988) reported that pteropodid bats, specifically flying foxes and the lesser dog-faced fruit bat (*Cynopterus brachyotis*), are considered pests by orchard owners interviewed in Malaysia and Indonesia and are therefore shot when they visit these orchards. Fruit growers considered bats to be particularly problematic for rambutan, langsat (*Lansium parasiticum*) and water apple (*Syzygium aqueum*), which are all important market fruits. The owner of one of the largest langsat orchards in Peninsular Malaysia revealed that if measures were not taken to protect his fruit crop several days prior to harvest, 20 % of the crop would be lost to bats. However, he also considered that simple protective measures could be undertaken such as shining bright lamps, lighting fires under the trees, or shooting to scare the bats away, in which case the damage would be negligible. This same orchard owner also appeared to display an understanding of the importance of pteropodids as seed dispersers—he considered that almost all of the langsat trees in his village resulted from seeds dropped by bats. His langsat fruit was typically harvested for sale in the local market.

Fujita and Tuttle (1991) conducted some preliminary investigations into bat pest control in Malaysia and Indonesia, interviewing six plantation/orchard owners and six professional hunters. Owners employed bounty hunters to eradicate bats during flowering and fruiting seasons who could earn up to USD 3 per bat, shooting as many as 100 in one night from a single plantation. A group of three to five hunters regularly patrolled an orchard, using bright lights to locate the bats. According to one hunter, up to seven bats could be hit with a single shot (Fujita 1988). These bats were killed in disproportionately large numbers despite plantation/orchard owners reporting that more significant damage was caused by other animals such as giant squirrels (*Ratufa* spp.), pig-tailed macaques (*Macaca nemestrina*), binturong (*Arctictis binturong*), Timor deer (*Cervus timorensis)* and bearded pigs (*Sus barbatus)*. A professional hunter employed by a pulp and paper plantation in Sabah (Malaysian Borneo) reported that in 1983 alone he purchased 2000 rounds of ammunition for sport shooting of flying foxes that were attracted to the eucalyptus flowers. He also reported that bats were killed in the thousands annually during 1983 and 1984, but that their numbers had been drastically reduced by 1985 (Fujita and Tuttle 1991). Using population models based on roost census data and numbers of hunting permits issued in Peninsular Malaysia, Epstein et al. (2009) found that rates of hunting were unsustainable and would lead to local extinction of *P. vampyrus*.

Gumal et al. (1998) acknowledged that in Sarawak (Malaysian Borneo), an increase in commercial fruit crops, coupled with the loss of habitats such as beach forests, mangroves and peat swamps, has resulted in flying foxes foraging in orchards and farms. This encroachment has led to them being labelled as pests, and it is reasonable to assume that a similar situation occurs in Sabah and Peninsular Malaysia.

On Tioman Island (Peninsular Malaysia), *P. hypomelanus* was reported by local people to feed on a wide range of cultivated fruit trees in their villages, where the bats also roost. This happens despite the fact that wild food resources are still widely available in nearby largely intact forest and has resulted in conflict with villagers despite the fruit being cultivated for personal consumption rather than a source of livelihood. Seeds of mango, cashew and rambutan have been found beneath day roosts, and people also frequently reported that the bats feed on langsat, mata kucing (*Euphoria malaiense*) and various types of *Syzygium* fruits. Durian (*D. zibethinus*) pollen has been found in flying fox faeces, and camera-trapping in durian trees has confirmed that *P. hypomelanus* feeds on durian flowers. Preliminary observations of feeding behaviour suggest that only the nectar is sought, leaving the flowers intact on the branch, and as such, these bats probably perform an important pollination service. Yet some villagers believe that the bats damage or remove the flowers, thereby affecting fruit set (S.A. Aziz, unpublished).

Farmers in Peninsular Malaysia use large, treble fishing hooks and monofilament line set in fruit orchard trees to capture flying foxes. This inhumane method is often lethal, and its efficacy in protecting crops has not been tested. One male *P. vampyrus* used in a satellite telemetry study was captured in a rambutan orchard in Johor, Malaysia, using this method and released after sustaining minor injuries (Epstein et al. 2009; K.J. Olival, unpublished). Gumal et al. (1998) concluded that there is a need to investigate non-lethal methods for protecting orchards and fruit gardens against bats.

In 2005, a newspaper article highlighted the overall decline of *Pteropus* in Malaysia, attributing it to logging and hunting (Teoh 2005). Interestingly, it cautioned that this would negatively affect cash crops such as durian (*D. zibethinus*), petai (*Parkia speciosa*), rambutan and langsat, highlighting the flying fox's role as a pollinator for these trees. However, some confusion may have arisen between flying foxes (*Pteropus* spp., *Acerodon* spp.) and smaller fruit bats such as *E. spelaea*, since Fujita (1988) and Fujita and Tuttle (1991) use the term to refer to all bats of the family Pteropodidae.

In southeast Thailand, fruit farmers stated that Lyle's flying fox (*Pteropus lylei*) damages less than 10 % of harvestable mangoes, and far fewer bananas, water apples (*Syzygium javanicum*) and santol (*Sandoricum koetjape*). Damage is reduced when fruit trees are mixed compared to monoculture systems. Farmers with mango monocultures treated flying foxes as pests, but most farmers with mixed fruit orchards did not regard them as such (S. Bumrungsri, unpublished). According to these farmers, these flying foxes feed mainly on several fig species, especially *F. religiosa* which is regarded as a sacred tree in Buddhist Thailand. These figs are common in the landscape, particularly in temples. Flying foxes also feed on flowers of the agate or hummingbird tree (*Sesbania grandiflora)*, commonly found across South and Southeast Asia and in villages in Thailand, where the flowers and young pods are consumed by people. Farmers also mentioned that flying foxes forage in groups of 10–15 individuals and keep returning to the same feeding area on consecutive nights (S. Bumrungsri, unpublished).

More recently, Weber et al. (2015) conducted GPS tracking of *P. lylei* in central Thailand. Tracked bats were found to forage mostly in farmland, plantations and gardens. All 34 recorded food plant species were noted to also be useful to local people, though not necessarily as fruits for sale or consumption. Thirty-one species were identified as fruit resources, and an unspecified 42 % of these were cash crops (therefore, the only species listed in Table 13.1 are ones that the authors know are cultivated by people in Southeast Asia for either fruits or flowers). Only mango, cashew, banana and tamarind were mentioned specifically as having high economic value or as being cultivated crops. Mangoes were also the most frequently eaten fruit, followed by bananas and tamarind. Such competition for resources between bats and humans was acknowledged as a potential source of conflict. Local farmers confirmed that flying foxes are hunted as an orchard pest in this area.

In Indonesia, Huang et al. (2014) have studied *Cynopterus* feeding in coffee (*Coffea* spp.) plantations in Sumatra. Most growers (93 % of 16 interviewed) reported that bats visit their plantations. Coffee berries are taken to feeding perches and the beans discarded after the pericarp is eaten. This study is now investigating the potential of marketing bat-discarded coffee beans as a premium wildlife product.

A recent dietary study on *P. giganteus* in the Mandalay region of central Myanmar (Win and Mya 2015) also interviewed local villagers to determine the extent of conflict between flying foxes and fruit tree owners. The bats were found to feed on 24 fruit species, 13 of which were also eaten by people. Of these, only three—guava, mango and tamarind—were of commercial importance. *Morinda angustifolia* and *Azadirachta excelsa* are used for medicinal purposes, while *Ceiba pentandra* is still used for stuffing pillows (a practice that is dying out in other Southeast Asian countries). Despite this, local people view the bats positively, and no conflict was reported. The authors of the study concede that a superabundance of mangoes is one reason why people are still willing to tolerate a certain amount of fruit loss.

13.2.5 Australia and Papua New Guinea

Australia has the oldest and most comprehensive records documenting the issue of flying foxes and fruit crop damage. Ratcliffe (1931) provided detailed reports on ‘depredations’ by flying foxes on both commercial orchards and garden trees in New South Wales (NSW) and Queensland. Although flying foxes were known to feed on bananas, citrus fruits, mangoes and grapes, losses were not significant enough for the bats to be considered ‘economic pests’. Slight losses were reported for papayas, some losses for pome fruit (fruits of the family Rosaceae having several seed chambers and an outer fleshy part, such as an apple or pear) and stone fruit (fruits of the genus *Prunus* with flesh or pulp enclosing a stone, such as a peach, nectarine, plum, or cherry), and heavy losses for figs (*Ficus* spp.). For some fruits such as bananas, mangoes and papayas, the regular practice of picking them before they ripen was often sufficient to avoid heavy losses to flying foxes.

Despite these known losses, the extent of flying fox damage to commercial fruit has seldom been quantified in Australia, even in more recent reports. Eby (1995) refers to ‘substantial financial loss to growers’ and lists a relatively large number of commercial exotic fruits on which *Pteropus* spp. feed, although damage was of particular concern to growers of stone fruits and banana. Stacey (1990) refers to heavy stone fruit losses during the prolonged drought conditions of 1986, with bats eating immature green fruit. Waples (2002) reported that most requests for licences to shoot flying foxes in NSW came from growers of stone fruits and lychee, but that damage was also reported to guava, mango, banana, pome fruits and coffee. Signs of damage include broken branches, clawed fruit and fruit remnants under trees (Comensoli 2002). Ullio (2002) reported that from 1995 to 2000, fruit growers in NSW suffered an annual gross market value loss of AUD 10.4 million due to consumption by flying foxes. When taking into account the resulting loss to affiliated industries such as packaging, employment, transport and marketing, the overall financial loss was estimated to be around AUD 26 million annually. Prior to 1998, on the north coast of NSW, only stone fruit, lychee and persimmon were consistently eaten by flying foxes in significant quantities (Rogers 2002). Losses increased dramatically from 1998, particularly in orchards without netting. The stone fruit industry suffered a loss of AUD 4–6 million (not including preharvest costs, which usually exceed AUD 20,000). Sixty per cent of orchards without netting suffered losses of 50–100 %, around AUD 45,000 per grower. The mandarin industry reports losing at least 40 % of its annual crop, while in 2001, an individual lychee grower reported a loss of more than AUD 500,000 in the unnetted section of her orchard (Rogers 2002). Comensoli (2002) measured the damage caused by flying foxes to his nectarine (*P. persica*) orchard, estimating that 20 % of ripe fruit was damaged over a period of 19 days, reducing the annual profit from his entire crop by 16 %. In Queensland, orchardists also suffered particularly high crop damage in the summer of 1998. The estimated total loss for that season was approximately AUD 10 million (Teagle 2002), with some growers having lost up to 90 % of their crop (Dewhurst 1998). It should be noted, however, that the above estimates of orchard losses have not been verified and originate primarily from growers.

Due to this perceived high economic loss, the Australian fruit industry considers species of *Pteropus* to be its main vertebrate crop pests (Ullio 2002). Yet it has been acknowledged, even among fruit growers, that increasing feeding by flying fox on commercial crops is due to the loss of natural food resources as the rainforests, heathland and *Melaleuca* swamps of Australia's eastern seaboard have been increasingly cleared for urban development (e.g. Bicknell 2002; Biel 2002; Gough 2002; Rogers 2002). As a result, Biel (2002) and Rogers (2002) proposed that fruit growers should be financially compensated for economic loss and that the wider community should also bear the cost of mitigation and biodiversity conservation.

Details of bat–grower conflict in Papua New Guinea are scant, but a report by Hicks (1967) stated that bats and birds together caused the loss of 8.7 % of cocoa (*Theobroma cacao*) pods from an orchard from 1962 to 1965.

13.2.6 The Pacific

Luskin (2010) studied the foraging behaviour of the Pacific flying fox (*Pteropus tonganus*) in a landscape mosaic in Fiji. He found that mean foraging density was four times higher in farmland compared to native dry forest, with high foraging competition taking place almost completely in farmland alone. Severe deforestation has resulted in a large bat population that has shifted away from feeding on flowers in forests to feeding more on fruits in farms. However, no observations were made on which type of fruits suffered predation. Farmland resources, with their higher fecundity, now appear to be the staple of *P. tonganus*' diet. Daily, crepuscular mass migration from forests to farmlands has reduced feeding density in forests, thus reducing the aggressive feeding interactions needed to catalyse effective seed dispersal necessary for forest regeneration (McConkey and Drake 2006). The loss of this ecological role could be disastrous for Pacific tropical dry forest, which is a critically endangered habitat (Myers et al. 2000). Also, while the abundance of farmlands has buffered the flying fox population from the effects of extensive deforestation, further research is needed to determine what damage or effects this may have on fruit crops, as well as flying fox nutrition.

In Japan, previous studies on the Ryukyu flying fox (*Pteropus dasymallus*) focused on diet and did not report any conflict with humans (e.g. Funakoshi et al. 1993; Nakamoto et al. 2007, 2009; Lee et al. 2009). In the Ryukyu Archipelago, Nakamoto et al. (2007) reported that Orii's flying fox (*P. dasymallus inopinatus*) on Iriomote-jima Island is a generalist forager, with almost 50 % of its diet consisting of cultivated or naturalised plants. The majority (67.9 %) of its diet throughout the year is composed of fruits. Although its main food resource is *Ficus microcarpa*, the subspecies appeared to adopt a varied diet through intense use of abundant planted trees, as a response to unstable food conditions in an urban environment. Some of these plants are from gardens, parklands and walkways, but others are agricultural plants from plantations. On Iriomotejima Island, Lee et al. (2009) found that the Yaeyama subspecies (*P.d. yayeyamae*) had a comparably less diverse diet and was more abundant in forest compared to cultivated areas, with figs again dominating its diet. Yet bats were still observed in larger groups frequenting villages containing fruit trees. Neither study mentioned predation of economically important fruit as being an issue of concern, and conflict with humans had not been previously identified by anyone as a threat for this particular species.

However, a more recent study by Vincenot et al. (2015) has revealed for the first time that farmers do indeed kill *P.d. yayeyamae*, illegally, because it feeds on crops. Face-to-face interviews and direct observations have shown that flying foxes are frequently killed either through netting, poison or physical beatings, to stop them from feeding in plantations of banana, citrus, guava, loquat, pineapple and sugar cane (*Saccharum officinarum*). This persecution has clearly contributed to continuing declines that were noticeable to interview respondents, and which contradicts the IUCN's decision in 2008 to downgrade the Red List status of *P. dasymallus* from endangered (EN) to near threatened (NT).

13.3 Food-Borne Zoonotic Disease Risk from Pteropodid Bats

An additional concern to crop damage caused by pteropodid bats is the potential for zoonotic disease transmission via fruit contaminated with bat excreta (i.e. saliva, urine, faeces). Old World fruit bats are natural reservoirs to a number of such diseases, including several emerging viruses that have limited or no pathogenicity in their bat hosts but high fatality rates in people. These include Ebola viruses (Leroy et al. 2005), Marburg virus (Towner et al. 2009), Nipah virus (Rahman et al. 2013), Hendra virus (Halpin et al. 2000), and lyssaviruses in Australia (Mackenzie et al. 2003) and Thailand (Lumlertdacha et al. 2005). While the transmission pathway for each virus is not always known, there is compelling evidence, in a small number of cases, that points to a food-borne route, most notably multiple spillover events of Nipah virus from *Pteropus giganteus* to people in Bangladesh (see below). Filoviruses (Ebola and Marburg) are also of great consequence to human health, as evident from the large west Africa outbreak of Zaire Ebola virus that began in early 2014. Much remains unknown about the natural hosts and ecology of filoviruses in bats (Olival and Hayman 2014), but Ebola virus may be transmitted from bats to humans through faeces (Swanepoel et al. 1996), but most likely through direct contact with blood (i.e. preparing hunted bats) (Leroy et al. 2009) or via contact with dead-end host carcasses (e.g. gorillas) (Leroy et al. 2004). Recent experimental studies have shown that Marburg virus can be excreted in bat saliva, answering important questions about its potential zoonotic spread via the oral route (Amman et al. 2014a). It has been postulated that bats and gorillas may share Ebola virus through contact at shared fruit resources, but this has not been verified and additional research is needed to better understand the ecological connections between bats and other mammal hosts in the transmission of these diseases (Groseth et al. 2007; Olival and Hayman 2014).

Henipaviruses (Hendra and Nipah viruses) are recently emerged paramyxoviruses that originate primarily from *Pteropus* spp. as their natural reservoir. Transmission of Hendra virus in Australia and Nipah virus in Malaysia from bats to intermediate or amplifying domestic animal hosts (horses and pigs, respectively) likely occurred though consumption of partially chewed fruit contaminated with bat saliva or ingestion of bat urine under bat foraging sites (Field et al. 2001; Chua et al. 2002). Henipaviruses have been shown experimentally to remain viable on the surface of mango and in other tropical fruit juices (lychee and papaya) from 2 h to 2 days depending on temperature and pH (Fogarty et al. 2008). Similarly, Chua et al. (2002) successfully isolated Nipah virus from a fruit in the wild that was partially eaten by *P. hypomelanus*. Thus, the risk of oral transmission of henipaviruses to humans via consumption of partially chewed fruit exists, although it is likely to be low. However, direct transmission of Nipah virus from bats to people occurs in Bangladesh nearly every year through the consumption of date palm sap, presumably contaminated with urine, saliva or faeces from infected *P. giganteus* (Luby et al. 2006; Rahman et al. 2012). Preventive measures are being used to block bats' access to date palm sap collection pots and reduce the risk of Nipah virus transmission (Nahar et al. 2010). Other mitigation measures that reduce the overall damage of crops by pteropodid bats will further mitigate any risk, however small, of zoonotic disease transmission via this route. Culling bat populations as a form of disease control is rarely effective and often has the opposite effect of increasing transmission and risk. This was recently demonstrated during an attempt to eradicate a population of *R. aegyptiacus* as a form of Marburg virus control, where prevalence of the virus significantly increased after the cull (Amman et al. 2014b). Additional approaches to reducing bat–human contact at potential disease interfaces should be developed, and disease mitigation should be carried out in a way that reduces risk without impacting bat populations.

13.4 Legislative Approach to Reducing Pteropodid Damage to Crops

13.4.1 Australia

Australia has 13 species of pteropodids, seven of which are flying foxes. Some are listed under the federal government's Environmental Protection and Biodiversity Conservation (EPBC) Act 1999 and several state wildlife protection laws.

Flying foxes became protected species in the State of New South Wales (NSW) in 1986 under the National Parks and Wildlife Act 1974. Since then, farmers and fruit growers have been required to obtain licences from the NSW National Parks and Wildlife Service (NPWS) in order to shoot flying foxes to protect their crops (Waples 2002). Licences are granted only when a NPWS representative has visited the orchard to inspect and assess whether the damage is severe enough to warrant culling (Comensoli 2002). Each licence allows a maximum of 50 flying foxes to be shot, and no more than two licences can be granted per landowner per season. Licence holders are required to submit reports on actual numbers of flying foxes killed (Waples 2002). However, in practice, this licensing system is far from perfect, as compliance monitoring and enforcement are neither practical nor feasible, and therefore, records can be unreliable (McLachlan 2002; Waples 2002; Thiriet 2010).

In 2001, the NSW government changed the listing of the grey-headed flying fox (*Pteropus poliocephalus*) from Protected to Vulnerable under the NSW Threatened Species Conservation Act 1995 (Eby and Lunney 2002). This resulted in negative reactions from the commercial fruit industry (e.g. Biel 2002; Bicknell 2002; Bower 2002; Comensoli 2002; Thiriet 2010), as it meant that even if shooting of the threatened species were still permitted for crop protection, it would be subject to a tighter licensing system, resulting in socio-economic repercussions, particularly for small growers (Bower 2002; Comensoli 2002; Ullio 2002; Waples 2002). The state government subsequently continued to allow shooting of the species for crop protection (Thiriet 2010). However, at the time of writing, the NSW government has now banned shooting of flying foxes as an orchard control method (G. Richards, unpublished).

In July 2011, in order to eliminate the need to issue shooting licences and to mitigate flying fox damage to crops, the NSW government introduced a AUD 5 million scheme to subsidise the cost of installing netting for commercial orchardists in the Sydney Basin and Central Coast regions, where impacts occur every year. Once a netting subsidy has been received, the orchardist is no longer eligible for a shooting licence for the netted area of the property. Subsidies are intended to meet half the cost of installing netting and are capped at AUD 20,000 per hectare. Orchardists are responsible for all ongoing maintenance and replacement costs. Not only are flying foxes (and parrots) excluded from the fruit crops, but hail damage is also reduced. This often means that the cost of netting is recovered in the season following its installation. Because netting in now subsidised, from July 2015, licences to shoot flying foxes as a crop protection measure will only be issued where damage to orchards is the result of special circumstances (e.g. the orchard is on terrain too steep to net). The issuing of such licences will eventually be phased out.

P. poliocephalus and the spectacled flying fox (*P. conspicillatus*) were listed as Vulnerable under the EPBC Act 1999, in 2001 and 2002, respectively. One year after its federal listing, *P. poliocephalus* was also listed as Vulnerable in the State of Victoria. Neither the little red flying fox (*P. scapulatus*) nor the black flying fox (*P. alecto*) is listed as threatened under any Australian legislation, and the State of Queensland has yet to list any flying fox species as threatened (Thiriet 2010).

In 2002, the State of Queensland banned the use of electric shocks for crop protection, though this was on grounds of animal cruelty rather than conservation. Prior to this, orchardists could receive a damage mitigation permit for electrocuting flying foxes on overhead grids. The use of such electric grids to kill a keystone species was later found to be in breach of the EPBC Act 1999 (which had led to the listing of *P. conspicillatus*), although this was construed as a negative impact on the world heritage values of a nearby Wet Tropics World Heritage Area rather than a biodiversity conservation issue. Shooting of *P. poliocephalus* and *P. conspicillatus* was still allowed for the purpose of crop protection, with an annual limit of up to 1.5 % of the lowest agreed national population estimate for the species. A quota of 30 animals per orchardist per month was implemented. However, in 2008, the state banned all shooting of flying foxes, again due to concerns over animal cruelty (Thiriet 2010).

In 2012, Queensland reintroduced shooting of flying foxes causing damage to commercial fruit, including *P. poliocephalus* and *P. conspicillatus*. However, shooting quotas for these two species are less than for the little red and black flying foxes, *P. scapulatus* and *P. alecto*. Fruit growers require permits to shoot, which are granted only if they can prove that non-lethal methods of control have failed. Such permits allow the use of shotguns and heavy shot on stationary but not on flying bats. Clear X-ray evidence in Australia (Richards et al. 2012; Divljan et al. 2009) and palpation of lead shot in live and dead bats in Madagascar, the Seychelles (P.A. Racey, unpublished) and Mauritius (V. Tatayah, pers. comm.) reveal that the use of shotguns results in wounding and is inhumane, because death is not instantaneous. Also, Thiriet (2010) pointed out that some bats that are shot may be lactating, and their young left behind in the colony will eventually starve to death. Shotguns were however banned in the Seychelles in the 1970s. The toxic effects of lead shot have been well documented for birds (Mateo 2009), and it is likely to have similar effects in bats.

In both Queensland and NSW, there has been very little (if any) monitoring by relevant authorities of numbers of bats shot in orchards. The only known scientific study was conducted near Sydney in 2007 (Divljan et al. 2009). Over a 140-day period, a total of 164 dead or injured flying foxes were collected and data were compiled from 136 carcasses. Eighty or so bats per week exceeded the number allowed by permits. The sex ratio was strongly skewed towards females (1:1.73), of which 54 (65 %) were lactating at the time. Thirteen of these were shot while carrying their dependent young, while 41 pups would have been left behind in the roost to die. Hence, the total estimate of flying foxes that died due to shooting in the orchard over the two-week period was 205. Collected bats suffered from various injuries, and at least 30 % (44 % including the pups left in the camp) were alive and unattended more than 8.5 h after shooting (Richards et al. 2012). This is in contravention of the definition of 'humane killing' and the Prevention of Cruelty to Animals Act 1979.

13.4.2 Cyprus

In Cyprus, *R. aegyptiacus* was officially declared a pest by the Department of Agriculture in the early 1900s. Destruction campaigns and programs to eradicate the species began in the late 1920s. As in Israel, fumigation of caves also depleted populations of insectivorous bats. In addition, bats were shot, with the government offering free cartridges and payment to participating hunters as well as payment for dead bats. These control campaigns finally ended in 1990 after there were very few bats left (Hadjisterkotis 2006). The species became legally protected after Cyprus law No. 24 of 1988 ratified the Convention on the Conservation of European Wildlife and Habitats. This was made possible when Cyprus became a candidate for European Union membership. As the Convention previously only protected insectivorous bats, in 1993 Cyprus added *R. aegyptiacus* to the EU list of protected bats in Annexes II and IV of the council directive 92/42/EEC on the conservation of natural habitats and of wild flora and fauna (Hadjisterkotis 2006).

13.4.3 Israel

In Israel, two laws protect animals outside nature reserves or national parks. 'The law for the protection of wild animals' concerns hunting and is considered to be stronger legislation than `The law for the protection of natural values'. The former aims mainly to regulate hunting (what, how and where?) and lists all protected mammals, including some non-local species. The second law aims to protect aniChironax melanocephalus are listed asmals, plants, fossils and speleothems.

R. aegyptiacus is protected by neither law and is considered a pest. Although it is legal to kill fruit bats, cruel killing is forbidden by the 'Animal welfare act'.

Fruit bat colonies are protected in national parks and nature reserves, but if the bats' foraging sites are outside protected areas, then they may be legally killed.

Israeli conservationists have had protracted negotiations with the Ministry of Agriculture regarding Israel joining the EUROBATS agreement. Although that is likely to happen in the near future, a derogation will be sought to maintain the pest status of *R. aegyptiacus*, at least for the immediate future (A. Streit, pers. comm.).

13.4.4 Japan

Pteropus dasymallus is one of the only two pteropodid species found in Japan, and as such, it is protected at both national and prefectural levels. Both the Daito (*P. dasymallus daitoensis*) and Erabu (*P.d. dasymallus*) subspecies are listed as critically endangered (CR) on the IUCN Red List, but *P.d. inopinatus* and *P.d. yayeyamae* are not even listed, and the latter two subspecies are only considered as NT in prefectural assessments (Vincenot et al. 2015).

Despite a severe lack of data on the population and conservation status of this species, the IUCN identified its threats only as habitat destruction, electrocution on power cables and occasional accidental entanglement in nets (Heaney et al. 2008). Yet Vincenot et al. (2015) have uncovered evidence of conflict between *P.d. yayeyamae* and humans on all fruit production islands in the Yaeyama archipelago that they visited. The only island without conflict, Kuroshima, focuses on cattle production instead. This conflict has led to severe declines in flying fox populations throughout the archipelago. It is likely that a similar situation occurs on Okinawa Island, where *P.d. inopinatus* occurs, as there is higher urbanisation and more agricultural fields there, and crop destruction by flying foxes was reported there in a 2013 Japanese-language news article. In the light of this new evidence, the conservation status of this species needs to be carefully reassessed, with population monitoring and conservation programmes being clearly necessary requirements.

13.4.5 Malaysia

In Malaysia, wildlife is governed under three distinct legislative systems according to the three main geopolitical regions: Peninsular Malaysia, Sabah and Sarawak. Protection of the country's two species of flying fox (*P. hypomelanus* and *P. vampyrus*) varies within and across each of the main geopolitical regions. In Peninsular Malaysia, the Department of Wildlife and National Parks (also known as PERHILITAN) regulates wildlife policy and hunting. For nearly 40 years, wildlife conservation policy was determined by the Protection of WildLife Act of 1972, which listed both flying fox species under Schedule II, or Protected Wild (Game) Animals. Hunting of both species is allowed with a permit, and there are no seasons or limits to the numbers of permits that may be issued by a state in Peninsular Malaysia. In 1990, under the Protection of Wild Life Amendment Order, a bag limit was set that allowed 50 bats to be shot under a single permit and the time of hunting was limited to 0700–1200 h and 0500–0700 h each day. Each licence costs MYR 25 (USD 8) (Teoh 2005). No other bats are listed. As in Australia, such a licensed hunting system is difficult to monitor and regulate.

A study by Epstein et al. (2009) evaluated the abundance and roost distribution of *P. vampyrus* in Peninsular Malaysia, finding that the number of hunting licences issued had doubled since 1996, and concluded that current levels were unsustainable and likely to cause local extinction within 6–81 years. Further, these estimates of hunting pressure from licence data were likely to be an underestimate as they did not include illegal hunting, and there was also a provision in the 1972 Act that allowed killing, shooting or removal of an unspecified number of any wild animal that is 'causing damage or there is reason to believe that it is about to cause serious damage to crops, vegetables, fruit, growing timber…if reasonable efforts to frighten away the wild animal have failed'.

The study by Epstein et al. (2009) was highlighted in the media (Burns 2009; Kandasamy 2009) and prompted a response from PERHILITAN that they would consider implementing a hunting ban as part of the then current review of the act. However, when the act was repealed in 2010 by the new Wildlife Conservation Act 2010 (Act 716), flying foxes had still not been moved from the 'Protected' list to the 'Totally Protected' list, meaning that licensed hunting is still permitted, and the provision for protecting crops (Part VI, sec 54) is also still permitted in the new legislation.

In February 2012, following lobbying and recommendations from conservation research group Rimba, the Terengganu state government implemented a state-wide moratorium on hunting of flying foxes (Rimba 2012). Prior to this, the State of Johor had banned hunting of all wildlife when its Sultan issued a royal decree to this effect (Charles and Benjamin 2010). However, to date, no nation-wide hunting ban has been announced by PERHILITAN at the federal level, and other bat species remain unprotected.

As in Peninsular Malaysia, in Sabah, the two flying fox species are currently listed under Schedule 3, sections 2, 25(2) as 'Protected species of animals for which hunting licence is required' under the Wildlife Conservation Enactment of 1997. However, there is no clear provision for shooting animals to protect crops without a licence, and no other bat species are legally protected.

In Sarawak, research by Gumal et al. (1998) successfully resulted in all bat species in the state being listed as 'Protected' in May 1998, under Part II of the Sarawak Wildlife Ordinance 1998 (with the exception of *Cheiromeles torquatus* that is listed in Part I, as 'Totally Protected'). The Sarawak Forest Department does not allow legal bat hunting and has implemented some of the strictest policies in Malaysia to regulate guns and ammunition and decrease the extent of wildlife poaching.

13.4.6 Mauritius and Madagascar

In 2006, the government of Mauritius proposed changes in legislation to allow culling of the only pteropodid on the island, the endemic *P. niger,* as a result of losses of marketable fruit, principally lychees. Any effect of this change was confounded, however, by existing legislation that prohibited the discharge of firearms after dark or with the aid of lights, and in the event, in one year, only six bats were officially killed. The proposal to cull an endemic species (albeit only in fruit orchards) on an island where two species (small Mauritian flying fox *P. subniger* and Rodrigues flying fox *P. rodricensis*) had already become extinct as a result of cyclones, habitat loss and overhunting was a major factor in the upgrading of the Red List status of *P. niger* in 2008 from Vulnerable to Endangered. Pressure on the government from growers of commercial fruit, particularly lychees, but also longans and mangoes, resulted in surveys of bat numbers by the National Parks and Conservation Service (NPCS). In November/December 2010, 49–56,000 bats were counted at 47 roost sites. This was broadly consistent with the results of an earlier count by Robyn (2007) of 12–16,000 bats at 24 of 57 known roosts. As a result, the Red List status of *P. niger* was downgraded from Endangered to Vulnerable in 2013.

Despite assurances from NPCS that there were no plans to cull bats, the National Terrestrial Diversity and National Parks bill was being considered by parliament in May 2012 and has been the subject of a public consultation. It allows for the culling of species that have attained high numbers and pest status. Irrespective of this, the Mauritian Wildlife Foundation, the main conservation NGO on the island, reports that up to 2000 bats are shot annually by hunters and fruit growers.

In Madagascar, bats are ‘animaux gibiers,’ i.e. game animals, and can be hunted legally although there is a close season coinciding with pregnancy and lactation. Officially, licences are required by hunters, but in practice, this is not usually observed, as enforcement is challenging to implement. Some hunters observe the close season (P.A. Racey, unpublished).

13.4.7 South Asia

In India, all pteropodid species with the exception of the Critically Endangered *Latidens salimalii* are categorised as vermin and included as such in Schedule V of the Indian Wildlife (Protection) Act 1972 and Amended Acts. However, only three of the thirteen species—*P. giganteus*, *R. leschenaultii* and *C. sphinx*—feed extensively on commercial fruit, and the remaining ten species forage mainly in forest where they play an important role in pollination and seed dispersal, and there is no evidence that they visit commercial orchards. The Indian government has ignored successive attempts by conservationists to have forest bats delisted (Singaravelan et al. 2009).

In Bangladesh, the newly revised Wildlife Preservation and Security Act 2012 protects all species of bats. Hunting is prohibited without government permission and a licence, and offenders can face imprisonment and/or a fine (Act translated from Bengali by A. Islam, pers. comm.).

In Pakistan, *P. giganteus* is listed in the fourth schedule of the Punjab Wildlife (Protection, Preservation, Conservation and Management) Act 1974, which specifically includes animals that have no legal protection and can be hunted.

In Sri Lanka, the Fauna and Flora Protection Ordinance 1937 (amended 2009) provides protection for all bat species in the country, and hunting is strictly prohibited. Bat roosts such as caves are not currently protected, but the Department of Wildlife Conservation is currently in discussion to protect such sites as refuges by law (W. Yapa, pers. comm.).

13.4.8 Thailand

In Thailand, all species of *Pteropus* (*P. hypomelanus*, *P. intermedius*, *P. lylei*, *P. vampyrus*), nectarivorous bats (*E. spelaea*, *Macroglossus minimus* and *M. sobrinus*) and *Chironax melanocephalus* are listed as ‘protected animals’ under the Wildlife Protection and Reservation Act 1992. Another 13 bat species found in Thailand, including all *Cynopterus* and *Rousettus,* are not protected. However, all animals are protected within designated areas, which include national parks, wildlife sanctuaries, and religious establishments (temples, mosques).

Out of a population of 38,000 bats forming 16 colonies of *P. lylei* in central Thailand, 90 % (13 colonies) are found in temples (Boonkird and Wanghongsa 2004), and thus their roosting colonies are well protected. In contrast, most known colonies of *P. vampyrus* and *P. hypomelanus* are found outside protected areas and therefore suffer from hunting and roost disturbance, except for colonies on oceanic islands. Generally, due to cheaper prices and greater abundance of fruit crops in Thailand, along with smaller population sizes of flying foxes, *Pteropus* spp. are less likely to be regarded as crop pests. However, smaller fruit bats such as *Cynopterus* spp. and *Rousettus* spp. are common and are still regarded as pests. Hunting and selling of flying foxes is widely known to be illegal. Attempts should be made to protect roosting sites outside designated protected areas.

13.5 Non-lethal Methods of Mitigation

13.5.1 Netting and Associated Tree Management

The only demonstrably effective method of preventing loss of fruit to bats and birds is full exclusion netting. The country in which this has been deployed to the greatest extent and most successfully is Australia where some large fruit orchards are enclosed in nets supported by cables, frames or posts (Minifie and Willis 1990; Campbell and Greer 1994; Gough 1992; Stacey 1992; Hall and Willis 1992). The netting has a mesh size of about 48 mm, is erected well above the height of the trees and is also attached to the ground at the edges (Fig. 13.1). Such orchards extend to 90 ha in area (G.C. Richards, unpublished), and the nets protect the crops from bats, other mammals (including possums), birds and hail. Estimates of the cost per hectare of netting vary widely from AUD 6,000 (from a conservationist) to AUD 60,000 (from a fruit grower) (Don't Shoot Bats 2013). Several

Fig. 13.1 Nets supported by frames in Australia over apples and stone fruit (*Photograph* Greg Richards)

state governments now subsidise the erection of netting for orchardists, and most of those interviewed considered that the structures pay for themselves at the first harvest.

But while netting may work for some, issues remain with its implementation in Australia, resulting in poor uptake among some growers (Gough 2002; Ullio 2002). Exclusion netting is costly and thus may not be economically feasible, particularly for smallholdings when flying fox damage is inconsistent and unpredictable from year to year (Slack 1990; Tidemann et al. 1997; Bower 2002; Gough 2002; McLachlan 2002; Rogers 2002; Ullio 2002). Many growers are reluctant to take on this added financial burden and are unlikely to net their crops (Ullio 2002). Bicknell (2002) pointed out that the financial cost of maintaining netting is too great, and it brings an added risk as a fire hazard. Comensoli (2002) further stated that the annual cost of leasing finance for netting outweighed the actual cost of flying fox damage to his crops. He and Ullio (2002) also pointed out that netting creates a microclimate within the orchard that results in poor fruit yield and inferior fruit quality—an experience echoed by other growers, with at least one case of netting in a lychee orchard resulting in a fungal disease (Bicknell 2002).

However, many orchards can be netted as long as they qualify for a state government subsidy, which is often 50 % of the cost. For example, the netted orchard shown in Fig. 13.1 was able to recover its costs at least by the second season, and with 18 ha (40 acres) now protected not just from bats, but also birds and hailstones, it produces top-quality fruit at high prices and with an environmentally-friendly tag. It used to be thought that because flying fox damage was sporadic and netting might have detrimental effects on crop growth, permanently netting an orchard was not viable for some orchards (Comensoli 2002; Rogers 2002; Ullio 2002). However, now that the industry has settled on a mesh size of 48 mm, so insect pollinators can freely access fruit trees, detrimental effects are no longer reported.

Netting is still not suitable for the banana industry, where plantations are often located on steep slopes that are impossible to net (Bower 2002; Rogers 2002; McLachlan 2002). In some cases, farmers who cannot afford to net have been forced out of business by heavy losses to flying foxes and other frugivores (Rogers 2002). This industry should investigate specific options and provide research funding for trials of innovative ideas, such as solar-powered ripening bags. To ensure that bananas ripen evenly, in Australia each bunch is covered with a plastic bag so that the ethylene by-product is evenly distributed. Once flying foxes smell the ripening aroma, they home in on bunches that they know to be palatable. A solar-powered bag with a low-voltage electric barrier would humanely deter flying foxes, and they would eventually learn not to tear bags open to feed.

A decade after the earlier reports, it is becoming increasingly accepted that netting of orchards is the only method of ensuring their full protection. In Australia, consumer expectations of high-quality fruit are acknowledged by major supermarket chains, so all fruit must be unmarked. Netting that excludes flying foxes, parrots and hail is now considered an industry standard by large producers, so it is only small family orchards that usually do not install nets. Because netting entire orchards is expensive (Reilly and Slack 1990), it can only be undertaken when large-scale farming of cash crops makes it cost-effective and justifies the investment.

Commercial crops are also protected by netting in Israel (Korine et al. 1999) and Thailand (Fig. 13.2) (S. Bumrungsri, unpublished), where fixed nets that cover the trees are most effective, although some growers also use mist nets despite their untested efficacy. They are usually lethal to bats, which are not always removed from the nets (C. Korine, pers. comm.). In Thailand, some fruit farmers also erect mist nets in their orchards, leaving tens or hundreds of nectarivorous bats (e.g. *E. spelaea*) to die (S. Bumrungsri, unpublished).

In some countries, such as Mauritius, entire lychee trees are netted and the government encourages this by subsidising 75 % of the cost of 10 nets per grower. However, individual growers may have 200–300 trees, and the method is applicable only to relatively low-growing orchard trees and not to the much older and larger 'backyard' trees which produce a significant proportion of the national lychee crop.

In Thailand, entire longan trees or groups of trees are covered by either plastic sheets or netting and the former also accelerate ripening (Fig. 13.3) (S. Bumrungsri, unpublished). Farmers actively prune these trees after harvesting, in order to maintain their low stature so that the trees are easily covered with netting during the next fruiting season. A cheaper method of mitigation used in

Fig. 13.2 Netted longan orchard in Thailand (*Photograph* Sara Bumrungsri)

Fig. 13.3 Longan trees covered by nets in Thailand (*Photograph* Sara Bumrungsri)

Mauritius and Cambodia involves the use of panicle nets consisting of small net bags commonly used to package vegetables, which are of an appropriate size to fit over an immature lychee panicle and can be reused from year to year (Fig. 13.4).

In Mauritius, trees are also pruned to make it easier to cover them with nets, but this involves some loss of productivity until they grow new fruit-bearing branches. When new orchards are planted, dwarf varieties are recommended (as bats prefer feeding on taller trees) and trees are now more widely spaced and are kept pruned to a height that facilitates the deployment of panicle or whole-tree nets. This lowers fruit production for the first three fruiting seasons, but production increases after that. When nets are supported by frames or poles, trees must also be pruned so that they do not grow into the net. This active pruning technique can also be applied to rambutan and lychee. Some nets are removed at the end of the fruiting season and replaced at the beginning of the next. However, most growers leave the nets in place for several seasons (V. Tatayah, pers. comm.).

Much fruit is picked before it has fully ripened and becomes attractive for flying foxes. Mango farmers in north Queensland stated in interviews (G.C. Richards, unpublished) that they harvested their crop just at the onset of ripening, well before it became soft enough to be highly attractive to bats. As well as being too hard to bruise during transport to markets as a high-quality product, there was negligible loss to the growers. By the time flying fox raids began to increase, the remaining crop was high on the trees and difficult to harvest and was left for wildlife.

Fig. 13.4 Net bags enclosing lychee panicles in Mauritius (*Photograph* Vikash Tatayah, Mauritian Wildlife Foundation)

In Bangladesh, a simple cost-effective method is used to prevent bats (including *P. giganteus* and smaller fruit bats, *Cynopterus* and *Rousettus* spp.) and other pests (e.g. birds) from accessing date palm sap during collection. This involves the use of bamboo skirts that cover the top of the collection pot and the shaved part of the palm tree (Nahar et al. 2010) and has been enthusiastically adopted by palm sap collectors (gachhis) (Fig. 13.5). Without it, date palm sap contaminated with bat faeces and urine is of lower quality and value, and, importantly, the risk of Nipah virus transmission is also reduced by using bamboo skirts over collection pots (Nahar et al. 2010).

13.5.2 Decoy Crops

A decoy crop produces less valuable or non-commercial fruit which is more attractive to bats than the crop to be harvested. Before selecting a plant species as a decoy crop, the feeding habits and preferences of the bats should be established. There have been many relevant studies. For example, in the Indian Ocean, Racey and Nicoll (1984) listed the food plants of the Seychelles flying fox (*Pteropus seychellensis*), while Nyhagen et al. (2005) did so for *P. niger* on Mauritius. Bollen and van Elsacker (2002) and Long and Racey (2007) studied the diet of the Madagascan flying fox (*Pteropus rufus)* in Madagascar and showed that bats feeding within 100 km of one another shared few food plants. The diet of another

Fig. 13.5 Bamboo skirt to prevent bats from accessing palm sap in Bangladesh. *Photograph* JH Epstein/EcoHealth Alliance

Malagasy endemic *Eidolon dupreanum* was described by Picot et al. (2007). Stier and Mildenstein (2005) studied the dietary habits of *P. vampyrus* and *Acerodon jubatus* in the Philippines. Parry-Jones and Augee (2001) and Williams et al. (2006) investigated food resources and the effect of food availability on the occupation of urban areas by *P. poliocephalus* in Australia, where Richards (1990) also described the diet of *P. conspicillatus*. Bumrungsri et al. (2007) reported on the diet of two species of *Cynopterus* in Thailand, and Hodgkison et al. (2003, 2004) studied nine fruit bat species in Peninsular Malaysia.

However, only a few studies have sought rigorously to establish feeding preferences: Korine et al. (1998) for *R. aegyptiacus*, Yapa et al. (1999) for *C. sphinx*, Nelson et al. (2005) for the Pacific flying fox (*Pteropus tonganus*), and Andrianaivoarivelo et al. (2012) for the Madagascan rousette (*Rousettus madagascariensis*). Bats were briefly taken into captivity to assess their fruit preferences. The first study compared fruits preferred by bats with those eaten by birds, and found that while bats ate 100 % of the introduced fruit species they were offered, only 14 % of native fruit species offered to them were actually consumed—suggesting that *R. aegyptiacus* only became common in the eastern Mediterranean with the introduction of new cultivated plants (Korine et al. 1998). The second study found that out of three different types of fruit offered, guava was the most preferred, followed by sea almond (*Terminalia catappa*) and mango, with fully ripe fruits being preferred over semi-ripe fruits. It concluded that this provided some support for farmers' claims that bats caused damage to their crops (Yapa et al. 1999). The third study tested fruit choice in relation to nutritional requirements. Flying foxes were found to prefer low-calcium, high-sugar fruits such as papayas, but although sugar was the primary basis for fruit selection, pregnant and lactating females required greater amounts of calcium. However, the flying foxes in this study consistently avoided figs, which are excellent sources of calcium (Nelson et al. 2005). In the last study, bats were found to prefer native and commercially unimportant figs (*F. polita*), rose apple (*Syzygium jambos*) and mountain apple (*S. malaccense*) to the cash crops of lychees and persimmon (Andrianaivoarivelo et al. 2012). These important results provide a perspective on the dietary preferences of pteropodids and should be repeated with other species.

There is convincing evidence that planting *Muntingia calabura*, which is very attractive to *C. sphinx*, can lessen the impact of these bats on commercial fruit. Singaravelan and Marimuthu (2006) showed that *C. sphinx* visited *Muntingia* more than any other wild or commercial fruit and recommended that it is planted around fruit orchards. Verghese's (1998) study on grapes in India found that less bat damage occurred closer to a mango orchard and suggested that presence of these trees deters the bats from feeding on grapes. However, it may be that the fruit bats simply show a stronger preference for feeding on mangoes (e.g. Ayensu 1974; Mahmood-Ul-Hassan et al. 2010). It would thus be useful to compare the results of Verghese's (1998) study with a similar study in the adjacent mango orchard.

Law et al. (2002) recommended planting trees which fruit in spring in Australia to relieve the flying fox damage suffered by orchardists at that time of year. Although the effectiveness of these decoy crops is yet untested, there is evidence that *P. poliocephalus* will cease consumption of commercial fruit if alternative native foods become available (Eby 1990). However, in order to be effective, the selection of plant species must be based on their high productivity and attractiveness to bats as well as producing fruit at the same time as the commercial crop. Local site conditions must also match the specific needs of the plant in order to ensure optimum growth. Most importantly, these food trees should not be planted in the immediate vicinity of orchards but located away from commercial fruit-growing areas in order to attract the bats away from orchards (Law et al. 2002). The authors also suggest that planting *Syzygium* around commercial fruit trees may reduce the feeding of bats on the latter. As these planting schemes still need to be tested for effectiveness, Law et al. (2002) suggested monitoring results through regular mapping and identifying dietary changes in the bats.

13.5.3 Deterrents/Aversion Agents

There is some evidence that strong smells such as rotting fish may deter bats from approaching ripening fruit and trials to investigate this are currently under way in Thailand (S. Bumrungsri, unpublished). Bicknell (2002) suggested that smoke could be used as an aversion agent, since it is known among Australian orchardists that it is disliked by flying foxes. On Tioman Island in Malaysia, anecdotal information from local communities relates that people build fires under roost trees in order to smoke out flying foxes, although the efficacy of this method is only temporary as it does not deter them from returning (S.A. Aziz, unpublished).

Over the last 30 years in Australia, deterrents used by fruit growers have included flashing and rotating lights, electronic distress sounds, gas-operated bird scare guns, electric shocks, and smell and taste deterrents. However, most of these are used in isolation and their effectiveness has not been systematically assessed, with results being mixed and most evidence anecdotal (Ullio 2002). A project to trial smell and taste deterrents was carried out by the Queensland Parks and Wildlife Service (QPWS) and the Queensland Flying-fox Consultative Committee (QFCC) in 2000. This involved three different commercial products for repelling animals, but none provided complete protection, and the results were ultimately inconclusive due to the small scale of the testing. A plant secondary compound was also tested, with more promising results, and further trials were planned (Teagle 2002), although the outcome is unknown. Bicknell (2002) considered that shooting to frighten, rather than shooting to kill, could also be an effective method.

A noise deterrent was developed in Australia in the late 1990s that reduced orchard crop losses caused by *P. conspicillatus* and *P. poliocephalus*, which was an adaptation of a bird deterrent known as the ’Phoenix Wailer’ (Phoenix Agritech Canada Ltd). In essence, it was a sound system with four stereo channels. Each channel had a speaker in the centre of the crop and another at a corner. Sounds were randomly played on each channel, with the sound appearing to come from the centre of the stereo pair. Pellet scars on wing membranes of a large proportion of flying foxes captured in Australia indicate that they had been targeted using shotguns, and therefore, the deterrent system also reproduced a shooting scenario. Sounds of humans (motorbikes, dogs barking) came from one channel, then randomly from another channel came sounds of shotguns, and then from another the screams of a wounded flying fox. Trials in several fruit-growing areas were successful, but the results were not accepted by the industry, which instead called for government trials although these were not implemented. The fruit-growing industry itself did not support independent trials, so this novel approach to mitigation has not been adopted (G.C. Richards, unpublished).

An ultrasonic repeller (Ultrason-X; Bird-X Inc, Chicago) was ineffective at preventing damage to longan panicles by *P. niger* in Mauritius. A similar device (Sonixgate, Tikod Trade Ltd. Tel-Aviv www.batman.co.il) is used in Israel in lychee orchards where it is popular with users, although its effectiveness has not been independently established (C. Korine, pers. comm.). Bomford and O'Brien (1990) reviewed the effectiveness of several sonic deterrent devices in animal damage control, although most tests did not involve bats. They pointed out that the efficacy of ultrasonic deterrents for bats was controversial, and there was no evidence that such devices had practical value. They concluded that broadcasting distress or alarm calls was probably the most promising noise deterrent method.

13.5.4 Combined Methods of Mitigation

In India, partially covering vulnerable sections of the canopy of fruit trees, illumination and scaring with noises saved 4.5, 6 and 11 % of the fruits of sapota, respectively (Chakravarthy and Girish 2003). However, the effectiveness of these methods was temporary, and for longer term protection, three methods were recommended: planting non-commercial species of figs attractive to the bats; dividing orchards into smaller plots so that trees may be covered with sprigs of foliage, thatch or nylon net; and covering bunches of grapes with dry sprigs of foliage, netting, use of firecrackers or electric fencing. Also in India, Verghese (1998) found that grapes in vineyards could be protected from bat damage if nylon netting is erected around the trellis-grown bower up to bower height, combined with using twigs and briers to cover canopy gaps in the bower.

A combination of lights, noises and plastic flags is widely used in Mauritius (V. Tatayah, pers. comm.).

13.5.5 Biological Control Agent—Weaver Ants Oecophylla longinoda

During an interview survey in Guinea, west Africa, almost half of farmers reported that bats fear the weaver ant *Oecophylla longinoda*, and more than half appreciate that orchards with abundant weaver ants experience less fruit damage due to the ants' protective role, possibly because bats are repelled by the smell of the ants. However, 40 % of farmers also felt that the weaver ant itself is also a form of pest, as it rolls up leaves and is a nuisance during harvest (Van Mele et al. 2009). Yet this species is considered by entomologists and ecologists to be a potential biological control agent (Van Mele 2008). Lokkers (1990) has also suggested the potential of using weaver ants to reduce fruit damage by bats in Australia. However, this proposed method would require a native weaver ant species and requires further research and field trials.

13.6 Recommendations and Issues for Future Consideration

According to opinions from both conservationists and some orchardists, shooting is not an effective means of mitigating flying fox damage to fruit crops, particularly when animal numbers are high (Hall and Richards 1987a, b; McLachlan 2002; Ullio 2002; Thiriet 2010). Most fruit damage occurs when the bats' native food supply is drastically lowered due to droughts or nectar washout (i.e. when heavy rain washes the nectar off the flowers), and killing does not prevent damage in orchards under high flying fox pressure. Because of the bats' mobility, shooting will not stop bats from foraging, as a continuous stream of animals will move into the site from further afield (Martin and McIlwee 2002). Shooting flying foxes has thus become an unnecessary persecution. Hundreds of thousands have been killed in Australia's east coast, even though for 80 years it has been known to be ineffective.

The most effective method to date for reducing crop loss not just to bats, but also to birds and hailstones, is full exclusion netting. If growers' estimates of orchard losses to animals have some credence, then their exclusion is the most appropriate management option. The implementation of such an effective mitigation measure should thus be explored in other countries that experience problems of bat damage to fruit crops. This requires full cooperation between the fruit industry, relevant managing authorities from the government, scientists and conservationists.

In addition to this, below we summarise some main issues that warrant more detailed attention and action in order to resolve the conflict between pteropodid bats and fruit growers.

13.6.1 Better Knowledge of Pteropodid Diet and Foraging Preferences

Studies from Cyprus, Israel, Madagascar and Pakistan have shown that fruit bats prefer native wild fruits compared to commercial fruit crops (Korine et al. 1999; Mahmood-Ul-Hassan et al. 2010; Del Vaglio et al. 2011; Andrianaivoarivelo et al. 2012). These findings can be used as a compelling argument in mitigating conflict with orchardists (Del Vaglio et al. 2011) and to prevent deliberate killing of bats for crop protection. However, examples from Australia, Fiji, India, Japan and Malaysia show that depletion of food resources due to habitat loss can drive flying foxes to feed in fruit orchards (Gumal et al. 1998; Verghese 1998; Tidemann 1999; Nakamoto et al. 2007; Luskin 2010). Any mitigation efforts therefore must ensure that wild food sources continue to be maintained in the long term, and where these have been depleted, tree-planting must be carried out to replenish the loss. This is especially important because Nelson et al. (2000) showed that there are negative nutritional consequences for flying foxes which change their diet from native to agricultural fruits.

However, Biel (2002) reported that even when much native blossom was available nearby, *P. poliocephalus* still preferred to feed on fruit crops, and Bower (2002) stated that it appears to prefer lychees 'over all naturally available foods'. Rogers (2002) reported that flying foxes on the North Coast of NSW were initially only a problem for the stone fruit, lychee and persimmon industries, but that once more of these orchards started adopting netting, the bats began moving on to bananas, coffee, mandarins and mangoes. This was exacerbated in 1999 and 2000 by a decrease in native food, with McLachlan (2002) reporting a similar issue for the 2000/2001 season. Yet there is some evidence that flying foxes will cease to feed on commercial fruit crops if their native food sources again become available in the wild (Eby 1990; Andrianaivoarivelo et al. 2012). The solution may thus consist of a careful selection of preferred tree species planted in appropriate locations away from fruit orchards (Law et al. 2002). Such methods are as yet unproven and require further trials and research.

13.6.2 Funding Interventions and Research to Mitigate the Pteropodid–Grower Conflict

Bicknell (2002) advocated an urgent need for funding research into non-lethal aversion agents to mitigate flying fox damage. Such research funds have not yet been made available in Australia. Individual government authorities have been reluctant to take ownership of the problem, while industry organisations do not view it as an industry-wide issue, as the majority of fruit growers in some parts of the country are not affected. Apart from research into specific mitigation methods, there is also a need to study netted orchards in order to determine the effects of netting—not just on the environment created under the net and on the ripening fruit, but also the implications of excluding other potential pollinators such as birds and insects. Ultimately, however, aversion agents and cheaper methods would be a preferred method for many orchardists in Australia compared to netting or even culling (Ullio 2002), and funds should be provided to develop and test such methods (Bicknell 2002; Bower 2002; Thiriet 2010). Thiriet (2010) also suggested that the dearth of such funding is caused by negative community attitudes and political considerations, which may influence the inaccurate conservation status of some species of flying foxes, such as Least Concern as in Queensland. The unpopularity of these species must thus be overcome in order to attract appropriate research funding.

Australian orchardists maintain that it is the government's responsibility, not theirs, to fund the research (Bicknell 2002) because they believe it was not orchards which caused the habitat loss driving this problem (Tidemann 1999). Bicknell (2002) pointed out that orchards provide flying foxes with food when wild resources are scarce. He also highlighted how government departments are responsible for releasing large areas of flying fox habitat for logging and agriculture and that therefore, the financial burden of protecting crops from flying foxes should be borne by the authorities. Biel (2002) echoed this concept of 'public good conservation', stating that flying fox conservation benefits the wider community, and cited examples of other projects that utilised the community benefit approach. He pointed out that the loss of native flying fox food in Australia was caused by ‘the people who lived in the cities’, since most fruit orchards were established on land that had already been previously cleared for cattle grazing. Fruit growers could thus be said to have revegetated the land, and therefore, it is unfair that they alone should bear the cost of protecting flying foxes. Martin and McIlwee (2002) agree with this and recommend that the cost of netting should be subsidised by federal funding.

13.6.3 Education of Growers and the Public

Apart from research into damage mitigation methods, there is also an urgent need to educate fruit growers and increase their awareness on the ecological and economic importance of pteropodid bats. Huang et al. (2014) found that in Sumatra, less than 20 % of coffee growers interviewed ($n = 16$) were aware that bats were pollinators, and none were aware that bats dispersed seeds. As demonstrated by Bumrungsri et al. (2008, 2009), pteropodids are major pollinators for some commercially important fruit trees, even when the bats may not be the most frequent visitors. In northern Queensland, *P. conspicillatus* plays a vital role in rainforest reproduction through pollination, and although these bats may affect the fruit industry, there has never been a full study of the economic value of flying foxes as pollinators of eucalypt hardwood forests in Australia. The majority of timber trees harvested on the east coast produce nectar and pollen only at night (P. Birt, unpublished). This means that as flying fox populations decrease, fewer timber trees will join the logging cycle.

More importantly, pteropodid bats play a major role in seed dispersal. The further that a fruit is dispersed from the parent tree, the greater the chance of any resulting seedlings surviving to maturity. Fighting over feeding territories (the squabbling heard at night) leads to the loser departing with a fruit in its mouth, and consuming it at a distance. This has been termed the ‘raiders versus residents’ seed dispersal model (Richards 1990), tested by McConkey and Drake (2006) in Tonga, where they showed that once numbers of flying foxes declined below a threshold where there was no conflict over feeding territories, then seed dispersal away from the parent tree ceased.

Therefore, while economic estimates of fruit loss are an important first step in quantifying the problem of crop damage, a cost–benefit analysis that takes into account the positive economic impact of ecosystem services provided by the same bat species (e.g. pollination and seed dispersal to maintain healthy forests) is needed. The resulting data must be shared and communicated to growers and orchardists. They will form a crucial component in mitigating conflict, as at least one example from an Australian orchardist shows that ignorance can lead to opinions that the ecological role of flying foxes is negligible. The orchardist claimed to have seen no evidence that flying foxes are essential to forests (Bicknell 2002). This shows that in some cases, feeding on fruit crops can create a negative bias among fruit growers against the beneficial aspects of bats. Therefore, bat conservation must also extend to educating and raising awareness of the farmers and fruit growers who bear the brunt of bat damage to their crops.

In Australia, NSW Agriculture suggested that in order to address and overcome the conflict between fruit growers and flying foxes, a NSW Flying-fox Consultative Committee should be formed along the lines of the Queensland Flying-fox Consultative Committee (QFFCC). This would include a dedicated Flying-fox Management Unit that would be responsible for population monitoring, community liaison, research and compensation to growers (Bower 2002). The QFFCC's role included providing a forum for multi-stakeholder consultation, providing advice on policy development, developing strategies to address crop damage, and disseminating information to stakeholders (Teagle 2002). This model of collaborative approach involving all interest groups should be adopted in other countries where pteropodid feeding is a serious concern for their respective fruit industries. However, support for this type of consultation is entirely dependent upon the policies of the government of the time. No consultative committees now exist in New South Wales or Queensland, and the government of the latter state actively supports the destruction of flying foxes in orchards.

In the Mascarene Islands, public education programmes about *P. rodricensis* on Rodrigues since 1998 have led to a sense of pride in this species among the inhabitants, despite the fact that the increasing bat population (>20,000 individuals on an island area of 109 km^2) damages the fruit on backyard trees and causes some discontent. While Rodriguans complain about loss of fruit, they are still tolerant of the bats, as a result of positive messages in schools and communities, and are less inclined to call for culling as a solution to the crop-raiding issue (V. Tatayah, pers. comm.).

13.7 Conclusions

Pteropodid bats can reduce the harvestable yield of a wide range of fruit crops, resulting in economic losses that can be severe. However, this problem appears to be caused, and exacerbated, by continuing loss of the bats' natural food, which happens when humans clear natural forests. Lethal methods to reduce fruit crop damage are ineffective and problematic, and thus, the best solution is to implement non-lethal mitigation such as fixed nets, deterrents and decoy trees. In some instances, a combination of some or all of these non-lethal methods may be required. However, further research and trials are required for some of these methods, and these would be aided by ecological research focusing specifically on feeding behaviour and dietary preferences of those pteropodid species implicated in crop damage. In addition, there is an urgent need to educate fruit growers, authorities and the general public about the important benefits and ecosystem services provided by pteropodid bats. Such information may work best when presented in economic terms and measurements, such as cost–benefit analyses, to make it immediately relevant to economies and livelihoods.

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References

Albayrak I, Asan N, Yorulmaz T (2008) The natural history of the Egyptian fruit bat, *Rousettus aegyptiacus,* in Turkey (Mammalia: Chiroptera). Turk J Zool 32:11–18

Amman BR, Jones MEB, Sealy TK et al (2014a) Oral shedding of Marburg virus in experimentally infected Egyptian fruit bats (*Rousettus aegyptiacus*). J Wildl Dis (ahead of print)

Amman BR, Nyakarahuka L, McElroy AK (2014b) Marburgvirus resurgence in Kitaka mine bat population after extermination attempts, Uganda. Emerg Infec Dis 20(10):1761–1764

Andrianaivoarivelo RA, Jenkins RKB, Petit EJ et al (2012) *Rousettus madagascariensis* (Chiroptera: Pteropodidae) shows a preference for native and commercially unimportant fruits. Endanger Species Res 19:19–27

Ayensu EA (1974) Plant and bat interactions in West Africa. Ann Mo Bot Gard 61:702–727

Bicknell JR (2002) The need for aversion agents for managing flying-foxes on crops and the difficulties in attracting research funds. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 63–69

Biel E (2002) The cost to orchardists in the management of the grey-headed flying-fox. Who pays? A community benefit approach. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 47–52

Bollen A, Van Elsacker L (2002) Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. Acta Chiropterol 4:33–47

Bomford M, O'Brien PH (1990) Sonic deterrents in animal damage control: a review of device tests and effectiveness. Wildl Soc Bull 18:411–422

Bower C (2002) Management issues in minimisation of damage by flying-foxes to horticultural crops. In: Eby P, Lunney D (eds) Managing the grey-headed glying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 77–79

Boonkird K, Wanghongsa S (2004) On the population number and distribution of flying foxes (*Pteropus lylei*) in central plain. In: 2003 Annual Report of Wildlife Research Division. Department of National Parks, Wildlife and Plant Conservation, Bangkok, pp 89–100 (In Thai)

Bumrungsri S, Leelapaibul W, Racey PA (2007) Resource partitioning in sympatric *Cynopterus* bats in lowland tropical rainforest, Thailand. Biotropica 39:241–248

Bumrungsri S, Harbit A, Benzie C et al (2008) The pollination ecology of two species of *Parkia* in southern Thailand. J Trop Ecol 24:467–475

Bumrungsri S, Sripaoraya E, Chongsiri T et al (2009) The pollination ecology of durian (*Durio zibethinus*) in southern Thailand. J Trop Ecol 25:85–92

Burns J (2009) Extinction threat to flying fox. BBC Online, 25 August, http://news.bbc.co.uk/2/hi/science/nature/8221132.stm. Accessed 5 Nov 2013

Campbell J, Greer N (1994) Controlling pest losses—why, how, how much? In: Bird and bat control for horticulture and aquaculture, Nambour, Queensland, 18 May 1994. Seminar proceedings, Department of Environment and Heritage, Queensland, pp 38–41

Chakravarthy AK, Girish AC (2003) Crop protection and conservation of frugivorous bats in orchards of hill and coastal regions of Karnataka. Zoos' Print J 18:1169–1171

Charles L, Benjamin N (2010) Ruler bans hunting of wildlife. The Star, 5 March

Chua KB, Koh CL, Hooi PS et al (2002) Isolation of Nipah virus from Malaysian island flying-foxes. Microb Infect 4:145–151

Clulow S, Blundell AT (2011) Deliberate insectivory by the fruit bat *Pteropus poliocephalus* by aerial hunting. Acta Chiropterol 13:201–205

Comensoli P (2002) The impact upon fruit growers of a decision to list the grey-headed flying-fox as a Vulnerable species under the NSW Threatened Species Conservation Act. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 53–55

Del Vaglio MA, Nicolau H, Bosso L et al (2011) Feeding habits of the Egyptian fruit bat *Rousettus aegyptiacus* on Cyprus island: a first assessment. Hystrix Ital J Mamm 22:281–289

Dewhurst (1998) Correspondence from Queensland Fruit and Vegetable Growers to DPI. Quoted by Teagle S 2002 op cit

Divljan A, Parry-Jones K, Eby P (2009) Report on deaths and injuries to grey-headed flying-foxes, *Pteropus poliocephalus* shot in an orchard near Sydney, NSW. Aust Zool 35:698–710

Dolbeer RR, Fiedler LR, Rasheed H (1988) Management of fruit bat and rat populations in the Maldive Islands, Indian Ocean. In: Crabb AC, Marsh RE (eds) Proceedings of the vertebrate pest conference, vol 13, pp 112–118. University of California, Davis

Don't Shoot Bats 2013. Lethal crop protection is not effective. http://www.dontshootbats.com/crop-protection.html. Accessed 18 November 2013

Eby P (1990) Seed dispersal and seasonal movements by grey-headed flying foxes and the implications for management. In: Slack J (ed) Flying-fox workshop proceedings. Wollongbar Agricultural Institute, Wollongbar, pp 28–32

Eby P (1995) The biology and management of flying foxes in NSW. NSW National Parks and Wildlife Service, Hurstville, NSW

Eby P, Lunney D (2002) Managing the grey-headed flying-fox *Pteropus poliocephalus* as a threatened species: a context for the debate. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 1–15

Entwistle AC, Corp N (1997) The diet of *Pteropus voeltzkowi*, an endangered fruit bat endemic to Pemba Island, Tanzania. Afr J Ecol 35:351–360

Epstein JH, Olival KJ, Pulliam JRC et al (2009) *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. J Appl Ecol 46:991–1002

Field H, Young P, Yob JM et al (2001) The natural history of Hendra and Nipah viruses. Microb Infect 3:307–314

Fleming TH, Kress WJ (2011) A brief history of fruit and frugivores. Acta Oecol 37:521–530

Fleming TH, Geiselman C, Kress WJ (2009) The evolution of bat pollination—a phylogenetic perspective. Ann Bot 104:1017–1043

Fogarty R, Halpin K, Hyatt AD et al (2008) Henipavirus susceptibility to environmental variables. Virus Res 132:140–144

Fujita F (1988) Flying foxes and economics. BATS Magazine 6(1). http://www.batcon.org/index.php/media-and-info/bats-archives.html?task=viewArticle&magArticleID=318. Accessed 3 March 2013

Fujita MS, Tuttle MD (1991) Flying foxes (Chiroptera, Pteropodidae)—threatened animals of key ecological and economic importance. Cons Biol 5:455–463

Funakoshi K, Watanabe H, Kunisaki T (1993) Feeding ecology of the northern Ryukyu fruit bat, *Pteropus dasymallus dasymallus*, in a warm-temperate region. J Zool Lond 230:221–230

Galil J, Stein M, Horoviz A (1976) On the origin of the sycamore fig (*Ficus sycomorus* L.) in the Middle East. Gard Bull XXIX:191–205

Gough JD (1992) Drift nets of the northern rivers. In: Blade K (ed) Fruit crop protection seminar. NSW National Parks and Wildlife Service, Australia, pp 14–17

Gough J (2002) The increasing need for netting fruit orchards against bat and bird damage and the increasing problems in affording netting. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 56–57

Groseth A, Feldmann H, Strong JE (2007) The ecology of Ebola virus. Trends Microbiol 15:408–416

Gumal MT, Irwan M, Brandah CJ et al (1998) The ecology and role of the large flying fox (*Pteropus vampyrus*) in Sarawakian rain forests—*Keluang embet embet*. Hornbill 2:82–95

Hadjisterkotis E (2006) The destruction and conservation of the Egyptian fruit bat *Rousettus aegyptiacus* in Cyprus: a historic review. Eur J Wildl Res 52:282–287

Hall LS, Richards GC (1987a) Crop protection and management of flying-foxes (Chiroptera: Pteropodidae). Aust Mammal 10:137–139

Hall LS, Richards GC (1987b) The flying-fox problem in eastern Australia. In: Proceedings of the 1987 Australian vertebrate pest control conference, Coolangatta, pp 279–283

Hall J, Willis B (1992) Netting orchards against flying foxes, birds and hail. In: Blade K (ed) Fruit crop protection seminar. NSW National Parks and Wildlife Service, Australia, pp 24–28

Halpin K, Young PL, Field HE, Mackenzie JS (2000) Isolation of Hendra virus from pteropid bats: a natural reservoir of Hendra virus. J Gen Virol 81:1927–1932

Harrison DL (1964) The Mammals of Arabia. Insectivora, Chiroptera, Primates. Ernest Bern Limited, London

Harrison DL, Bates PJJ (1991) The Mammals of Arabia. Harrison Zoological Museum, 2nd edn. Lakeside Printing, London

Harrison ME, Cheyne SM, Darma F et al (2011) Hunting of flying foxes and perceptions of disease risk in Indonesian Borneo. Biol Cons 144:2441–2449

Heaney L, Rosell-Ambel G, Tabaranza B et al (2008) Pteropus dasymallus. IUCN Red List of Threatened Species. Version 2015.3. http://www.iucnredlist.org. Accessed 25 July 2015

Hicks PG (1967) Observations on the diseases and conditions of cocoa pods in Papua and New Guinea—Pod losses 1962–1965. P N G Agr J 19:5–9

Hodgkison R, Balding ST, Zubaid A et al (2003) Fruit Bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. Biotropica 35:491–502

Hodgkison R, Balding ST, Zubaid A et al (2004) Temporal variation in the relative abundance of fruit bats (Megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. Biotropica 36:522–533

Huang JC-C, Jazdzyk E, Nusalawo M, et al (2014) Is Bat coffee a potential "wing-wing" tool for biodiversity conservation in southwestern Sumatra? Paper presented at the 16th international bat research conference, Hotel Herradura, San José, 11–15 Aug 2013, Bat Res News (in press)

IUCN (2014) IUCN Red List of Threatened Species. Version 2014.2. http://www.iucnredlist.org. Accessed 10 Nov 2014

Izhaki I, Korine C, Arad Z (1995) The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in eastern Mediterranean habitats. Oecologia 101:335–342

Kandasamy D (2009) Flying foxes facing extinction. The Malay Mail, 2 Sept

Khan MSU, Hossain J, Gurley ES et al (2011) Use of infrared camera to understand bats' access to date palm sap: implications for preventing Nipah virus transmission. EcoHealth 7:517–525

Kingston T (2010) Research priorities for bat conservation in Southeast Asia: a consensus approach. Biodivers Conserv 19:471–484

Korine C, Izhaki I, Arad Z (1998) Comparison of fruit syndromes between the Egyptian fruit-bat (*Rousettus aegyptiacus*) and birds in East Mediterranean habitats. Acta Oecol 19:147–153

Korine C, Izhaki I, Arad Z (1999) Is the Egyptian fruit-bat *Rousettus aegyptiacus* a pest in Israel? An analysis of the bat's diet and implications for its conservation. Biol Cons 88:301–306

Kunz TH, de Torrez EB, Bauer D et al (2011) Ecosystem services provided by bats. Ann NY Acad Sci 1223:1–38

Lane DJW, Kingston T, Lee BPY-H (2006) Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia. Biol Cons 131:584–593

Law B, Eby P, Somerville D (2002) Tree-planting to conserve flying-foxes and reduce orchard damage. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 84–90

Lee Y-F, Takaso T, Chiang T-Y et al (2009) Variation in the nocturnal foraging distribution of and resource use by endangered Ryukyu flying foxes (*Pteropus dasymallus*) on Iriomotejima Island, Japan. Contr Zool 78:51–64

Leroy EM, Rouquet P, Formenty P et al (2004) Multiple Ebola virus transmission events and rapid decline of central African wildlife. Science 303:387–390

Leroy EM, Kumulungui B, Pourrut X et al (2005) Fruit bats as reservoirs of Ebola virus. Nature 438:575–576

Leroy EM, Epelboin A, Mondonge V et al (2009) Human Ebola outbreak resulting from direct exposure to fruit bats in Luebo, Democratic Republic of Congo, 2007. Vector-Borne Zoonotic Dis 9:723–728

Lewis RE, Harrison DL (1962) Notes on bats from the Republic of Lebanon. Proc Zool Soc Lond 138:473–486

Lobova TA, Geiselman CK, Mori SA (2009) Seed dispersal by bats in the neotropics. New York Botanical Garden, New York (Mem New York Bot Gard 101)

Lokkers C (1990) Colony dynamics of the green tree ant (*Oecophylla smaragdina* Fab.) in a seasonal tropical climate. PhD dissertation, James Cook University

Long E, Racey PA (2007) An exotic plantation crop as a keystone resource for an endemic megachiropteran, *Pteropus rufus* in Madagascar. J Trop Ecol 23:1–11

Luby SP, Rahman M, Hossain MJ et al (2006) Foodborne transmission of Nipah virus, Bangladesh. Emerg Infect Dis 12:1888–1894

Lumlertdacha B, Boongird K, Wanghongsa S et al (2005) Survey for bat lyssaviruses, Thailand. Emerg Infect Dis 11:232–236

Luskin MS (2010) Flying foxes prefer to forage in farmland in a tropical dry forest landscape mosaic in Fiji. Biotropica 42:246–250

Mackenzie JS, Field HE, Guyatt KJ (2003) Managing emerging diseases borne by fruit bats (flying foxes), with particular reference to henipaviruses and Australian bat lyssavirus. J Appl Microbiol 94:59S–69S

Madkour G (1977) *Rousettus aegyptiacus* (Megachiroptera) as a fruit eating bat in A.R. Egypt. Agric Res Rev 55:167–172

Mahmood-Ul-Hassan M, Gulraiz TL, Rana SA et al (2010) The diet of Indian flying-foxes (*Pteropus giganteus*) in urban habitats of Pakistan. Acta Chiropterol 12:341–347

Makin D, Mendelssohn H (1987) Israel wipes out its bats. Ecologist 16:1–2

Marshall AG (1983) Bats, flowers and fruit: evolutionary relationships in the Old World. Biol J Linn Soc 20:115–135

Martin L, McIlwee AP (2002) The reproductive biology and intrinsic capacity for increase of the grey-headed flying-fox *Pteropus poliocephalus* (Megachiroptera), and the implications of culling. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 91–108

Mateo R (2009) Lead poisoning in birds in Europe and the regulations adopted by different countries. In: Watson RT, Fuller M, Pokras M et al (eds) Ingestion of lead from spent ammunition: implications for wildlife and humans. The Peregrine Fund, Boise, Idaho, pp 71–98

Meyer C, Struebig M, Willig M (in press) Responses of tropical bats to habitat fragmentation, logging and deforestation. In: Kingston T, Voigt CC (eds) Bats in the anthropocene. Springer, New York, pp 63–94

McConkey KR, Drake DR (2006) Flying foxes cease to function as seed dispersers long before they become rare. Ecology 87:271–276

McLachlan B (2002) NPWS operational management of commercial crop damage by flying-foxes—licensing in practice, a far north coast perspective. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 80–83

Mickleburgh S, Hutson AM, Racey PA (1992) Old World Fruit Bats—an action plan for their conservation. IUCN, Gland

Mickleburgh S, Waylen K, Racey PA (2009) Bats as bushmeat—a global review. Oryx 43:217–234

Minifie G, Willi B (1990) Duranet cloth and supporting systems. In: Slack JM (ed) Flying fox workshop proceedings, Wollongbar Agricultural Institute, Wollongbar. NSW Agriculture and Fisheries, Australia, pp 47–55

Moran S, Keidar H (1993) Checklist of vertebrate damage to agriculture in Israel. Crop Prot 12:171–182

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nahar N, Sultana R, Gurley ES et al (2010) Date palm sap collection: exploring opportunities to prevent Nipah transmission. EcoHealth 7:196–203

Nakamoto A, Kinjo K, Izawa M (2007) Food habits of Orii's flying-fox, *Pteropus dasymallus inopinatus*, in relation to food availability in an urban area of Okinawa-jima Island, the Ryukyu Archipelago, Japan. Acta Chiropterol 9:237–249

Nakamoto A, Kinjo K, Izawa M (2009) The role of Orii's flying-fox (*Pteropus dasymallus inopinatus*) as a pollinator and seed disperser on Okinawa-jima Island, the Ryukyu Archipelago, Japan. Ecol Res 24:405–414

Nelson SL, Miller MA, Heske EJ et al (2000) Nutritional consequences of a change in diet from native to agricultural fruits for the Samoan fruit bat. Ecography 23:393–401

Nelson SL, Masters DV, Humphrey SR et al (2005) Fruit choice and calcium block use by Tongan fruit bats in American Samoa. J Mammal 86:1205–1209

Nyhagen DF, Turnbull SD, Olesen JM et al (2005) An investigation into the role of the Mauritian flying fox, *Pteropus niger*, in forest regeneration. Biol Cons 122:491–497

Oleksy R, Racey PA, Jones G (2015) High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. Glob Ecol Conserv 3:678–692

Olival KJ, Hayman DTS (2014) Filoviruses in Bats: current knowledge and future directions. Viruses 6:1759–1788

Parry-Jones KA, Augee ML (2001) Factors affecting the occupation of a colony site in Sydney, New South Wales by the grey-headed flying-fox *Pteropus poliocephalus* (Pteropodidae). Aust Ecol 26:47–55

Phillips WWA (1980) Manual of Mammals of Sri Lanka (Part 1). Wild Life and Nature Protection Society of Sri Lanka

Picot M, Jenkins RBK, Ramilijoana O et al (2007) The feeding ecology of *Eidolon dupreanum* (Pteropodidae) in eastern Madagascar. Afr J Ecol 45:645–650

Price V (2013) Trouble in paradise: mapping human-wildlife conflict in the western Indian Ocean. Unpublished MSc thesis, Imperial College, London, UK

Qumsiyeh MB (1980) New records of Bats from Jordan. Säugetierkd Mitt 1:36–39

Qumsiyeh MB, Disi AM, Amr ZS (1992) Systematics and distribution of the bats (Mammalia: Chiroptera) of Jordan. Dirasat 19B:101–118

Racey PA, Nicoll ME (1984) Mammals. In: Stoddart DR (ed) Biogeography and ecology of the Seychelles Islands. Dr W Junk, The Hague, pp 607–626

Rahman MA, Hossain MJ, Sultana S et al (2012) Date palm sap linked to Nipah virus outbreak in Bangladesh, 2008. Vector-Borne Zoonotic Dis 12:65–72

Rahman SA, Hassan L, Epstein JH et al (2013) Risk factors for Nipah virus infection among pteropid bats, Peninsular Malaysia. Emerg Infect Dis 19:51–60

Ramlugun TMRRS (2013) An assessment of fruit bat damage caused by the Mauritian fruit bat (*Pteropus niger*) in a litchi (*Litchi chinensis*) orchard. BSc thesis, University of Mauritius

Ratcliffe FN (1931) The flying fox (*Pteropus*) in Australia. Report for co-operative work conducted on behalf of the Council for Scientific Research, the New South Wales Department of Agriculture, and the Queensland Home Secretary's Department, Melbourne

Reilly T, Slack J (1990) Cost and returns of netting low-chill stonefruit orchards. In: Slack JM (ed) Flying fox workshop proceedings. Wollongbar Agricultural Institute, Wollongbar, 22 August 1990. NSW Agriculture and Fisheries, Australia, pp 61–65

Richards GC (1990) The Spectacled flying fox, *Pteropus conspicillatus*, in north Queensland. 2. Diet, feeding ecology and seed dispersal. Aust Mammal 13:25–31

Richards GC, Hall LS, Parish S (2012) A natural history of Australian Bats: working the night shift. CSIRO Publishing, Melbourne

Roberts TJ (1997) The Mammals of Pakistan. Oxford University Press, Karachi

Robyn S (2007) Suivi et essai d'estimation de la population de chauve-souris frugivore (*Pteropus niger*) a l'Ile Maurice (monitoring and population estimate of a fruit bat [*Pteropus niger*] in Mauritius). Université Paul Cézanne, Memoir de Stage

Rogers J (2002) The economic and social implications of flying-fox predation on the north coast of NSW. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 58–62

Rimba (2012) Special update: Terengganu protects flying foxes! http://myrimba.org/2012/02/16/special-update-terengganu-protects-flying-foxes/. Accessed 19 May 2013

Scanlon AT, Petit S, Sternberg LDS (2013) Insectivory in Fijian flying foxes (Pteropodidae). Aust J Zool 61:342–349

Singaravelan N (2002) Foraging behaviour of fruit bats in orchards. PhD thesis, Madurai Kamaraj University

Singaravelan N, Marimuthu G (2006) *Muntingia calabura*—an attractive food plant of *Cynopterus sphinx*—deserves planting to lessen orchard damage. Acta Chiropterol 8:239–245

Singaravelan N, Marimuthu G, Racey PA (2009) Do all fruit bats deserve to be listed as vermin in the Indian Wildlife (Protection) & Amended Acts—a critical review. Oryx 43:608–613

Simmons N (2005) Chiroptera. In: Wilson DE, Reeder DAM (eds) Mammals of the World—a taxonomic and geographic reference. Johns Hopkins University Press, Baltimore, pp 312–529

Slack J (1990) Flying-fox damage in low-chill stone fruit orchards. In: Slack JM (ed) Flying-fox workshop proceedings. NSW Agriculture and Fisheries, Wollongbar, NSW, pp 55–60

Spitzenberger F (1979) Die Säugetierfauna Zyperns. Teil II: Chiroptera, Lagomorpha, Carnivora und Artiodactyla. Ann Nat Hist Mus 82:439–465

Srinivasulu C, Srinivasulu B (2002) Greater short-nosed fruit bat (*Cynopterus sphinx*) foraging and damage in vineyards in India. Acta Chiropterol 4:167–171

Stacey P (1990) Fruit industry focus-exotic fruit industry, NSW North Coast. In: Slack JM (ed) Flying fox workshop proceedings, Wollongbar Agricultural Institute. NSW Agriculture and Fisheries, Australia, pp 13–16

Stacey P (1992) To net or not to net. In: Blade K (ed) Fruit crop protection seminar. NSW National Parks and Wildlife Service, Australia, pp 20–23

Stier SC, Mildenstein TL (2005) Dietary habits of the world's largest bats: the Philippine flying foxes, *Acerodon jubatus* and *Pteropus vampyrus lanensis*. J Mammal 86:719–728

Struebig MJ, Harrison ME, Cheyne SM et al (2007) Intensive hunting of large flying foxes *Pteropus vampyrus natunae* in Central Kalimantan, Indonesian Borneo. Oryx 41:390–393

Swanepoel R, Leman PA, Burt FJ et al (1996) Experimental inoculation of plants and animals with Ebola virus. Emerg Infect Dis 2:321–325

Teagle S (2002) Queensland Flying-fox Consultative Committee—formation, outcomes and future strategies. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. Royal Zoological Society of New South Wales, Mosman, NSW, pp 109–116

Teoh TH (2005) Logging and hunting killing bats. The Star, 5 June

Thiriet D (2010) Flying fox conservation laws, policies and practices in Australia—a case study in conserving unpopular species. Australas J Nat Resour Law Policy 13:161–194

Tidemann CR (1999) Biology and management of the grey-headed flying-fox, *Pteropus poliocephalus*. Acta Chiropterol 1:151–164

Tidemann R, Kelson SI, Jamieson G (1997) Flying-fox damage to orchard fruit in Australia—incidence, extent and economic impact. Aust Biol 10:179–186

Towner JS, Amman BR, Sealy TK et al (2009) Isolation of genetically diverse Marburg viruses from Egyptian fruit bats. PLoS Path 5:e1000536

Ullio L (2002) To net or not to net that is the question! But is it the answer? In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. R Zool Soc New South Wales, Mosman, NSW, pp 70–76

Van Mele P (2008) The importance of ecological and socio-technological literacy in R&D priority setting: the case of a fruit innovation system in Guinea, West Africa. Int J Agric Sust 6:183–194

Van Mele P, Camara K, Vaysierres JF (2009) Thieves, bats and fruit flies: local ecological knowledge on the weaver ant *Oecophylla longinoda* in relation to three 'invisible' intruders in orchards in Guinea. Int J Pest Manage 55:57–61

Verghese A (1998) Non-destructive control of the bat, *Cynopterus sphinx* Vahl (Chiroptera: Pteropodidae) in grapes (*Vitis vinifera* Linnaeus) in India. Int J Pest Manage 44:81–85

Vincenot CE, Koyama L, Russo D (2015) Near threatened? First report of unsuspected human-driven decline factors in the Ryukyu flying fox (*Pteropus dasymallus*). Mammal Biol 80:273–277

Waples K (2002) Review of the NPWS policy on the mitigation of commercial crop damage by flying-foxes. In: Eby P, Lunney D (eds) Managing the grey-headed flying-fox as a threatened species in NSW. R Zool Soc New South Wales, Mosman, NSW, pp 39–46

Weber N, Duengkae P, Fahr J et al (2015) High-resolution GPS tracking of Lyle's flying fox between temples and orchards in central Thailand. J Wildl Manage 79:957–968

Williams NSG, McDonnell MJ, Phelan GK et al (2006) Range expansion due to urbanization: increased food resources attract grey-headed flying-foxes (*Pteropus poliocephalus*) to Melbourne. Aust Ecol 31:190–198

Win SS, Mya KM (2015) The diet of the Indian Flying Fox *Pteropus giganteus* (Brünnich. 1782) (Chiroptera: Pteropodidae) in Myanmar—conflicts with local people? J Threat Taxa 7:7568–7572

Yapa WB, Kumarasinghe J, Digana PMCB et al (1999) Food preferences (three food types) of Sri Lankan short-nosed fruit bat *Cynopterus sphinx* (Chiroptera) in a semi-natural condition. Vidyodaya J Sci 8:109–116

Chapter 14
Bats and Buildings: The Conservation of Synanthropic Bats

Christian C. Voigt, Kendra L. Phelps, Luis F. Aguirre, M. Corrie Schoeman, Juliet Vanitharani and Akbar Zubaid

Abstract Humans have shared buildings with bats for thousands of years, probably as early as first humans built primitive huts. Indeed, many bat species can be defined as synanthropic, i.e., they have a strong ecological association with humans. Bats have been observed using buildings as roosting and foraging sites, temporary shelters, for reproduction and hibernation. A synanthropic lifestyle may result in direct fitness benefits owing to energetic advantages in warmer roosts, which may ultimately lead to more rapid gestation and faster development of juveniles, or by being less exposed to natural predators in urban environments. All

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Luis F. Aguirre, M. Corrie Schoeman, Juliet Vanitharani and Akbar Zubaid: Contributed equally, listed alphabetically.

C.C. Voigt (✉)
Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research,
Berlin, Germany
e-mail: ccvoigt@googlemail.com

K.L. Phelps
Department of Biological Sciences, Texas Tech University, Lubbock, USA

L.F. Aguirre
Centro de Biodiversida y Genetica, UniversidadMajor de San Simon, Cochabamba, Bolivia

M. Corrie Schoeman
School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

J. Vanitharani
Department Advanced Zoology and Biotechnology and Research Centre, Sarah Tucker
College, Palayamkottai, Tirunelveli, Tamil Nadu, India

A. Zubaid
School of Environmental and Natural Resource Sciences, Faculty of Science and Technology,
Universiti Kebangsaan Malaysia, 43600 Bangi, Malaysia

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these benefits may allow bats to use buildings as stepping stones to exploit habitats otherwise devoid of roosting structures and may even lead to the expansion of geographic ranges. Yet, the coexistence with humans also comes with some risks. Bats may be exposed to chemical pollutants, particularly preservation chemicals used on lumber or during pest control measures. Bats may also be at risk of direct persecution or they may die accidently if trapped within buildings. In general, eviction of bats from buildings should follow the general rule of avoidance–mitigation–compensation. When considering conservation measures for synanthropic bats, it is most important to assess the role of the building for different life stages of bats. Construction work at buildings should be conducted in a manner that minimizes disturbance of bats. Artificial roosts can replace lost roosts, yet bats will often not accept alternative roosts. Demographic changes in human populations may lead to the abandonment of buildings, for example, in rural areas and to increased conflicts in urban areas when old buildings are replaced by new buildings or when previously unoccupied space in buildings is renovated. We advocate maintenance and enhancement of roosts for synanthropic bats, in addition to outreach and education campaigns, to improve the tolerance of humans for synanthropic bats.

14.1 Introduction

14.1.1 What Is the Purpose of This Review?

Bats are nocturnal mammals that spend the daytime in dark places (Kunz 1982; Kunz and Lumsden 2003). Usually, they depend on natural roosting structures such as caves, crevices, foliage, branches, tree trunks, and hollows among many others. Bats most likely used buildings as roosts when humans started to build primitive huts thousands of years ago. Indeed, some bat species, such as the hairy split-faced bat, *Nycteris macrotis*, inhabit thatched huts in Africa that are likely similar to the earliest buildings of humans (Poché 1975).

In this chapter, we focus on bats that use man-made buildings that are coinhabited by humans. We refer to these bats as synanthropic species, or species that are “ecologically associated with humans (Merriam-Webster’s dictionary). We do not use synanthropic species in the context of bats living in anthropogenically shaped landscapes; rather, this topic is covered in Chap. 2 (Reichel-Jung and Threlfall 2015). Nonetheless, we address certain aspects of bats living in other man-made structures unoccupied or abandoned by humans.

Synanthropic bat species have benefited from the expansion of human populations, and some species have likely expanded their geographic distribution as humans moved into new habitats worldwide. Yet this close association has disadvantages when synanthropic bats are faced with threats from humans. Currently, about a quarter of all bat species are considered threatened or near threatened, and one of the most prominent threats is loss of roost sites and disturbance at roosts (Mickleburgh et al. 2002). Therefore, this chapter is timely, and we hope that it will contribute to the conservation of synanthropic bats.

14.1.2 Relevant Natural History Features of Synanthropic Bats

Along the fast–slow continuum of life, bats are considered to be in the slow lane, even though most other mammals of similar size are in the fast lane (Barclay and Harder 2003; Bielby et al. 2007). Bats have low reproductive rates that are associated with exceptionally long life spans, a feature most obvious in insectivorous bats from temperate zones (Wilkinson and South 2002; Munshi-South and Wilkinson 2010). Long life spans may predispose bats to inhabit relatively permanent structures, such as in buildings, since some bat species are loyal to their roost over many years and form long-term social relationships with other colony members (Kerth et al. 2011).

Similar to other small mammals, bats exhibit relatively high mass-specific metabolic rates (McNab 2002). Many bats are also heterothermic, reducing their body temperature and consequently metabolic rate, during periods of adverse conditions, such as low resource abundance (insects, fruits, or nectar), low ambient temperature, or high rainfall (Geiser 2004). Most notably, temperate zone bats employ extended torpor when they hibernate in winter. Apart from hibernation, almost all bats use torpor on a daily basis as an energy-saving strategy (Speakman and Thomas 2003; Willis et al. 2006). During daytime torpor, bats may use passive rewarming when ambient temperatures peak during the warmest part of the day (Turbill et al. 2003). The use of radiant heat created by the exposure of building exteriors to sunshine likely saves synanthropic bats significant amounts of energy since they do not depend on endogenous heat production in brown adipose tissue (Geiser and Drury 2003). This could be a selective advantage for bats using sun-exposed buildings instead of dark caves as daytime roosts or hibernacula (Lausen and Barclay 2006; Halsall et al. 2012).

14.1.3 Which Bat Species Use Buildings?

The order Chiroptera comprises 19 living families, with at least one species in each family known to roost in buildings (Figs. 14.1 and 14.2), with the notable exceptions of Furipteridae, Mystacinidae, Myzopodidae, Natalidae, and Thyropteridae. Quite often, only local residents are aware of the occurrence of synanthropic bat species. The chapter on bats and urbanization (Reichel-Jung and Threlfall 2015) provides a meta-analytic perspective on bats living in urban landscapes. Many of the species included in their analysis also roost in buildings; thus, the general patterns derived from their study may also hold true for aspects of roost choice in synanthropic bats.

Fig. 14.1 Example of synanthropic bats that use both natural roosts and buildings. The greater sac-winged bat, *Saccopteryx bilineata*, shown here in Costa Rica, forms colonies in the cavities formed by large buttress roots of canopy trees. In the absence of such trees, this species will roost on the exterior walls of buildings (or inside if the building is abandoned as shown in the *right picture*; © *left picture* Knörnschild M, right picture Voigt CC)

Fig. 14.2 Colony of *Megaderma lyra* under a tin roof of a building in India

14.1.4 Human–Bat Conflict in Buildings and the Legal Protection of Synanthropic Bats

Buildings constructed specifically as human dwellings are usually well maintained and protected against opportunistic invasions by unwanted animals. Unfortunately, synanthropic bats are unwanted by most humans, which generate conflicts (Gareca et al. 2007). Accordingly, synanthropic bats are persecuted virtually worldwide, even if the legal framework may define this action as criminal. Documented cases of humans removing bats from buildings are apparent across the entire geographic range of synanthropic bats (e.g., Merzlikin 2002), but most cases remain unnoticed by law enforcement agencies even where bats are legally protected. Indeed, bats are legally protected in only a few countries. For example, bats are protected in countries of the European Union according to the Habitats Directive (Council Directive 92/43/EEC). Also, migratory bats are specifically protected in countries that have signed the United Nations convention on the “Conservation of Migratory Species of Wild Animals” (Lyster 1989). In some countries, conservationists have established action plans for threatened bat species, including suggestions for protecting synanthropic bats (Aguirre et al. 2010). However, these recommendations have not yet been converted into some form of legal framework. In African and Asian countries, bats are not protected under specific legislation. In summary, the level of protection of synanthropic bats by national or international legislation is highly variable and clearly deficient.

14.2 How Do Bats Find and Use Buildings?

Since most bat species are not capable of constructing their own roosts (Kunz 1982; Kunz and Lumsden 2003), they depend largely on preexisting roosting structures, either of natural or of artificial origin. Therefore, roost sites are likely a limited resource for bats (Kunz 1982; Kunz and Lumsden 2003), such that buildings may constitute an important substitute for natural roosts (Lisón et al. 2013). Buildings may resemble rocks or cavelike structures, which may attract bats into crevices or attics. Once one or a few bats establish a roost in a building, other bats may recognize the newly established roosts by olfactory or acoustic cues. The importance of nonsocial information such as visual and temperature-related cues and social sensory cues, e.g., conspecific echolocation calls, has recently been confirmed as important information for the common noctule bat, *Nyctalus noctula*, to initiate roost exploration (Ruczyński et al. 2007). Presumably, noctule bats use the same set of cues for exploring buildings as temporary shelters or hibernacula (Bihari 2004; Kozhurina and Gorbunova 2004; Szodoray-Parádi et al. 2004; Cel’uch and Kaňuch 2005; Cel’uch et al. 2006; Bačkor et al. 2007).

14.2.1 Buildings as Foraging Sites

Buildings are rarely used by bats as foraging sites, although abandoned buildings may develop into small urban ecosystems. For example, Aspetsberger et al. (2003) found that cockroaches (Blattodea: Blaberidae), sharing the space under the metal roof of a building with little free-tailed bats, *Chaerephon pumilus*, comprised more than 60 % of the diet of the bats. Yet, most observations of foraging at buildings are bats hunting insects around illuminated buildings. Artificial lighting is known to attract insects, and consequently, bats may chase insects close to illuminated buildings (Rydell 1991, 1992; Rydell and Racey 1995; Pavey 1999; Rowse et al. 2015).

14.2.2 Buildings as Shelters During Foraging Bouts

Buildings provide structures that can be used by bats as a temporary shelter. For example, buildings are often used by bats as a shelter to digest food items gathered during their most recent foraging bout (Ormsbee et al. 2007). This behavior has been observed in many species, including tropical carnivorous species such as the greater false vampire bat, *Megaderma lyra*, in India (Subbaraj and Balasingh 1996), and the greater slit-faced bat, *Nycteris grandis*, in southern Africa (Fenton et al. 1990) as well as temperate insectivorous bats such as Leisler's bat, *Nyctalus leisleri*, in Europe (Shiel et al. 1999), and the pallid bat, *Antrozous pallidus*, in the USA (Lewis 1994). In general, the temporary use of buildings by foraging bats may be the first step toward a more permanent occupation of buildings.

14.2.3 Buildings as Maternity Roosts

Females of many synanthropic bats use buildings as maternity roosts. Sometimes adult males share the same roost, but often the sexes are segregated. According to our literature survey, at least 35 bat species form maternity colonies in buildings. Energetic advantages and reduced predation risk may be benefits for female bats that give birth and raise their young in buildings. Harbusch and Racey (2006) reported that the serotine bat, *Eptesicus serotinus*, selected old buildings with slate roofing for maternity roosts, largely because such buildings tend to have small holes and fissures allowing easy access. Also, such buildings offered suitable temperatures of about 22 °C during gestation and lactation periods, a critical parameter for the survival of offspring (Harbusch and Racey 2006). Further, many species that form maternity colonies in buildings show high levels of site fidelity and natal philopatry, with female young returning to the same roosts to reproduce when they mature (Harbusch and Racey 2006). This could initiate a tradition of using buildings instead of natural roosts in local bat populations.

14.2.4 Buildings as Swarming Sites

Several European bats, such as common pipistrelle bats, *Pipistrellus pipistrellus*, and parti-colored bats, *Vespertilio murinus*, swarm at large buildings during autumn (Kanuch et al. 2010; Šuba et al. 2010). Usually, swarming occurs after juveniles have fledged and as they start to disperse from their natal roost. In Marburg, Germany, common pipistrelles swarm between mid-August and late September not only at tall buildings, such as historic towers, castles, and churches, but also at large multistory buildings. Interestingly, bat researchers recorded almost exclusively juvenile bats during swarming events (Kanuch et al. 2010; Šuba et al. 2010), and therefore, it was argued that swarming was related to roost exploration (Smit-Viergutz and Simon 2000). Yet, a social function of swarming behavior has also been suggested, for example, for *Vespertio murinus* (Kanuch et al. 2010; Šuba et al. 2010). To the best of our knowledge, swarming of bats at buildings has not been observed in countries outside of Europe.

14.2.5 Buildings as Hibernacula

Many bat species are known to hibernate in buildings, presumably because building interiors rarely reach freezing temperatures, turning them into ideal hibernation sites for bats. For many of these species, natural hibernacula include not only caves, rock crevices, and rock screes, but also tree hollows. Michaelsen et al. (2013) reported that in Norway, hibernating bats prefer anthropogenic structures rather than natural subground hibernacula, but the reason for this preference was unknown. Bats, such as big brown bats, *Eptesicus fuscus*, hibernating in walls of heated buildings expose themselves to ambient temperatures of 2–5 °C which are created by the balance between warm interior temperatures from heated rooms and cold ambient temperatures from the outside (Whitaker and Gummer 1992). In addition, bats hibernating in buildings may also benefit from occasional passive rewarming, when being exposed to mild exterior temperatures. *Nyctalus noctula* usually forms maternity colonies in tree roosts, yet in Central and northern Europe, they frequently use prefabricated buildings, i.e., multistory buildings consisting of prefabricated concrete walls that are assembled at the construction site. Throughout continental Europe, large numbers of noctule bats hibernate in such buildings in crevices at about 5–10 m aboveground, sometimes forming winter aggregations of a few thousand individuals (Zahn et al. 2000; Kozhurina and Gorbunova 2004; Cel'uch and Kaňuch 2005; Cel'uch et al. 2006). Bats in subtropical and tropical zones may also use buildings during adverse conditions and employ torpor, yet their biology is largely unknown and therefore in need of further studies.

14.3 Benefits of a Synanthropic Lifestyle in Bats

14.3.1 Increased Fitness of Bats Using Buildings

Bats would not use buildings as roosts without a proximate (ecological or physiological) or ultimate (evolutionary) benefit. In the following, we will discuss three potential benefits for bats using buildings, which seem to be linked to increased fitness over the short or long term.

Reduced predation risk In general, bats face only a few predators compared to non-volant mammals of similar size (Sibly and Brown 2007). Yet some birds, mammals, and even invertebrates hunt bats on a regular basis (Gillette and Kimbrough 1970; Speakman 1991; Altringham 1996; Nyffeker and Knörnschild 2013). Roosts in buildings could reduce the exposure of bats to predators if predators avoid anthropogenic environments. For example, snakes and giant centipedes hunt neotropical bats at the entrance of caves, and many of these species are less abundant or even absent in an urban environment (Molinari et al. 2005; Esbérard and Vrcibradic 2007). In North America, big brown bats, *E. fuscus*, seem to be less exposed to predators when roosting in buildings than in natural roosts (Lausen and Barclay 2006). However, clustered emergence of bats from roosts in buildings may point to antipredatory behavior in synanthropic bats in urban environments (Speakman et al. 1995; Duvergé et al. 2008; but see Irwin and Speakman 2003).

Energetic benefits Bats may survive periods of adverse weather conditions, such as heavy rain or low ambient temperatures, by roosting in a warm and dry building. The energetic benefits for bats roosting in buildings may manifest particularly during critical life history stages, such as reproduction and hibernation.

Buildings may provide conditions that are beneficial for reproducing female bats. For example, elevated ambient temperatures in attics seem to be ideal for pregnant and lactating bats. Angolan free-tailed bats, *Mops condylurus*, inhabit maternity roosts under corrugated steel roofs of houses that often exceed 40 °C during the day (Maloney et al. 1999), enabling them to maintain ideal growth conditions throughout the reproductive period without expending a lot of energy (Vivier and van der Merwe 2007). Their use of hot roosts may even be linked to increased reproductive rates (Bronner et al. 1999). Higher roost temperatures in attics seem to be also favorable for the development of juveniles of European greater mouse-eared bats, *Myotis myotis*. This species forms large clusters of individuals in natural cave roosts, presumably to benefit from huddling and sharing of body heat (Dietz et al. 2009). In buildings, however, greater mouse-eared bats usually form smaller colonies, and these smaller clusters may be energetically feasible only because *Myotis myotis* may benefit from exogenous instead of endogenous heat when roosting in warm attics (Zahn 1999). The use of different locations depending on reproductive state has been confirmed for other species as well, including Rafinesque's big-eared bats, *Corynorhinus rafinesquii* (Roby et al. 2011). Similar to attic-roosting *Myotis myotis*, thermal benefits have also been suggested for *Eptesicus fuscus*. Pregnant big brown bats rarely entered torpor when roosting at favorable ambient conditions in buildings (Lausen and Barclay 2006). The avoidance of torpor may be advantageous for fetal development. For example, big brown bats gave birth earlier when roosting in buildings than when roosting in natural roosts. Furthermore, juveniles from buildings fledged one to two weeks earlier than conspecifics born in natural roosts (Lausen and Barclay 2006). Similarly, building-dwelling bats gave birth earlier than their conspecifics roosting in foliage or trees (Kurta 2010). These temporal differences could translate to important advantages for building-roosting juveniles; for example, they have more time to explore new roosts and foraging sites and to prepare for the onset of hibernation.

Hibernating bats may also benefit from thermal advantages in buildings. For example, thermoregulation of *E. fuscus* hibernating in buildings was more similar to that of tree-dwelling species than to that of cave-hibernating conspecifics (Halsall et al. 2012). The authors argued that bats hibernating in buildings may benefit to a larger extent from passive rewarming (Halsall et al. 2012), which may lead to massive savings of crucial fat depots (Turbill et al. 2003; Geiser and Drury 2003). This notion is also supported by the observation that some bats, such as *Nyctalus noctula*, choose crevices behind sun-exposed walls when hibernating in buildings (Bihari and Bakos 2001).

In addition to thermal benefits, synanthropic bats may also benefit by reducing their travel distance and thus time to foraging sites, resulting in substantial energetic savings from reduced commuting distances (Knight and Jones 2009).

Presence of social or mating partners If buildings are selected as roost sites by a single bat, conspecifics may follow to benefit from social advantages (Kerth 2008). These secondary social benefits for synanthropic bats are identical to those of conspecific roosting in natural roosts. Briefly, bats that form large colonies in buildings may be less exposed to predators because of the dilution effect. They may as well benefit from information transfer and by cooperation among members of the same social unit. Clustered emergence of bats from a roost may constitute an antipredator behavior (Speakman et al. 1995), yet clustered emergence may be disrupted in large colonies due to bottleneck effects (Speakman et al. 1999). Gillam et al. (2011) found non-random patterns when pit-tagged *Eptesicus fuscus* emerged from buildings, indicating that these bats may form social bonds that likely influence their foraging. Information transfer might also be involved during swarming at buildings as observed in some temperate zone bats (Kanuch et al. 2010; Šuba et al. 2010). Finally, bats may explore buildings in search of mating partners. For example, buildings are known to be used as mating roosts in a number of species, such as greater sac-winged bats, *Saccopteryx bilineata* (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976), greater mouse-eared bats, *Myotis myotis* (Dietz et al. 2009), spear-nosed bat, *Phyllostomus hastatus* (Santos et al. 2003), and free-tailed bats, such as *Tadarida brasiliensis* and *Mops condylurus* (Vivier and van der Merwe 2001).

14.3.2 Enhanced Access to Habitats by Using Buildings as Ecological Stepping Stones

Extending the aforementioned argument that bats may benefit from using buildings as shelters by shortening travel distances to foraging habitats, one could argue that bats may even be able to explore and exploit new habitats by using buildings as ecological stepping stones. For example, some uniform and homogenous agricultural habitats, such as the former prairies of the Midwestern USA, are nearly void of roosting structures. Therefore, it is almost impossible for aerial-hawking insectivorous bats to use these habitats, unless artificial roosting structures are available. Here, buildings may present pivotal resources for bats to survive in an otherwise hostile environment. Farm buildings, villages, and cities may create structurally complex islands used by bat colonies (Coleman and Barclay 2012a), and this could possibly lead to an increase in local species richness. Some synanthropic bats, such as *Mops condylurus*, are capable of using exceedingly hot roosts (40 °C) which allow them to colonize habitats that other bats with a lower tolerance toward high roost temperatures are not able to exploit (Maloney et al. 1999), suggesting that heat tolerance might be favorable for bats with a synanthropic lifestyle.

In forested areas, buildings may provide roosting structures for cave-roosting bats, i.e., for bats that do not use tree hollows or crevices. By using buildings as roosts, these bats may gain access to other habitats. For example, in a forest habitat in Central Europe, bats that typically do not occupy tree cavities, such as *Eptesicus serotinus* and *Vespertilio murinus*, will instead inhabit buildings. By doing this, they gain access to insect-rich forest habitats (Mazurska and Ruczyński 2008).

Buildings can also provide roosting sites for cave-roosting bats in urban areas. For example, *Otomops martiensseni* exploits buildings only in the city of Durban, South Africa, while elsewhere in its range it uses caves as roosts. Despite the reduced availability of food and intensive large-scale agricultural land use in the surrounding landscape, the species is quite common in Durban (Fenton et al. 2002). Similarly, Moutou's free-tailed bat, *Mormopterus francoismoutoui*, uses a variety of human structures (e.g., roof slats, window shutters) across the island of La Réunion, Mauritius, yet it was thought to be restricted to roosts in lava tubes and crevices along cliff faces before the colonization of the island by European settlers (~AD 1500; Goodman et al. 2008a). Seemingly, this species has profited from the large-scale changes that occurred on this island over the past centuries. In summary, buildings may present an important resource for synanthropic bats that could increase foraging ranges of individual bats as well as the diversity of local bat assemblages.

14.3.3 Expansion of Geographic Ranges

The use of buildings as roosts may also lead to the expansion of a species' geographic range (Kunz and Reynolds 2003). Some temperate bat species such as greater mouse-eared bats, *Myotis myotis*, and lesser and greater horseshoe bats, *Rhinolophus hipposideros* and *Rhinolophus ferrumequinum*, respectively, predominantly form maternity roosts in caves in southern Europe but occupy mostly attics of large buildings (e.g., churches and castles) in more northern regions of their geographic ranges where cave temperatures are too cold to host cave-roosting maternity colonies (Dietz et al. 2009). The notch-eared bat, *Myotis emarginatus*, also uses buildings as maternity roosts in the northernmost part of their range in Europe (Dekker et al. 2013). Frafjord (2007) observed a small nursery colony of the northern bat, *Eptesicus nilssonii*, in the attic of a cabin at the northern extent of the species range. The roost was only occupied when human inhabitants heated the house for their own use, giving support to the idea that bats benefited from the warmer roost temperatures. The use of buildings as a driving force to reach more northern limits of their geographic ranges (in the Northern hemisphere) has been suggested for *E. nilssonii* and soprano pipistrelles, *Pipistrellus pygmaeus*, in Norway (Michaelsen et al. 2004), *Pipistrellus pipistrellus*, in Sweden (Ahlen et al. 2004), and *Eptesicus fuscus*, in North America (McAlpine et al. 2002). Bats may also benefit from favorable thermal conditions in buildings at higher elevations and may thus go beyond their normal elevational range. For example, a maternity colony of the rare eastern small-footed myotis, *Myotis leibii*, was found roosting in a high-elevation cabin above the previously known elevational limits for this species (O'Keefe and LaVoie 2011).

A similar argument can be made for hibernating bats in buildings. Strelkov (2002) made the point that the ability of some European bat species, such as *Nyctalus noctula*, to hibernate in buildings may have enabled them to overwinter in more northern regions than when using exclusively natural roosts. By doing so, *Nyctalus noctula* are closer to their breeding ranges when arousing from hibernation in spring, which gives them an advantage in terms of time and energy in relation to conspecifics that migrate to more southern areas. This could lead to the expansion of this species' geographic range northward.

14.4 Negative Consequences of a Synanthropic Lifestyle in Bats

14.4.1 Decreased Fitness Owing to Direct Threats

Humans The foremost direct threat for synanthropic bats are humans. The co-occupancy of buildings by bats and humans gives rise to various conflicts. Interestingly, many early papers that discuss bats in buildings deal largely with the eradication or control of bats roosting in buildings (e.g., Silver 1935; Daver 1953; Kunz et al. 1977; Barclay 1980). These papers were gradually replaced by descriptive papers about the biology of synanthropic bats and eventually by those focusing on conservation topics. Nonetheless, eradication of bats from buildings is an eminent, yet mostly undocumented, problem, in all regions of the world. Unfortunately, there are no data available on the number of bats killed each year by closing entrances to daytime roosts in buildings, by destroying roosts, or by fumigating or poisoning bats. In many countries, bats are considered pests or vermin. Therefore, eradication of whole colonies is commonly practiced. In some African countries, synanthropic molossids are consumed by humans as a delicacy (Goodman et al. 2008b), and the bats' distinct odor is regarded favorably from a culinary perspective (Allen et al. 1917), yet synanthropic bats as a form of bushmeat is rather the exception (Mildenstein and Tanshi 2015).

Buildings as traps Buildings may act as traps for bats, when bats that enter a building through open windows or structural gaps are unable to find the exit (Gaisler 1998). In Europe, *Pipistrellus pipistrellus* is most often trapped during autumn swarming (Pfalzer and Weber 2007; Kanuch et al. 2010). Bats may also be killed if they become trapped in wire mesh that is used to protect buildings from feral pigeons (König and Neumann 1996).

Predators Bats may also be killed by synanthropic predators. Some birds of prey, e.g., European kestrels and tawny and barn owls, specialize on bats that use buildings as roosts (Kovats et al. 2008; Lesiński et al. 2013; Mikula et al. 2013). Indeed, the high density of kestrels in Rome, Italy, is thought to be related to the abundance of feral pigeons, swifts, and bats (Salvati et al. 1999). In the Neotropics, great kiskadees, *Pitangus sulphuratus*, have been observed hunting *Myotis nigricans* and *Myotis albescens* when bats emerged from a building (Fischer et al. 2010). African goshawks, *Accipiter tachiro*, have attacked molossid bats, *Mops condylurus* and *Chaerephon pumilus*, near their roosts in buildings (Fenton et al. 1994). Synanthropic bats that fall to the ground or fly close to the ground may be captured and killed by domestic cats (Bruijn 1990; Ancillotto et al. 2013). Snakes and invertebrates have also been observed hunting bats in or at buildings (Esbérard and Vrcibradic 2007; Nyffeler and Knörnschild 2013).

In some cases, natural predators may have devastating effects on bats, in particular when they specialize on hunting emerging bats at the entrance of roosts. Synanthropic owls are especially efficient predators of bats in or around buildings. An effective protective measure is to install a small water hose above the entrance of a colony that is triggered by the presence of a perching predator (pers. communication K. Kugelschafter, Fig. 14.3). Since owls are puzzled by the sudden stream of water, they immediately leave the entrance without any harm done to the predator (pers. commun. K. Kugelschafter).

Pathogens Mühldorfer et al. (2012) reported that one-third of bat deaths in Germany were due to bacterial infections. According to this study, viral infections were less important as a natural cause of death, even though rabies infections are documented in some populations of synanthropic bats (O'Shea et al. 2012; Racey et al. 2013). Yet it is unknown to what extent bats suffer from rabies and whether disease dynamics are exacerbated in synanthropic species because of their specific choice of buildings.

14.4.2 Decreased Fitness Owing to Indirect Threats

Roosting in buildings, particularly in urban environments, may provide fitness benefits for bats. However, Coleman and Barclay (2012b) concluded that urban bats did not perform better in terms of body condition, reproductive rate, and number of weaned juveniles compared to rural bats. Indeed, bats seemed to perform best in the transition zone between urban and rural sites, and thus, the authors summarized that the process of urbanization may be universally detrimental to bats (Coleman and Barclay 2012b).

Fig. 14.3 Method to repel owls from the entrance of bat colonies in Germany. Water flows from the overhead water hose when the perching owl (*Strix aluco*) interrupts a light beam at the entrance to a colony of greater mouse-eared bats (*Myotis myotis*) (copyright Kugelschafter K)

Chemical pollutants Indirect threats for synanthropic bats are numerous, yet because of their subtle nature, it is more difficult to pinpoint indirect mortality risks. Chemical pollutants are likely an indirect threat for bats roosting in buildings (Mitchell-Jones et al. 1989; Bayat et al. 2014). Wood used in buildings is usually treated by chemicals such as chlorinated hydrocarbons to prevent rotting caused by fungi or insects. Bats roosting in buildings are in close contact with wooden structures and thus may be exposed to chemical preservatives such as lindane, pentachlorophenol, and pyrethroids (Racey and Swift 1986; Boyd and Myhill 1988; Mitchell-Jones et al. 1989; Shore et al. 1990, 1991; Bennet and Thies 2007). Most often, bats do not die immediately after contact with treated wood but instead suffer sublethal effects that cause, for example, immune suppression (Corrao et al. 1985; Clark and Shore 2001). Sometimes, bats are eradicated from buildings using poisons, and these poisons continue to persist so that bats may be exposed to toxic residues for extended periods after application. Poisoning is usually a gradual process that is exacerbated in temperate bats via the accumulation of toxic compounds in fat tissue and seasonal mobilization of these compounds during migration and hibernation (Mitchell-Jones et al. 1989; Bayat et al. 2014). Since the introduction of alternative bat-friendly chemical treatments of wood in buildings, mortality caused by chlorinated hydrocarbons has decreased markedly (Bayat et al. 2014), yet from a global perspective, the problem of slow poisoning of synanthropic bats in buildings remains an issue.

Parasites Patterson et al. (2007) found that bats inhabiting relatively permanent roosts, such as caves and buildings, carry more ectoparasites than bats that roost in temporal structures, such as leaves or tree hollows. Buildings may provide ectoparasites, e.g., streblid flies, bed bugs (*Cimex* spp.), or reduviid bugs (Triatominae; Reduviidae), an ideal substrate for egg laying and larval development. As female bats may be immunosuppressed during pregnancy, they may suffer from heavy parasite infestation during reproduction (Christe et al. 2000; Pearce and O'Shea 2007). The combined effect of inflammation and immune challenge may then increase oxidative stress and consequently reduce longevity in house-dwelling bats (Schneeberger et al. 2013; Lilley et al. 2014). Endoparasites are poorly studied in synanthropic bats. *Leishmania braziliensis* occurs in Brazilian house-dwelling bats, yet it is unknown whether roost choice and colony dynamics are different from those of conspecifics roosting in natural roosts and whether building roosts may impose a higher risk of contracting these parasites (Shapiro et al. 2013).

14.5 Consequences for Humans Sharing Buildings with Bats

14.5.1 Benefits of Sharing a Building with Bats

There are several direct benefits for humans when sharing buildings with synanthropic bats. Bats provide essential ecological services (e.g., pest suppression, pollination, seed dispersal) near houses, villages, and cities (Jones et al. 2009; Kunz et al. 2011; Ghanem and Voigt 2012). For example, synanthropic bats, such as molossids, feed on large quantities of insects that are vectors of human diseases, such as dengue, yellow fever, and chikungunya fever (Andrianaivoarivelo et al. 2006; Goodman et al. 2008b). In tropical and subtropical regions, bats are important seed and pollen dispersers. Orchards in house gardens may largely benefit from the cost-free ecosystem services provided by pollinating bats. Insectivorous bats have the ability to reduce insect herbivory in temperate forests (Böhm et al. 2011), tropical forests (Kalka et al. 2008), and tropical agricultural fields (Williams-Guillén et al. 2008; Maas et al. 2013). Thus, the presence of synanthropic bats comes with large, yet mostly unacknowledged, benefits to humans. Lastly, bats are an integral component of our natural heritage, and thus, they have intrinsic value (Soulé 1985).

14.5.2 Pathogen and Parasite Exposure

Viruses Bats inhabiting buildings may be reservoir hosts of viruses. For example, North American *Eptesicus fuscus* and Eurasian *Eptesicus serotinus* are both synanthropic species roosting in buildings, and they are known for their relatively high prevalence of rabies (Zorya 2002; O'Shea et al. 2012; Racey et al. 2013). In Dutch populations of *Eptesicus serotinus*, bats exhibited a 21 % seroprevalence for lyssavirus (Van der Poel et al. 2005), yet is unknown how many of these positive cases were infectious. In another Dutch study, 30 % of sampled bats that bit humans tested positive for European bat lyssaviruses (Takumi et al. 2009). Other synanthropic bat species may carry lyssaviruses, such as the molossid bats *Tadarida brasiliensis* or *Nyctinomops macrotis* in North and South America, or vespertilionid bats such as *Eptesicus furinalis* in South America (Clark et al. 1996; Uieda 1998; Passos et al. 1998; de Almeida et al. 2011; Favi et al. 2012) or nycterid bats such as *Nycteris thebaica* in Zimbabwe (Foggin 1988). In Kenya, SARS-like coronaviruses (CoVs) were identified in a *Chaerephon* spp. (Tong et al. 2009), and in South Africa, bat-derived CoVs that are closely related to the MERS-CoV were found in *Neoromicia capensis* (Corman et al. 2014). Frequent roost switching of synanthropic bats may increase the transmission risk of the rabies virus to humans (Ellison et al. 2007), particularly when humans try to evict bats from houses (Streicker et al. 2013). In general, precautionary measures should be taken when handling synanthropic bats: (1) Do not touch or handle bats without gloved hands, and (2) in case of a bat bite, immediately proceed to the appropriate facility for post-exposure prophylactics. A more detailed treatment of bat-related diseases is provided in Chap. 10 (Schneeberger and Voigt 2016).

Bacteria Bacterial infections are one of the primary causes of natural death in temperate bats (Mühldorfer et al. 2012), and many of the documented bacterial strains are relevant to human health. For example, bats may act as a reservoir for *Bartonella/Burkholderia* bacteria, which can be transmitted to humans via bed bugs (Saenz et al. 2013). Bat ticks, specifically *Argas vespertilionis*, collected from a human-inhabited building were documented to carry *Borrelia*, *Rickettisa*, and *Ehrlichia* species (Socolovschi et al. 2012). *Staphylococcus nepalensis* was detected in guano samples from mixed *M. myotis* and *M. blythii* summer roosts, and guano in or near buildings may pose a significant threat to human health (Vandzurova et al. 2013). To our knowledge, no direct infection of humans with bat-related bacterial strains has been described. Overall, synanthropic bats have the potential to transmit zoonotic diseases, yet as outlined by Mühldorfer et al. (2011), there is no evidence, at least for temperate zone bats, that they pose a greater health risk to humans than other wildlife species.

Parasites Besides bat-specific ectoparasites, bats may also carry generalist ectoparasites that could infect humans as well. For example, bed bugs (*Cimex* spp.) could possibly switch between bat roosts and rooms inhabited by humans (Pearce and O'Shea 2007). Bat ticks have been suggested to cause inflammatory responses in humans living in a building with bats in the attic (Labruna et al. 2014). Ticks associated with bats, and known to bite humans, may also be carriers of bacteria or viruses that can cause disease in humans. For example, *Carios kelleyi* collected from residential and community buildings in Jackson County, Iowa, tested positive for *Rickettsia* (Loftis et al. 2005). In addition, some endoparasites are threats to human health, yet many depend on an invertebrate host as a vector for transmission to humans. For example, in Brazil, *Leishmania braziliensis* occur in some synanthropic bat species that serve as a reservoir host for leishmaniasis but require sand flies as a vector (Shapiro et al. 2013).

Fungus Environments soiled with large accumulations of guano may harbor *Histoplasma capsulatum*, a fungal pathogen that causes histoplasmosis. When roosts in attics, roofs, and other rooms are not cleaned on a regular basis, guano accumulates creating a greater risk to humans (Bartlett et al. 1982; Martins et al. 2000). Humans can develop histoplasmosis after inhaling the microscopic spores of *H. capsulatum*, often while participating in activities that disturb a heavily contaminated environment. While histoplasmosis is rarely fatal, infections in individuals with weakened immune systems can become severe (Martins et al. 2000), yet it is questionable that infections by *H. capsulatum* can be traced back to bats.

14.5.3 Noise, Odor, Dust, and Activity

Although echolocation calls emitted by most bats in open space are not audible to humans, many social vocalizations of bats are noticeable because they are typically below the 20 kHz auditory threshold of humans. These vocalizations may be particularly evident at times of the year when pups use contact calls to attract their returning mothers. Such vocalizations combined with noises caused by terrestrial locomotion of bat inhabitants, e.g., molossid bats moving through small crevices below tin roofs, can be a nuisance for human inhabitants. In addition, humans sometimes complain about bat-related odors and dust (Razafindrakoto et al. 2011).

14.5.4 Harmful Bats

Bat feces is suggested to have antigenic properties, causing skin rashes in susceptible humans (Alonso et al. 1998), yet detailed studies are lacking. To our knowledge, there is only one bat species worldwide that could be directly harmful to humans. The common vampire bat, *Desmodus rotundus*, consumes mammalian blood but is restricted to Latin America. Although this species feeds primarily on livestock animals, e.g., cattle (Delpietro et al. 1992; Voigt and Kelm 2006), vampire bats may feed on sleeping humans not protected inside buildings (Schneider et al. 2001; Carvalho-Costa et al. 2012). Though vampire bats are not known to inhabit occupied buildings, in some areas of South America, these bats inhabit abandoned buildings next to occupied houses (Mialhe 2013). Besides the potential of contracting rabies via a bite, humans can suffer from inflammation, secondary infections, and blood loss. Overall, humans are not a regular victim for vampire bats.

14.5.5 *Destruction of Buildings Caused by Bat Excreta*

Bats may inhabit buildings over many years, or even centuries, and accumulated feces and urine may cause severe damage to buildings. For example, bat guano was the cause of damage to some buildings of the UNESCO World Heritage Centre—Angkor monuments in Cambodia. Apparently, salts in excretions of bats are eroding the sandstone of some ancient buildings (Hosono et al. 2006). In most cases, structural damage can be prevented by removing accumulations of guano. Plastic sheets can be placed over exposed structures to protect them and facilitate the removal of urine and guano; in addition, wooden boards placed directly under roosts may also be helpful in collecting bat excreta from roosts inside buildings.

14.6 Conservation of Bats in Buildings: Avoidance, Mitigation, and Compensation

The protection of synanthropic bats and their roosts should occur in a tri-level hierarchical pattern. First, it should be determined whether bat roosts can be preserved, e.g., left untouched, even when construction work is carried out near the roost. Second, if construction work affects the roost, developers and architects should mitigate the impact on the bat colony (mitigation). Lastly, if bat roosts are going to be lost, when, for example, barns are converted into apartments (Briggs 2004), appropriate compensation measures should be practiced in order to offer bats an alternative roost. Although this general approach may not be applicable in all countries, particularly when the legal framework is lacking, we will elaborate on it in the remainder of the chapter.

Conservation guidelines for bats in buildings have been formulated in various countries, including those from the European Union (Table 14.1; Marnell and Prsetnik 2010). Conservation networks (Kingston et al. 2016, Chap. 16) could use these and our recommendations to develop further region-specific guidelines for the protection of local synanthropic bats.

14.6.1 *General Considerations for the Conservation of Bats in Buildings*

Monitoring of colonies Monitoring of bat colonies, particularly maternity colonies, in buildings needs to be conducted with appropriate care (Kunz and Reynolds 2003). In some countries, it is legally forbidden to disturb bats in their roosts, particularly during the maternity period. Kunz and Reynolds (2003) suggested conducting evening emergence counts at roost exits to monitor maternity colonies without disturbing bats.

Table 14.1 List of Web-based resources pertaining to the conservation of synanthropic bats (sorted alphabetically according to continent or country)

Country	Web address
EU	http://www.eurobats.org/sites/default/files/documents/publications/publication_series/pubseries_no4_english_2nd_edition.pdf
France Australia Latin America	http://www.sfepm.org/chiropteres.htm http://ausbats.org.au/#/bats-in-your-house/4569171536 http://www.relcomlatinoamerica.net/images/PDFs/PROTOCOLO.pdf
Germany	http://www.nabu.de/tiereundpflanzen/saeugetiere/fledermaeuse/aktivwerden/01506.html
Ireland	http://www.batconservationireland.org
Italy	http://biocenosi.dipbsf.uninsubria.it/chiroptera/
Netherlands	http://www.vzz.nl
Russia	http://zmmu.msu.ru/bats/popular/v_dome.htm
UK UK UK UK	http://www.bats.org.uk/pages/bats_and_buildings.html http://www.bedsbatgroup.org.uk/wordpress/?page_id=3429 http://jncc.defra.gov.uk/page-2861 http://www.naturalengland.org.uk/ourwork/regulation/wildlife/species/bats.aspx
USA USA	http://www.conservewildlifenj.org/protecting/projects/bat/buildings/ http://www.nature.nps.gov/biology/wns/assets/docs/2012BatsInBuildingsWebinarOdegard.pptx

Life stages of bats For effective protection of synanthropic bats, it is crucial to understand the purpose of the buildings being used as roosts by bats. We have outlined several possibilities for why bats use buildings. Since bats may be particularly vulnerable during their reproductive period and during hibernation, roosts that are used by bats during these life stages are of prime concern for conservation efforts. The central recommendation for such roosts is to leave them untouched, unless gradual deterioration of the building may destroy the roost.

Human occupancy Usually, disturbance of synanthropic bats by humans is detrimental to colonies. For example, de Boer et al. (2013) showed for the Netherlands that hibernacula in buildings were more suitable for bats when disturbance by humans was low. However, it should be noted that some studies report that synanthropic bats tend to leave roosts when humans no longer use buildings, possibly because buildings are no longer heated (Frafjord 2007). In Poland, Sachanowicz and Wower (2013) found evidence that the gradual deterioration of buildings caused an impoverishment of species in the local assemblages of attic-dwelling bats. Therefore, human occupancy of buildings may be a benefit in some circumstances and a disadvantage in others, depending on the species involved and the specific life stages.

Interior of roosts The size and spatial structure of building interiors affects the occupancy by synanthropic bats. For example, the availability of sufficient space and optimal microclimatic conditions seem to be beneficial for attic-dwelling bats, such as the endangered Townsend's big-eared bat *Corynorhinus townsendii*

(Betts 2010) and Rafinesque's big-eared bat, *Corynorhinus rafinesquii* (Loeb and Zarnoch 2011). In addition to roost compartments, relatively higher ambient temperatures in roost interiors are also relevant for bats inhabiting buildings (Entwistle et al. 1997). *Eptesicus fuscus* prefer old buildings with galvanized (tin) roofs that are also taller than surrounding buildings, most likely because of higher temperatures and wider temperature gradients in these buildings (Williams and Brittingham 1997). For some hibernating bats, the size and number of hiding places may contribute to the quality of hibernacula in buildings.

Exterior of roosts Synanthropic bats not only depend on suitable roosting interiors, but also depend on the quality of the surrounding environment, e.g., for foraging or drinking. Suitable roost entrances are critical for some bats, particularly for fast-flying species with a low ability to maneuver (Neubaum et al. 2007). For example, *Nyctalus noctula* roosting in buildings preferred roosts that were located at the top floors (Bihari 2004; Cel'uch and Kaňuch 2005). Molossids, e.g., *Chaerephon ansorgei*, and vespertilionids, e.g., *Neoromicia capensis*, that inhabit crevices or narrow spaces under roofs are capable of landing and crawling through narrow roost entrances, whereas horseshoe bats, e.g., *Rhinolophus clivosus*, and slit-faced bats, e.g., *Nycteris thebaica*, require an opening large enough to fly through since they usually do not crawl (Monadjem et al. 2010). Other species, such as *Pipistrellus pipistrellus*, are generalists with respect to their roost preference, i.e., they do not prefer specific structural attributes of buildings (Jenkins et al. 1998). It is also noteworthy that some species may require several roosts in separate buildings to establish a stable colony, e.g., greater horseshoe bats, *Rhinolophus ferrumequinum* (Maltagliati et al. 2013), eastern pipistrelles, *Pipistrellus subflavus* (Whitaker 1998), and *Eptesicus fuscus* (Ellison et al. 2007; O'Shea et al. 2012).

Additional landscape elements, such as vegetation and water sources, have been suggested to promote bat populations in cities (Neubaum et al. 2007). Trees in the vicinity of roosts were beneficial for pipistrelle bats, *Pipistrellus pipistrellus*, not only as foraging grounds but also as a protection against aerial predators, thus enabling bats to increase their nocturnal foraging activity substantially by emerging earlier from their roost (Jenkins et al. 1998). Brown long-eared bats, *Plecotus auritus*, preferred buildings situated close to woodland and water (Entwistle et al. 1997; Moussy 2011).

Illumination of buildings at night by streetlamps reduces the quality of roosts for some bats. For example, European *Rhinolophus ferrumequinum*, *Myotis emarginatus*, *and Myotis oxygnathus* emerged later at sunset from roosts when buildings were illuminated. Also, body mass and forearm length were smaller in juveniles from illuminated buildings than in those from not illuminated. In the worst case, roosts are abandoned after direct lighting of the buildings in which the roost is located (Boldogh et al. 2007).

Eviction of bats from roost Eviction of bats from houses is practiced worldwide, yet it is against the law in some countries. The corresponding authorities may grant concessions if there is no alternative to the exclusion of bats from roosts. Yet, in many countries, it is a legal requisite that appropriate measures are practiced to compensate for the loss of a roost. The permanent closure of roost exits or the destruction of a roost should only be considered during times when bats are not using the roost, e.g., outside the reproduction or hibernation period. Otherwise, bats may be trapped and killed, which is against animal welfare. If roosts are destroyed or closed, bats may switch to alternative roosts (Neilson and Fenton 1994). After eviction of *Eptesicus fuscus* from buildings, females produced fewer offspring at alternative sites, even though foraging behavior remained constant (Brigham and Fenton 1986). Relocation of bats to nearby habitats usually fails because bats will return to their original roost in most cases. Lastly, the permanent eviction of bats from roosts may increase the frequency of roost switching. In the case of species with a high prevalence of rabies infections, it is predicted that the rabies transmission risk may increase due to more, and possibly undirected, movements of evicted bats around buildings (e.g., *Eptesicus fuscus*, Streicker et al. 2013). Therefore, roost closures might have unforeseen and unwanted side effects for public health.

14.6.2 Avoiding or Mitigating Roost Losses in Buildings

Roosts are key resources for bats since many species are limited by roost availability (Kunz 1982; Kunz and Lumsden 2003). Therefore, a prime conservation effort should be the protection of existing roosts and possibly the enhancement of their quality. If private or commercial development of buildings is an inevitable conflict with synanthropic bats, appropriate measures should be practiced, particularly when the species is endangered and/or protected.

Reduction of human disturbance Disturbance of bat roosts in buildings can lead to a variety of outcomes, ranging from direct effects when people disturb building roosts to indirect effects of noise and light pollution. Bats seem to adjust quickly to noise, yet as Rowse et al. (2015) point out, some species may be quite sensitive to artificial light. For example, *Pipistrellus pipistrellus* are quite tolerant to artificial light during foraging, but altered their emergence behavior when exposed to different light intensities at their daytime roost (Down et al. 2003). Directing artificial light at roost entrances may have a negative impact on bats roosting in buildings (Boldogh et al. 2007). Adjusting the regime of artificial light near a colony and reducing the light spill from neighboring buildings or streetlamps should be considered to improve the quality of roosts in buildings.

It is important to recognize that human visits to hibernacula of bats in buildings might cause bats to arouse from hibernation, a process that is energetically costly and causes bats to deplete their fat depots which increases the risk of starvation (Speakman and Thomas 2003). Therefore, it is necessary to cease visitations to known hibernacula to minimize impacts on hibernating bats.

The impact of disturbance caused by structural work in buildings, e.g., renovation of roof structures or attics, can have severe consequences for synanthropic bats. Indeed, colonies will abandon roosts because of this disturbance. To minimize these negative impacts, construction work should only take place during the annual period when bats are not using the roost. For example, renovation of attics used by bats as maternity roosts should only occur after juveniles fledge or when colony members leave the roost to hibernate in another location. Minimizing disturbance is also vital for protecting hibernacula, and construction work at these sites should not be conducted during the hibernation period.

Conservation of smaller-sized roosts Reduction of the size of bat roosts inside buildings might be acceptable if the only alternative is the complete loss of a roost. For example, attics or barns are sometimes converted to apartments or houses, respectively. If bats are roosting in an attic or barn, a small part of it could be separated from the space used by humans and this smaller space could be designated for the exclusive use by bats. However, it should be noted that many bat species roosting in attics or barns prefer large and complex structures with some variation in microclimate conditions. A decrease in size and structural complexity of the roost space may lead to the gradual decline in colony size and possibly complete loss. Therefore, a reduction in roost size may best be accompanied by the provision of new artificial roosts that are suitable for the specific bat species (Figs. 14.4 and 14.5; Kunz and Reynolds 2003).

Fig. 14.4 Artificial bat roost on the exterior of the Leibniz Institute for Zoo and Wildlife Research building in Berlin, Germany. *Nyctalus noctula* use the roost during autumn

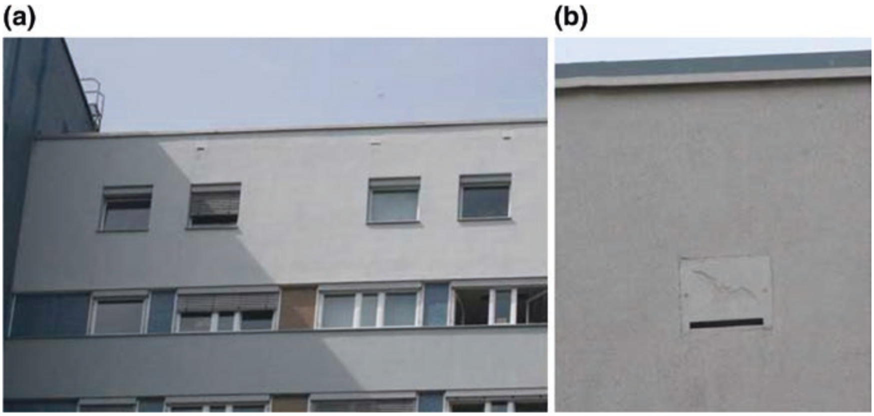

Fig. 14.5 Artificial bat roosts embedded into the external insulation layer of a renovated public building in Berlin, Germany: **a** row of artificial roosts within the top floor of a seven-story building; **b** detail of a single artificial roost (the horizontal exit is at the base). Such roosts are suitable as hibernation sites and stopover sites during migration for noctule bats, *Noctula noctula*, in Europe, yet they may not host as many individuals as buildings before renovation

14.6.3 Compensating for Lost Roosts

Sometimes it is inevitable that roosts in buildings are lost. The addition of artificial bat boxes near previously occupied buildings can successfully compensate in some instances. For example, colonies of *Pipistrellus pygmaeus* and *Plecotus auritus* and various other species throughout Europe benefited from artificial roosts when the original roost was destroyed (Anonymous 2006; Beck and Schelbert 1999). Artificial bat roosts were also provided for and accepted by South American *Molossus molossus* when roosts in buildings were destroyed (Alberico et al. 2004). In North America, *Eptesicus fuscus*, and *Myotis lucifugus*, will occupy artificial bat boxes installed at buildings that formerly housed colonies (Brittingham and Williams 2000). For example, the Bat House Research Project in the Kruger National Park, South Africa, has recently provided new accommodation for bats in the Letaba Rest Camp in an effort to help identify the most effective way to remove bats from buildings within the park (http://www.krugerpark.co.za/krugerpark-times-2-11-bat-accommodation-19864.html). Similar attempts to provide alternative roosting structures for synanthropic bats have been successful in the USA; for example, artificial roosts have been built on the campus of the University of Florida to host populations of *Tadarida brasiliensis* and other native bats (https://www.flmnh.ufl.edu/index.php/bats/home/).

These success stories should not imply that roosts in building are replaceable by artificial structures and that bats will readily occupy artificial roosts. Sometimes, for unknown reasons, bats avoid artificial roosts in buildings completely. Therefore, protection of existing roosts should be considered prior to attempting the use of artificial roosts.

14.6.4 *Loss of Roosts Due to Demographic Changes in the Human Population*

Demographic changes in human populations of many countries are turning rural areas into areas nearly devoid of humans. As a result, buildings are abandoned and, due to a lack of maintenance, deteriorate over time. Shortly after abandonment, many synanthropic bat species benefit, likely due to the reduced disturbance by humans. Deserted buildings may provide new roosting structures for bats, e.g., for *Hipposideros nicobarulae* in Myanmar (Douangboupha et al. 2012). Yet in the long run, synanthropic bats may vanish from these sites when buildings deteriorate (Sachanowicz and Wower 2013). Another effect of demographic changes involves movement and thus concentration of people in urban areas. Following this, previously unused buildings, even in industrial areas, or unoccupied space under the roof of buildings are converted into houses or apartments to host the influx of people in cities. This may cause losses of roosting opportunities for synanthropic bats. In China, like in many Asian countries, a vast number of old buildings are demolished during the process of modernization and this reduces the density of roosts significantly for synanthropic bats (Zhang et al. 2009).

14.7 Examples of Good Practice

14.7.1 *Example 1: The Outreach Program for the "Bat-Friendly House"*

To conserve synanthropic bat species, education appears to be the prime method to protect bat roosts in buildings. Kingston (2016, Chaps. 17 and 18) address various outreach approaches. Here, we focus on a specific German-based conservation program called "bat-friendly house." Directed by a consortium of nonprofit organizations (spearheaded by the "Naturschutzbund" Germany) and federal and local authorities and bat conservationists, the program has created a "Bat-Friendly House" award for owners who protect bat colonies in their buildings. The major goal of this program is to support populations of synanthropic bats by maintaining or even enhancing their roosts and to involve local people in the protection of bats. Several hundred houses have been deemed bat-friendly in the federal states of Hessen, Schleswig-Holstein and Northrine-Westfalia and others in Germany. The award ceremony is usually accompanied by a press campaign to raise awareness about the conservation of bats that use building as their roosts. Similar programs have been initiated in other EU countries.

14.7.2 *Example 2: Renovated Buildings Designated for Bat Conservation Purposes*

There are many examples of buildings that were renovated successfully to mitigate the human–bat conflict or to protect endangered bats. The details of the vast majority of these cases have not been documented or published. Yet, it is encouraging to read about some of the examples on Web pages or in the gray literature of nongovernmental organizations (Table 14.1). The EUROBATS publication, available at www.eurobats.org, provides examples of successful projects throughout Europe. Many of these examples underline that the details of specific conservation efforts depend largely on the biology of the target bat species and on local circumstances, ranging from the building in question, the overall legal framework, and the funding agencies and the authorities and persons involved. We have summarized some general features in the next section that might be relevant for many synanthropic bats, but we cannot provide a comprehensive overview of all projects. We have also refrained from repeating case studies that have already been described in detail at other places. Instead, we focus on a single example that we consider successful because it combines efficiently the practical aspects of protecting a building for an endangered bat species, preservation and enhancement of suitable habitats, and a community-based outreach program to facilitate the acceptance and thus continuation of the project beyond the funding period.

Protection of the last maternity colony of greater horseshoe bats, *Rhinolophus ferrumequinum,* in Germany According to surveys over the past decades, populations of greater horseshoe bats, *Rhinolophus ferrumequinum*, are on the decline throughout Europe (Ransome and Hutson 2000; Dietz et al. 2009; Spitzenberger et al. 2010). Although some parts of southern Germany were inhabited previously by this species, today they are virtually absent from Germany except for a maternity colony found in 1992 in Hohenburg, a small village located in northeastern Bavaria adjacent to a large military training area. Because of its rarity, this species is categorized as "Threatened by Extinction" in the national red list of mammals for Germany.

The colony occupied a house and adjacent farm buildings that were built in the sixteenth century. Since the 1980s, the buildings have not been inhabited or used by humans (Fig. 14.6). Thus, the complex deteriorated and was nearly to the point of collapse when the colony was discovered. In 1992, there were 21 adults, yet it is unknown how large the colony had been before its discovery.

After initial monitoring of the bats in the colony and their feeding habits, it was decided in 2011 to apply for a grant from the European Union which supports biodiversity projects. Since the funding scheme required complementary funding sources, the applicants, namely the "Landesbund für Vogelschutz e.V.," a German NGO devoted to protecting national biodiversity, contacted additional partners, such as "Bayerischer Naturschutzfonds," "Bundesanstalt für Immobilienaufgaben," and "Naturpark Hirschwald," to reach the critical financial needs for achieving the conservation plan.

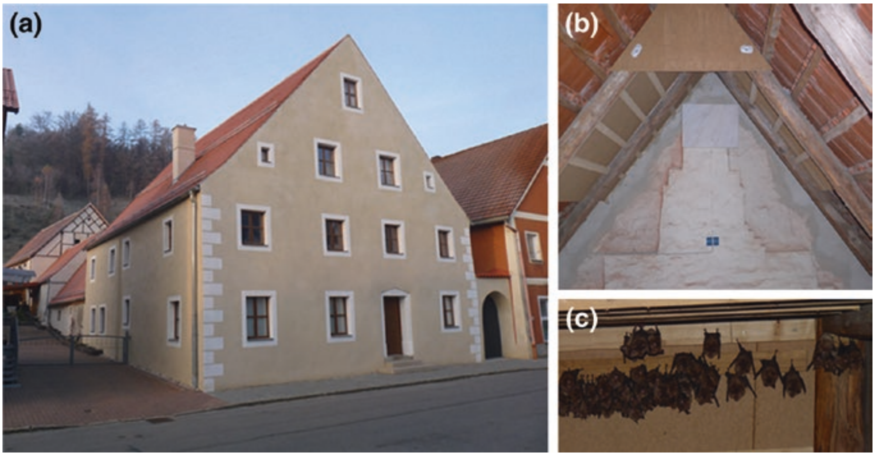

Fig. 14.6 Building complex that hosts the last maternity roost of the greater horseshoe bat, *Rhinolophus ferrumequinum*, in Germany (**a**). Bats most often use the attic of the largest backyard building (**b**). The attic ceiling functions as a heat trap where warm, upward moving air is trapped; this is the preferred roosting area for the colony (**c**)

Based on an initial investment made by the German government in support of small and intermediate companies during the 2011 bank crisis, it was first decided to renovate the complex of buildings after bats left for hibernation in nearby caves. Developers were faced with the difficult task of renovating a building complex that was protected by law, while at the same time keeping the roosting requirements of greater horseshoe bats in mind. The majority of space inside the building complex was designated for the exclusive use by bats. The ground floor level of the main buildings was transformed into an education center and some office space for the project coordinator. The fact that several attics and rooms with variable microclimatic conditions were available to the colony likely contributed to the success of the project. This is consistent with observations of roost use by greater horseshoe bats elsewhere. For example, Maltagliati et al. (2013) pointed out that the largest nursery colony of *Rhinolophus ferrumequinum* in Italy uses several buildings. The Hohenburg house was carefully modified to include some further beneficial structures for bats. For example, workers built a so-called heat dome inside the attic where warm, upward moving air is trapped in a structure that is used by bats as a roosting site (Fig. 14.6b, c). Furthermore, they created a 1-m^2 pool of water (3 cm depth) at which bats may drink. Finally, roost exits were constructed in a way that prevents predators, e.g., stone martens and domestic cats, from entering the building.

Second, it was understood that horseshoe bats would not survive if adjacent habitat structures degenerate by forest succession. Therefore, they designed a strategy to protect and indeed improve habitat structures for *Rhinolophus ferrumequinum*, a strategy that has proven successful for other synanthropic bats as well

(Murphy et al. 2012). Accordingly, a strategic plan was developed to protect foraging habitats and enhance the quality of landscape elements. Efforts are currently underway to convert forests into so-called Hutewald, which is an extensive forest used by livestock as pasture that resembles a landscape park. Furthermore, nearby hibernacula in natural caves were protected by fences to minimize disturbance of roosting bats.

Finally, the project includes an outreach program in which local people are informed about the progress of the project and engaged in fulfilling the working plan. The education center is equipped with monitors to provide real-time views into the bat colony. Project workers explain the goals of the project and show visitors the emergence of colony members at dusk. By using bat detectors and by direction observation, visitors learn firsthand about the biology of this fascinating species. Lastly, interested people might also visit the Web page of the project and observe bats using the Webcam (http://www.lbv.de/unsere-arbeit/life-natur-projekte/life-projekt-hufeisennase.html). Local hotels and restaurants in Hohenburg and adjacent villages have benefited from tourists and bat enthusiasts who come to this area for the single purpose of learning more about the Hohenburg colony of *Rhinolophus ferrumequinum*.

Since its discovery, the size of the colony has increased fourfold, numbering 94 adult *Rhinolophus ferrumequinum* and 37 juveniles in 2013 (pers. comm. Rudolf Leitl). Currently, efforts are underway to provide appropriate roosting structures in buildings and protected hibernacula in the nearby area to offer a suite of habitats for the expanding Hohenburg colony with the ultimate goal to establish further colonies in the larger region.

14.8 Synthesis and Outlook

Synanthropic bats are, by definition, in close contact with humans. Although this contact bears some risks to both humans and bats, it also provides opportunities to promote bat conservation. Practical aspects regarding the conservation of synanthropic bats in buildings, such as how to construct a new roost or enhancement of an existing building roost, should be one part of conservation efforts. From our point of view, it is equally important to engage in outreach programs and communicate with building owners about the conservation value of synanthropic bats (see also Kingston et al. 2016). With respect to research directions, we identify the following questions that need to be addressed:

1. What sensory cues do bats use to explore buildings as potential night or day roosts?
2. What are the differences in microclimate between natural and building roost sites, particularly in tropical and subtropical regions?
3. Is use of building roosts a learned behavior? Do local populations establish a tradition of inhabiting buildings?

4. Is swarming behavior unique to European bats?
5. Are there differences in the way bats use buildings between areas or continents where buildings have been in place for many centuries compared with areas where humans have only built houses recently.
6. Do tropical and subtropical bats also use buildings for extended periods of torpor, similar to hibernation of temperate zone bats?
7. What is the selective benefit for synanthropic bats inhabiting roosts in buildings compared with conspecifics inhabiting natural roosts? Why do some species commonly hibernate in buildings and others do not (see also Rintoul and Brigham 2014)?
8. Do tropical and subtropical bats exhibit similar expansions of geographic ranges when thermal benefits of using buildings as roosts are not the predominant driving benefit?
9. Is it possible to estimate the monetary value of ecosystem services provided by synanthropic bats?
10. To what extent have the geographic ranges of synanthropic bats changed in response to the coinhabitation of buildings?

Apart from these basic research questions, we need to engage in larger conservation efforts to protect synanthropic bats in developing countries, taking into account their ecological and economic value. Synanthropic bats face an uncertain future in many temperate countries due to political measures and specific programs to improve building standards, e.g., building modernization in the European Union that involves increased insulation of exterior walls has led to the large-scale eviction of synanthropic bats from buildings. We also see a strong incentive to coordinate conservation efforts to protect populations of synanthropic bats. Bats that live in the same buildings as humans could be ambassadors for the conservation of bats if other successful outcomes are replicated and publicized to a general audience. We conclude that synanthropic bats coinhabiting buildings with humans may provide good opportunities to teach humans in both urban and rural environments about wildlife species, particularly bats.

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References

Aguirre LF, Moya MI, Arteaga BLL, Galarza MMI, Vargas EA, Barboza Marquez K, Peñaranda DA, Pérez-Zubieta JC, Terán VMF and Tarifa T (2010) Plan de acción para la conservación de los murciélagos amenazados de Bolivia. BIOTA-PCMB, MMAA-VBCC-DGB, UICN-SSC-BSG, CBG-UMSS. Cochabamba, Bolivia

Ahlen I, Bach L, Johansson T (2004) Första kolonin av pipistrell funnen i Sverige: a common pipistrelle *Pipistrellus pipistrellus* colony found in Sweden. Fauna och Flora 99:16–17

Alberico M, Saavedra-R CA, Paredes HG (2004) Criterios para el diseno e istalacion de casas para murcielagos: Proyecto CPM (Cali, Valle del Cauca, Colombia). Actualidades Biologicas 26:5–11

Allen JA, Lang H, Chapin JP (1917) The American Museum Congo expedition collection of bats. Am Mus Nat Hist 37:405–478

Alonso A, Irañeta SG, Rodríguez SM, Scavini LM, Rodríguez SR (1998) Bat feces as an indoor allergen. J Investig Allergol Clin Immunol 8:365–369

Altringham JD (1996) Bats: biology and behavior. Oxford University Press, United Kingdom

Ancillotto L, Serangeli MT, Russo D (2013) Curiosity killed the bat: domestic cats as bat predators. Mamm Biol 78:369–373

Andrianaivoarivelo AR, Ranaivoson N, Racey PA, Jenkins RKB (2006) The diet of three synanthropic bats (Chiroptera: Molossidae) from eastern Madagascar. Acta Chiropterol 8:439–444

Anonymous (2006) A review of the success of bat boxes in houses. Scottish Natural Heritage commissioned report 160:1–41

Aspetsberger F, Brandsen D, Jacobs DS (2003) Geographic variation in the morphology, echolocation and diet of the little free-tailed bat, *Chaerephon pumilus* (Molossidae). Afr Zool 38:245–254

Barclay RMR (1980) Comparison of methods used for controlling bats in buildings. J Wildl Manage 44:502–506

Barclay RMR, Harder LD (2003) Life histories of bat: life in the slow lane. In: Kunz TH, Fenton MB (eds) Bat ecology. Chicago University Press, pp 209–25

Bartlett PC, Vonbehren LA, Tewari RP, Martin RJ, Eagleton L, Isaac MJ, Kulkarni PS (1982) Bats in the belfry: an outbreak of histoplasmosis. Am J Pubic Health 72:1369–1372

Bayat S, Geiser F, Kristiansen P, Wilson SC (2014) Organic contaminants in bats: trends and new issues. Env Intern 63:40–52

Beck A, Schelbert B (1999) Fledermauskästen als Ersatz für zerstörte Quartiere an Bauten. Mitt der Aargauischen Naturforschenden Ges 35:115–127

Bennet BS, Thies ML (2007) Organochlorine pesticide residues in guano of Brazilian free-tailed bats, *Tadarida brasiliensis* Saint-Hilaire, from east Texas. B Environ Contam Tox 78:191–194

Betts BJ (2010) Thermoregulatory mechanisms used in a maternity colony of Townsend's big-eared bats in northeastern Oregon. Northwest Nat 91:288–298

Bielby J, Mace GM, Binina-Emonds OR, Cardillo M, Gittleman JL, Jones KE, Orme CD, Purvis A (2007) The fast-slow continuum in mammalian life history: an empirical reevaluation. Am Nat 169:748–757

Bihari Z (2004) The roost preference of *Nyctalus noctula* (Chiroptera, Vespertilionidae) in summer and the ecological background of their urbanization. Mammalia 68:329–336

Bihari Z, Bakos J (2001) Roost selection of *Nyctalus noctula* (Chiroptera, Vespertilionidae) in urban habitat. In: Woloszyn BW (ed) Proceedings of the European Bat Research Symposium, Poland, pp 29–39

Boehm SM, Wells K, Kalko EKV (2011) Top-down control of herbivory by birds and bats in the canopy of temperate broad-leaved oaks (*Quercus robur*). PLoS ONE 6(4):e17857

Boldogh S, Dobrosi D, Samu P (2007) The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. Acta Chiropterol 9:527–534

Boyd IL, Myhill DG (1988) Uptake of gamma-HCH (lindane) by pipistrelle bats and its effect on survival. Environ Pollut 51:95–111

Bradbury JW, Emmons L (1974) Social organization of some Trinidad bats. I Emballonuridae Z Tierpsychol 36:137–183

Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in Emballonurid bats. I. Field studies. Behav Ecol Sociobiol 1:337–381

Briggs P (2004) Effect of barn conversion on bat roost sites in Hertfordshire, England. Mammalia 68:353–364

Brigham RM, Fenton MB (1986) The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Can J Zool 64:1128–1133

Brittingham MC, Williams LM (2000) Bat boxes as alternative roosts for displaced bat maternity colonies. Wildlife Soc B 28:197–207

Bronner G, Maloney SK, Buffenstein R (1999) Survival tactics within thermally-challenging roosts: heat tolerance and cold sensitivity in the Angolan free-tailed bat, *Mops condylurus*. S Afr J Zool 34:1–10

Bruijn Z (1990) Domestic cat *Felis catus* as a predator of bats. Lutra 33:30–34

Carvalho-Costa FA, Tedesqui VL, Monteiro MDN, Bóia MN (2012) Outbreaks of attacks by hematophagous bats in isolated riverine communities in the Brazilian Amazon: a challenge to rabies control. Zoonoses Public Health 59:272–277

Cel'uch M, Kaňuch P (2005) Winter activity and roosts of the noctule (*Nyctalus noctula*) in an urban area (central Slovakia). Lynx 36:39–45

Cel'uch M, Danko Š, Kaňuch P (2006) On urbanisaton of and *Pipistrellus pygmaeus* in Slovakia. Vespertilio 9–10:219–221

Christe P, Arlettaz R, Vogel P (2000) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). Ecol Lett 3:207–212

Clark DR, Shore RF (2001) Chiroptera. In: Shore RF, Rattner BA (eds) Ecotoxicology of wild mammals. Wiley, pp 159–214

Clark DR, Lollar A, Cowman DF (1996) Dead and dying Brazilian free-tailed bats (*Tadarida brasiliensis*) from Texas: rabies and pesticide exposure. Southwest Nat 41:275–278

Coleman JL, Barclay RMR (2012a) Urbanization and the abundance and diversity of prairie bats. Urban Ecosyst 15:87–102

Coleman JL, Barclay RMR (2012b) Influence of urbanization on demography of little brown bats (*Myotis lucifugus*) in the prairies of North America. PLoS ONE 6(5):e20483

Corman V, Ithete NL, Richards LE, Schoeman MC, Preisler W, Drosten C, Drexler JF (2014) Rooting the phylogenetic tree of MERS-Coronavirus by characterization of an ancestral virus from an African Bat. J Virol. doi:10.1128/JVI.01498-14

Corrao A, Catalano E, Zava B (1985) Destructive effects of chlorinated pesticides on a bats colony (Chiroptera). Mammalia 49:125–130

Daver SR (1953) Eradicating bats from bungalows. J Bombay Nat Hist Soc 51:734–735

de Almeida MF, Favoretto SR, Martorelli LFA, Trezza-Netto J, Campos ACD, Ozahata CH, Sodre MM, Kataoka APAG, Sacramento DRV, Durigon EL (2011) Characterization of rabies virus isolated from a colony of *Eptesicus furinalis* bats in Brazil. Rev Inst Med Trop Sao Paulo 53:31–37

de Boer WF, van de Koppel S, de Knegt HJ, Dekker JJA (2013) Hibernation site requirements of bats in man-made hibernacula in a spatial context. Ecol Appl 23:502–514

Dekker JJA, Regelink JR, Jansen EA, Bringkmann R, Limpens HJGA (2013) Habitat use by female Geoffroy's bats (*Myotis emarginatus*) at its two northernmost maternity roosts and the implications for their conservation. Lutra 56:111–120

Delpietro HA, Marchevsky N, Simonetti E (1992) Relative population densities and predation of the common vampire bat (*Desmodus rotundus*) in natural and cattle-raising areas in northeast Argentina. Prev Vet Med 14:13–20

Dietz C, von Helversen O, Nill D (2009) Bats of Britain, Europe and northwest Africa. A & C Black, London

Douangboupha B, Bumrungsri S, Satasook C, Soisook P, Bu SSH, Aul B, Harrison DL, Pearch MJ, Thomas NM, Bates PJJ (2012) A new species of small Hipposideros (Chiroptera: Hipposideridae) from Myanmar and a reevaluation of the taxon *H. nicobarulae* Miller, 1902 from the Nicobar islands. Acta Chiropterol 13:61–78

Down NC, Beaton V, Guest J, Polanski J, Robinson SL, Racey PA (2003) The effects of illuminating the roost entrance on emergence behavior of *Pipistells pygmaeus*. Biol Conserv 111:247–252

Duvergé PL, Jones G, Rydell R, Ransome RD (2008) Functional significance of emergence timing in bats. Ecography 23:32–40

Ellison LE, O'Shea TJ, Neubaum DJ, Bowen RA (2007) Factors influencing movement probabilities of big brown bats () in buildings. Ecol Appl 17:620–627

Entwistle AC, Racey PA, Speakman JR (1997) Roost selection by the brown long-eared bat *Plecotus auritus*. J Appl Ecol 34:399–408

Esbérard CEL, Vrcibradic D (2007) Snakes preying on bats: new records from Brazil and a review of recorded cases in the Neotropical region. Rev Bras Zool 24:848–853

Favi M, Bassaletti A, Lopez J, Rodriguez L, Yung V (2012) Epidemiological description of rabies reservoir in bats in the metropolitan region: Chile 2000–2009. Rev Chil de Infectologia 28:223–228

Fenton MB, Swanepoel CM, Brigham RM, Cebek J, Hickey MBC (1990) Foraging behaviour and prey selection by large slit-faced bats (*Nycteris grandis*; Chiroptera: Nycteridae). Biotropica 22:2–8

Fenton MB, Rautenbach IL, Smith SE, Swanepoel CM, Grosell J, van Jaarsveld J (1994) Raptors and bats: threats and opportunities. Anim Behav 48:9–18

Fenton MN, Taylor PJ, Jacobs DS, Richardson EJ, Bernard E, Bouchard S, Debaeremaeker KR, ter Hofstede H, Hollis L, Lausen CL, Lister JS, Rambaldini D, Ratcliffe JM, Reddy E (2002) Researching little-known species: the African bat *Otomops martiensseni* (Chiroptera: Molossidae). Biodivs Conserv 11:1583–1606

Fischer E, Munin RL, Longo JM, Fischer W, De Souza PR (2010) Predation on bats by great kiskadees. J Field Ornithol 81:17–20

Foggin CM (1988) Rabies and rabies-related viruses in Zimbabwe: historical, virological and ecological aspects. Dissertation, University of Zimbabwe

Frafjord K (2007) Foretrekker nordflaggermus *Eptesicus nilssonii* oppvarma hus? Do northern bats *Eptesicus nilssonii* prefer heated building as roosts? Fauna 60:239–245

Gaisler J (1998) Bat thanatocenosis with *Eptesicus serotinus*, *Vespertilio murinus* and *Nyctalus leisleri* in a building. Folia Zool 47:313–315

Gareca E, Rey-Ortiz G, Aguirre LF (2007) Relación entre el conocimiento acerca de los murciélagos y las actitudes de cinco grupos sociales de Cochabamba. In: Aguirre LF (ed) Historia natural, distribución y conservación de los murciélagos de Bolivia. Fundación Simón I, Patiño, Santa Cruz, pp 99–103

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66:239–274

Geiser F, Drury RL (2003) Radiant heat affects thermoregulation and energy expenditure during from torpor. J Comp Physiol 173:55–60

Ghanem SJ, Voigt CC (2012) Increasing awareness of ecosystem services provided by bats. Adv Stud Behav 44:279–302

Gillam EH, O'Shea TH, Brigham RM (2011) Nonrandom patterns of roosts emergence in big brown bats, *Eptesicus fuscus*. J Mammal 92:1253–1260

Gillette DD, Kimbrough JD (1970) Chiropteran morality. In: Slaughter BH, Walton DW (eds) About bats. Southern Methodist University Press, pp 262–283

Goodman SM, Jansen van Vuuren B, Ratrimomanarivo F, Probst J-M, Bowie RCK (2008a) Specific status of populations in the Mascarene Islands referred to *Mormopterus acetabulosus* (Chiroptera: Molossidae), with description of a new species. J Mammal 89:1316–1327

Goodman SM, Ratrimomanarivo FH, Ranivo J, Cardiff SG (2008b) The hunting of microchiropteran bats in different portions of Madagascar. Afr Bat Con News 16:4–7

Halsall AL, Boyles JG, Whitaker JO (2012) Body temperature patterns of big brown bats during winter in a building hibernaculum. J Mammal 93:497–503

Harbusch C, Racey PA (2006) The sessile serotine: the influence of roost temperature on philopatry and reproduction phenology of *Eptesicus serotinus* (Schreber, 1774)(Mammalia: Chiroptera). Acta Chiropterol 8:213–229

Hosono T, Uchida E, Suda C, Ueno A, Nagagawa T (2006) Salt weathering of sandstone at the Angkor monuments, Cambodia: identification of the origins of salts using sulfur and strontium isotopes. J Archeol Sci 33:1541–1551

Irwin NR, Speakman JR (2003) Azorean bats *Nyctalus azoreum*, cluster as they emerge from roosts, despite the lack of avian predators. Acta Chriopterol 5:185–192

Jenkins EV, Laine T, Morgan SE, Cole KR, Speakman JR (1998) Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. Anim Behav 56:909–917

Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) Carpe noctem: the importance of bats as bioindicators. Endangered Species Res 8:93–115

Kalka MB, Smith AR, Kalko EKV (2008) Bats limit arthropods and herbivory in a tropical forest. Science 320:71

Kanuch P, Fornuskova A, Bartonicka T, Bryja J, Rehak Z (2010) Do two cryptic pipistrelle bat species differ in their autumn and winter roosting strategies within the range of sympatry? Folia Zool 59:102–107

Kerth G (2008) Causes and consequences of sociality in bats. Bioscience 58:737–755

Kerth G, Perony N, Schweitzer F (2011) Bats are able to maintain long-term social relationships despite the high fission-fusion dynamics of groups. P Zool Soc Lond. doi:10.1098/rspb.2010.2718

Kingston (2016) Cute, Creepy, or crsipy- how values, attitudes and norms shape human behavior toward bats. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 571–588

Kingston T, Aguirre L, Armstrong K, Mies R, Racey P, Rodríguez-Herrera, Waldien D (2016) Networking networks for global bat conservation. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 539–566

Knight T, Jones G (2009) Importance of night roosts for bat conservation: roosting behaviour of the lesser horseshoe bat *Rhinolophus hipposideros*. Endangered Species Res 8:79–86

König H, Neumann F (1996) Drahtgitter zur Taubenabwehr als Fledermausfallen. Wire mesh as unintentional bat traps. Fauna und Flora (Rheinland-Pfalz) 21:141–143

Kovats D, Habarics B, Urban H (2008) Épületlakó denevérfajok populációdinamikai vizsgálata gyöngybaglyok jelenlétében, a Szatmár-Beregi Tájvédelmi Körzet területén. The changes of population of house-dwelling bat colonies in the presence of barn owls (*Tyto alba*) in the Szatmar-Bereg landscape protection area (Hungary). Deneverkutatas 4:59–73

Kozhurina EI, Gorbunova YA (2004) Hibernation of bats in the Volga Delta. Plecotus 7:104–105

Kunz TH (1982) Roosting ecology of bats. In: Kunz TH (ed) Ecology of bats. Plenum Press, New York, pp 1–56

Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 3–90

Kunz TH, Reynolds DS (2003) Bat colonies in buildings. In: O'Shea TJ, Bogan MA (eds) Monitoring trends in bat populations of the United States and territories: problems and prospects. US Geological Survey, Biological resources discipline, information and technology report, pp 91–102

Kunz TH, Anthony ELP, Rumage WT III (1977) Mortality of little brown bats following multipiple pesticide applications. J Wildl Manag 41:476–483

Kunz TH, Braun de Torrez E, Bauer DM, Lobova TA, Fleming TH (2011) Ecosystem services provided by bats. Ann Ny Acad Sci 1223:1–38

Kurta A (2010) Reproductive timing, distribution, and sex ratios of tree bats in Lower Michigan. J Mammal 91:586–592

Labruna MB, Marcilia A, Ogrzewalska M, Barros-Attesti DM, Dantas-Torres F, Fernandes AA, Leite RC, Venzal JM (2014) New records and human parasitism by *Ornithodoros mimon* (Acari: Argasidae) in Brazil. J Med Entomol 51:283–287

Lausen CL, Barclay RMR (2006) Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. J Mammal 87:362–370

Lesiński G, Kasprzyk K, Gryz J (2013) Bats taken by the tawny owl in relation to its roosting sites. North-west J Zool 8:247–251

Lewis SE (1994) Night roosting ecology of pallid bats (*Antrozous pallidus*) in Oregon. Am Midl Nat 132:219–226

Lilley TM, Stauffer J, Kanerva M, Eeva T (2014) Interspecific variation in redox status regulation and immune defense in five bat species: the role of ectoparasites. Oecologia 175:811–823

Lisón F, Palazón JA, Calvo JF (2013) Effectiveness of the natura 2000 network for the conservation of cave-dwelling bats in a Mediterranean region. Anim Conserv 16:528–537

Loeb SC, Zarnoch SJ (2011) Seasonal and multiannual roost use by Rafinesque's big-eared bats in the coastal plain of South Carolina. Conserv Manage East Big-Eared Bats—US Forest Serv Gen Techn Rep SRS 145:111–121

Loftis AD, Gill JS, Schriefer ME, Levin ML, Eremeeva ME, Gilchrist MJR, Dasch GA (2005) Detection of *Rickettsia*, *Borrelia*, and *Bartonella* in *Carios kelleyi* (Acari: Argasidae). J Med Entomol 43:473–480

Lyster S (1989) The convention on the conservation of migratory species of wild animals (the "Bonn Convention"). Nat Resour J 29:979–1000

Maas B, Cough Y, Tscharntke T (2013) Bats and birds increase crop yield in tropical agroforestry landscapes. Ecol Lett 16:1480–1487

Maloney SK, Bronner G, Buffenstein R (1999) Thermoregulation in the Angolan free-tailed bat *Mops condylurus*: a small mammal that uses hot roosts. Physiol Zool 72:385–396

Maltagliati G, Agenlli P, Cannicci S (2013) Where and at what time? Multiple roost use and emergence time in greater horseshow bats (*Rhinolophus ferrumequinum*). Acta Chiropterol 15:113–120

Marnell F, Prsetnik P (2010) Protection of overground roosts for bats. Eurobats Publication Series 4, pp 1–57

Martins P, Neves C, Lopes AA, Santos Q, Araújo NN, Pereira M (2000) Histoplasmosis presenting as acute respiratory distress syndrome after exposure to bat feces in a home. Braz J Infect Dis 4:103–106

Mazurska K, Ruczynski I (2008) Bats select buildings in clearings in Bialowieza Primeval forest. Acta Chiropterol 10:331–338

McAlpine DF, Muldoon F, Forbes GJ, Wandeler AI, Makepeace S, Broders HG, Goltz JP (2002) Over-wintering and reproduction by the big brown bat, *Eptesicus fuscus*, in New Brunswick. Can Field Nat 116:645–647

McNab BK (2002) The physiological ecology of vertebrates: a view from energetics. Cornell University Press, New York

Merzlikin IR (2002) On some causes of bat mortality in Sumy region (Northeastern Ukraine). Plecotus 113–115

Mialhe PJ (2013) Characterization of *Desmodus rotundus* (E. Goeffroy, 1810) (Chiroptera, Phyllostomidae) shelters in the municipality of Sao Pedro—SP. Braz J Biol 73:521–526

Michaelsen TC, Tore C, Grimstad KJ, Anonby JE (2004) Noen interessant funn av dagoppholdssted for flaggermus. Some interesting discoveries of day roosts for bats in Norway. Fauna (Oslo) 57:54–61

Michaelsen TC, Olsen O, Grimstad KJ (2013) Roosts used by bats in late autumn and winter at northern latitudes in Norway. Folia Zool 62:297–303

Mickleburgh SP, Hutson AM, Racey PA (2002) A review of the global conservation status of bats. Oryx 36:18–34

Mikula P, Hromada M, Tryjanowski P (2013) Bats and swifts a food of the European kestrel (*Falco tinnunculus*) in a small town in Slovakia. Ornis Fennica 90:178–185

Mildenstein T, Tanshi I (2016) Direct exploitation of bats. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 325–363

Mitchell-Jones AJ, Cooke AS, Boyd IL, Stebbings RE (1989) Bats and remedial timber treatment chemicals. Mammal Rev 18:93–110

Molinari J, Gutiérrez EE, Asecencão AA, Nassar JM, Arends A, Márquez RJ (2005) Predation by giant centipedes, *Scolopendra gigantea*, on three species of bats in a Venezuelan cave. Carribean J Sci 41:340–346

Monadjem A, Taylor PJ, Cotterill FPD, Schoeman MC (2010) Bats of central and southern Africa: a biogeographic and taxonomic synthesis. Wits University Press, Johannesburg

Moussy C (2011) Selection of old stone buildings as summer day roost by the brown long-eared bat *Plecotus auritus*. Acta Chiropterol 13:101–111

Mühldorfer K, Speck S, Wibbelt G (2011) Diseases in free-ranging bats from Germany. BMC Vet Res 7:61

Mühldorfer K, Speck S, Kurth A, Lesnik R, Freuling C, Müller T, Kramer-Schadt S, Wibbelt G (2012) Diseases and causes of death in European bats: dynamics in disease susceptibility and infection rates. PLoS ONE 6:e29773

Munshi-South J, Wilkinson GS (2010) Bats and birds: exceptional longevity despite high metabolic rates. Ageing Res Rev 9:12–19

Murphy SE, Greenaway F, Hill DA (2012) Patterns of habitat use by female brown long-eared bats presage negative impacts of woodland conservation management. J Zool (Lond) 288:177–183

Neilson AL, Fenton MB (1994) Responses of little brown myotis to exclusion and to bat houses. Wildl Soc Bull 22:8–14

Neubaum DJ, Wilson JR, O'Shea TJ (2007) Urban maternity roost selection by big brown bats in Colorado. J Wildl Manage 71:728–736

Nyffeler M, Knörnschild M (2013) Bat predation by spiders. PLoS ONE 8:e58120

O'Keefe JM, LaVoie M (2011) Maternity colony of eastern small-footed myotis (*Myotis leibii*) in a historic building. Southeast Nat 10:381–383

O'Shea TJ, Neubaum DJ, Neubaum MA, Cryan PM, Ellison LE, Stanley TR, Rupprecht CE, Pape WH, Bowen RA (2012) Bat ecology and public health surveillance for rabies in an urbanizing region of Colorado. Urban Ecosyst 14:665–697

Ormsbee PC, Kiser J, Perlmeter SI (2007) The importance of night roosts to the ecology of forest bats. In: Lacki MJ, Hayes JP, Kurta A (eds) Bats in forests: conservation and management. John Hopkins University Press, Baltimore, pp 129–152

Passos EC, Carrieri ML, Dainovskas E, Camara M, Silva MMS (1998) Isolamento do virus rabico em morcego insectivoro, *Nyctinomops macrotis*, no municipo de Diadema, SP (Brasil)—Isolation of rabies virus in an insectivorous bat *Nyctinomops macrotis*, in southeastern Brazil. Rev Saude Publica 32:74–76

Patterson BD, Dick CW, Dittmar K (2007) Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). J Trop Ecol 23:177–189

Pavey CR (1999) Foraging ecology of the two taxa of large-eared horseshoe bat, *Rhinolophus philippinensis*, on Cape York Peninsula. Australian Mammal 21:135–138

Pearce RD, O'Shea TJ (2007) Ectoparasites in an urban population of big brown bats (*Eptesicus fuscus*) in Colorado. J Parasitol 83:518–530

Pfalzer G, Weber C (2007) Invasionen der Zwergfledermaus (*Pipistrellus pipistrellus*) im Stadtgebiet von Kaiserslautern (BRD, Rheinland-Pfalz). Mass invasions of the common pipistrelle bat (*Pipistrellus pipistrellus*) in the city of Kaiserslautern (Germany, Rhineland-Palatine). Fauna und Flora in Rheinland-Pfalz Beiheft 35:212–219

Poché RM (1975) The bats of National Park W, Niger, Africa. Mammalia 39:39–50

Racey P, Swift SM (1986) The residual effects of remedial timber treatments on bats. Biol Conserv 35:205–214

Racey PA, Hutson AM, Lina PHC (2013) Bat rabies, public health and European bat conservation. Zoonoses Public Health 60:58

Ransome R, Hutson AM (2000) Action plan for the conservation of the greater horseshoe bat in Europe (*Rhinolophus ferrumequinum*). Nature and environment 109, Council of Europe Publishing, Strasbourg

Razafindrakoto N, Harwll A, Jenkins R (2011) Bats roosting in public buildings: a preliminary assessment from Moramang, Eastern Madagascar. Madagascar Conserv Dev 5:85–88

Reichel-Jung K, Threlfall CG (2016) Urbanization and its effects on bats—a global meta-analysis approach. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 13–28

Rintoul JLP, Brigham RM (2014) The influence of reproductive condition and concurrent environmental factors on torpor and foraging patterns in female big brown bats (*Eptesicus fuscus*). J Comp Physiol B 184:777–787

Roby PL, Gumbert MW, Sewell PL, Brewer SW (2011) Characteristics of roosts used by Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) on camp Mackall, North Carolina. Conserv Manage East Big-Eared Bats—US For Serv Gen Tech Rep SRS 145:101–110

Rowse EG, Lewanzik D, Stone EL, Harris S, Jones G (2016) Dark matters: the effects of artificial lighting on bats. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 187–207

Ruczyński I, Kalko EKV, Siemers BM (2007) The sensory basis of roost finding in a forest bat, *Nyctalus noctula*. J Exp Biol 217:3607–3615

Rydell J (1991) Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*. Ecography 14:203–207

Rydell J (1992) Exploitation of insects around streetlamps by bats in Sweden. Funct Ecol 6:744–750

Rydell J, Racey PA (1995) Street lamps and the feeding ecology of insectivorous bats. Sym Zool S 67:291–307

Sachanowicz K, Wower A (2013) Assemblage structure and use of anthropogenic roosts by bats in the eastern Carpathians: case study in the Bieszczady National Park (SE Poland). Ital J Zool 80:139–148

Saenz VL, Maggi RG, Breitschwerdt EB, Kim J, Vargo EL, Schal C (2013) Survey of *Bartonella* spp. in US bed bugs detects *Burholderia multivorans* but not *Bartonella*. PLoS ONE 8:e73661

Salvati L, Manganaro A, Fattorini S, Piattella E (1999) Density, nest spacing, breeding success and diet of a kestrel *Falco tinnunculus* urban population. Alauda 67:47–52

Santos M, Aguirre LF, Vázquez LB, Ortega J (2003) Phyllostomus hastatus. Mamm Species Acc 722:1–6

Schneeberger K, Voigt CC (2016) Zoonotic viruses and conservation of bats. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 263–282

Schneeberger K, Czirják GÁ, Voigt CC (2013) Inflammatory challenge increases measures of oxidative stress in a free-ranging long-lived mammal. J Exp Biol 216:414–4519

Schneider MC, Aron J, Santos-Burgoa C, Uieda W, Ruiz-Velazco S (2001) Common vampire bat attacks on humans in a village of the Amazon region of Brazil. Pan Am J Pub Hlth 25:260–268

Shapiro JT, de Costa Lima Junior MS, Dorval ME, de Oliveira França A, Cepa Matos Mde F, Bordignon MO (2013) First record of *Leishmania braziliensis* presence detected in bats, Mato Gross do Sul, southwest Brazil. Acta Tropica 128:171–174

Shiel CB, Shiel RE, Fairley JS (1999) Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. J Zool 249:347–358

Shore RF, Boyd IL, Leach DV, Stebbings RE, Myhill DG (1990) Organochlorine residues in roof timber treatments and possible implications for bats. Environ Pollut 64:179–188

Shore RF, Myhill DG, French MC, Leach DV, Stebbings RE (1991) Toxicity and tissue distribution of pentachlorophenol and permethrin in pipistrelle bats experimentally exposed to treated timber. Envioron Pollut 73:101–118

Sibly RM, Brown JH (2007) Effets of body size and lifestyle on evolution of mammal life histories. Proc Nat Acad Sci 104:17707–17712

Silver J (1935) Eliminating bats from buildings, vol 109. United States Department of Agricultural leaflet, pp 1–5

Smit-Viergutz K, Simon M (2000) Eine vergleichende Analyse des sommerlichen Schwärmverhaltens der Zwergfledermaus (45 kHz Ruftyp, *Pipistrellus pipistrellus* Schreber, 1774) an den Invasionsorten und am Winterquartier. A comparative analysis of the summertime swarming behavior of the common pipistrelle (*Pipistrellus pipistrellus* Schreber, 1774, 45 kHz call type) at the sites of the invasion and in the hibernaculum. Myotis 38:69–89

Socolovschi C, Kernif T, Raoult D, Parola P (2012) Borrelia, Rickettsia, and Ehrlichia species in bat ticks, France, 2010. Emer Infect Dis 18:1966–1975

Soulé ME (1985) What is conservation biology? Bioscience 35:727–734

Speakman JR (1991) The impact of predation by birds on bat populations in the British Isles. Mammal Rev 21:123–142

Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats: In: Kunz TH, Fenton MB (eds) Bat ecology. Chicago University Press, pp 430–409

Speakman JR, Stone RE, Kerslake JL (1995) Temporal patterns in the emergence behaviour of pipistrelle bats, *Pipistrellus pipistrellus*, from maternity colonies are consistent with an anti-predator response. Anim Behav 50:1147–1156

Speakman JR, Irwin N, Tallach N, Stone R (1999) Effect of roost size on the emergence behaviour of pipistrelle bats. Anim Behav 58:787–795

Spitzenberger F, Weiss E, Sackl P (2010) Massive population decline of the critically endangered greater horseshoe bat, *Rhinolophus ferrumequinum* (Schreber, 1774) in Styria, south-eastern Austria, between the mid-1990s and 2009 (Mammalia, Chiroptera). Joannea Zool 11:5–17

Streicker DG, Franka R, Jackson FR, Rupprecht CE (2013) Anthropogenic roost switching and rabies virus dynamics in house-roosting big brown bats. Vector-borne Zoonot 13:498–504

Strelkov PP (2002) Material on wintering of migratory bat species (Chiroptera) on the territory of the former USSR and adjacent regions, Part 2. *Nyctalus noctula*. Plecotus 5:35–56

Šuba J, Vietniece D, Petērsons G (2010) The parti-coloured bat *Vespertilio murinus* in Riga (Latvia) during autumn and winter. Environ Exp Biol 8:93–96

Subbaraj R, Balasingh J (1996) Night roosting and lunar phobia in Indian false vampire bat *Megaderma lyra*. J Bombay Nat Hist Soc 93:1–7

Szodoray-Parádi F, Szodoray-Parádi A, Sike T (2004) Building dwelling bats survey in Satu Mare County, Romania. Sau Mare, Studii şi Comunicăre, Seria Ştiinţele Naturale 4–5:196–200

Takumi K, Lina PHC, van der Poel WHM, Kramps JA, Van Der Giessen JWB (2009) Public health risk analysis of European bat lyssavirus infection in the Netherlands. Epidemiol Infect 137:803–809

Tong S, Conrardy C, Ruone S, Kuzmin IV, Guo X, Tao Y, Niezgoda M, Haynes L, Agwanda B, Breiman RF, Anderson LJ, Rupprecht CE (2009) Detection of novel SARS-like and other coronaviruses in bats from Kenya. Emerg Infect Dis 15:482–485

Turbill C, Körtner G, Geiser F (2003) Natural use of heterothermy by a small, tree-roosting bat during summer. Physiol Biochem Zool 76:868–876

Uieda W (1998) Rabies in the insectivorous bat *Tadarida brasiliensis* in southeastern Brazil. Rev Saude Publ 23:484–485

Van der Poel WH, Van der Heide R, Verstraten ERAM, Takumi K, Lina PHC, Kramps JA (2005) European bat lyssaviruses, the Netherlands. Emerg Infect Dis 11:1854–1859

Vandzurova A, Backor P, Jarvorsky P, Pristas P (2013) *Staphylococcus nepalensis* in the guano of bats (Mammalia). Vet Microbiol 164:116–121

Vivier L, van der Merwe M (2001) Aspects of the histology of reproduction in the female Angolan free-tailed bat *Mops condylurus* (Microchiroptera: Molossidae) in Mpumalanga, South Africa. J Zool 254:495–504

Vivier L, van der Merwe M (2007) The incidence of torpor in winter and summer in the Angolan free-tailed bat, *Mops condylurus* (Microchiroptera: Molossidae), in a subtropical environment, Mpumulanga, South Africa. Afr Zool 42:50–58

Voigt CC, Kelm DH (2006) Host preference of the common vampire bat (*Desmodus rotundus*; Chiroptera) assessed by stable isotopes. J Mammal 87:1–6

Whitaker JO Jr (1998) Life history and roost switching in six summer colonies of eastern pipistrelles in buildings. J Mammal 79:651–659

Whitaker JO Jr, Gummer SL (1992) Hibernation of the big brown bat, *Eptesicus fuscus*, in buildings. J Mammal 73:312–316

Wilkinson GS, South JM (2002) Life history, ecology and longevity in bats. Aging Cell 1:124–131

Williams LM, Brittingham MC (1997) Selection of maternity roosts by big brown bats. J Wildl Manage 61:359–368

Williams-Guillén K, Perfecto I, Vandermeer J (2008) Bats limit insects in a neotropical agroforestry system. Science 320:70

Willis CKR, Brigham RM, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging bats. Naturwissenschaften 93:80–83

Zahn A (1999) Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*. J Zool 247:275–280

Zahn A, Christoph C, Christoph L, Kredler M, Reitmeier A, Reitmeier F, Schachenmeier C, Schott T (2000) Die Nutzung von Spaltenquartieren an Gebaeuden durch Abendsegler (*Nyctalus noctula*) in Suedostbayern. The use of crevices in buildings as roosts by the noctule (*Nyctalus noctula*) in southeast Bavaria. Myotis 37:61–76

Zhang LB, Zhu GH, Jones G, Zhang SY (2009) Conservation of bats in China: problems and recommendations. Oryx 43:179–182

Zorya AV (2002) Contribution of bats to spreading rabies on the territory of Kharkov region and prevention of conflict sutations “man-bat”. Plecotus et al. Supplement: pars specialis 118–120

Chapter 15
Conservation Ecology of Cave Bats

Neil M. Furey and Paul A. Racey

Abstract Caves and other subterranean sites such as mines are critical to the survival of hundreds of bat species worldwide, since they often provide shelter for most of a nation's bat fauna. In the temperate zone, caves provide roosts for hibernation and for some species, breeding in summer, whereas in warmer regions, they support high species richness year round and enormous colonies that maintain substantial ecosystem services. Due to the solubility of the substrate, the highest densities of caves occur in karst landscapes. Given their importance for bats, relatively few studies have investigated factors involved in cave selection, although current evidence suggests that the density and size of caves are the best predictors of species diversity and population sizes. Thermal preferences have been established for some cave-dwelling species as well as their vulnerability to disturbance, particularly during hibernation and reproduction. Growth in limestone quarrying and cave tourism industries worldwide severely threatens cave-dwelling bats, in addition to loss of foraging habitat, hunting for bushmeat, incidental disturbance and disruptive guano harvesting. Apparent declines of cave bats in Europe and North America also pose serious concerns, as do global climate change predictions. The main conservation response to threats to cave bats in these continents

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N.M. Furey (✉)
Fauna & Flora International (Cambodia Programme), No. 19, Street 360,
Boeng Keng Kang 1, PO Box 1380, Phnom Penh 12000, Cambodia
e-mail: neil.furey@fauna-flora.org

P.A. Racey
Centre for Ecology and Conservation, College of Life and Environmental Sciences,
University of Exeter, Cornwall Campus, Treliever Road, Penryn TR10 9EZ, UK
e-mail: p.a.racey@exeter.ac.uk

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has been gating, but this remains relatively untested as a means of protecting colonies in other regions. Research on sustainable harvesting of bats as bushmeat and their responses to different types of human disturbance at caves and loss of surrounding foraging habitats is required. More caves of outstanding importance for bats at national and international levels also require protection.

15.1 Introduction

Bats fly mainly at night and spend the day in roosts which provide shelter from extremes of temperature, other climatic variables and predators. The most widely used day roosts occur in caves and because of the global abundance of surface carbonate rock (Fig. 15.1), in karstic caves. However, caves in other rock formations, as well as mines, wartime fortifications and other underground situations, are also used by roosting bats, because all provide a relatively cool and constant environment compared to that outside. Although the term 'cave-dependent' is often applied to bats, and will be used in this review, it is recognized that while their need for day roosts is incontrovertible, dependency is difficult to establish. The threats to such roosts and the bats they shelter also have much in common and for that reason this chapter will consider all such roost types, which will often be referred to collectively as caves. We aim to review the importance of such sites for the maintenance of bat biodiversity. We consider those factors which make caves important for bats and whether bats select caves with particular features. Our main aim however is to highlight the threats to bats in caves and the ways in which these may be mitigated.

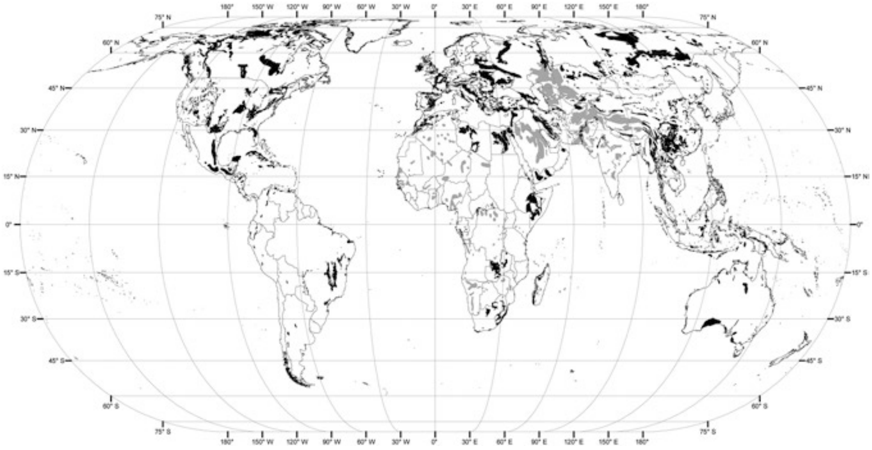

Fig. 15.1 Global distribution of carbonate rocks (© Paul Williams, University of Auckland, NZ)

15.2 Why Do Cave Bats Matter?

The largest aggregations of living vertebrates are found in caves, and in the 1950s and early 1960s, midsummer colonies of adult Mexican free-tailed bats (*Tadarida brasiliensis*) in 17 caves in the south-western USA were estimated to total 150 million individuals (McCracken 2003; Russell and McCracken 2006) (Fig. 15.2). In contrast, the largest number of tree-roosting bats in any location is currently estimated at 8 million for the straw-coloured fruit bat (*Eidolon helvum*) in a small area of swamp forest in Kasanka National Park, Zambia (Racey 2004). Large aggregations are characteristic of molossid bats in caves in both Old and New Worlds and despite repeated efforts to harness modern technology such as Doppler radar (Horn and Kunz 2008) and thermal infrared video (Betke et al. 2008), accurate counting of the numbers involved has proved elusive. Not surprisingly however, the evening emergence of such colonies attracts significant numbers of tourists around the world every year. For example, an amphitheatre at the entrance to Carlsbad caverns, New Mexico has allowed visitors to observe the dusk departure (and dawn return) of a large colony of *T. brasiliensis* over several decades, although the US National Parks Service have banned the use of flash photography in recent times because of concerns that it disturbs the bats (Altringham 2011).

The survival of many bat species worldwide depends upon natural caves and other underground sites such as mines (Mickleburgh et al. 2002). For instance, of

Fig. 15.2 Evening emergence of *T. brasiliensis* from Frio cave in Texas, USA (© Merlin D. Tuttle, Bat Conservation International, www.batcon.org)

39 bat species in temperate America (north of Mexico), 18 rely substantially on caves (46 %), including 13 species that dwell in them all year round, while the remaining five depend on caves for hibernation sites (McCracken 1989). Of the 40 European bat species for which information is available, 28 are found in caves during hibernation and a few all year round (Dietz et al. 2009). Arita (1993a) documented similarly high levels of occupancy in subtropical Mexico, where 60 of the 134 bat species known (45 %) regularly use caves. Even higher occupancy has been found in China, where 77 % of the known bat fauna (101 of 131 species) roosts in caves and other subterranean habitats (Luo et al. 2013) and similar figures exist for Puerto Rico and North Vietnam (Rodriguez-Durán 2009; Furey et al. 2010). Because cave-roosting bats spend at least half their lives inside caves (Kunz 1982), protection of these sites is central to their conservation. Due to the solubility of calcium carbonate, caves are found in particularly high density in karstic areas and research in Southeast Asia suggests they may serve as population reservoirs subsidizing bat species diversity in fragmented landscapes that could otherwise decline over time (Struebig et al. 2009).

The ecological services provided by cave bats have been documented in recent years (Boyles et al. 2011; Kunz et al. 2011). In Texas, *T. brasiliensis* fly up to 900 meters before dispersing to forage over crops, and include in their diet important pests such as cotton bollworm moth (*Helicoverpa zea*). The proportion of such pests in their faeces allows the economic value of such predation to be estimated, which includes a reduction in the number of costly pesticide applications required (Cleveland et al. 2006). In Thailand, the wrinkle-lipped free-tailed bat (*Chaerephon plicatus*) consumes economically significant amounts of white-backed planthoppers (*Sogatella furcifera*) which are major pests of rice crops (Leelapaibul et al. 2005; Wanger et al. 2014). The dawn bat (*Eonycteris spelaea*) which forms colonies of up to 20,000 individuals in SE Asian caves (Medway 1958) is the primary pollinator of durian (*Durio zibethinus*), a high value fruit (Bumrungsri et al. 2009) and a commonly eaten tree bean (*Parkia speciosa*) (Bumrungsri et al. 2008), alongside other economically important plant species (Bumrungsri et al. 2013).

Mining the guano of cave-dwelling bats is a worldwide phenomenon as the undigested remains of insects are rich in nitrogen and phosphates (Gillieson 1996). This is particularly true in Asia, where bat guano is a major source of fertilizer whose sale and use features prominently in many local economies (Leh and Hall 1996; Leelapaibul et al. 2005; Aye 2006). This has resulted in overharvesting and disturbance of cave roosting bats (Bumrungsri et al. 2013), exacerbated by cave modifications made to assist guano extraction (Elliot 1994). Allied to this, the guano produced by bats constitutes a primary source of energy in cave ecosystems and survival of a considerable proportion of the terrestrial invertebrate fauna in tropical caves is dependent upon its continued deposition. These communities include a suite of highly-adapted and narrowly-endemic arthropods (often referred to as guanophiles or guanobionts) which complete their entire life cycle in or around guano piles (Deharveng and Bedos 2012).

15.3 Life in Caves

Caves confer important advantages in the form of permanent, thermally stable and humid environments which protect bats against inclement weather and reduce loss of body water (Kunz 1982; Gunn 2003; Avila-Flores and Medellin 2004). Added to this are potential benefits in reduced predation risk and thermoregulatory advantages derived from aggregating in large numbers. Disbenefits may include increased commuting costs in foraging, higher incidence of parasites and disease transmission, and possibly greater intraspecific foraging competition (Kunz 1982). Although caves that permit human access are necessarily the ones about which most is known, bats also roost extensively in smaller inaccessible rock cavities. For example, four overwintering colonies of noctule bats (*Nyctalus noctula*), comprising about a thousand individuals, were reported in vertical crevices 1–2 m in both height and depth and 5–7 cm in breadth in calcareous lakeside cliffs in Romania (Barbu and Sim 1968). In Madagascar, Malagasy straw-coloured fruit bats (*Eidolon dupreanum*) often roost in such crevices high on cliffs, where they are less accessible to hunters (Mackinnon et al. 2003).

While caves have the disadvantage of being uncommon in many areas and may be located far from suitable foraging sites (Bradbury 1977), roost fidelity is greatest among bat species that use caves and buildings (Lewis 1995). This is thought to stem in part from their permanency, although many caves are unsuitable as roosts, particularly those that are too cold or warm to promote efficient thermoregulation (Kunz 1982). Caves can be viewed as largely azonal habitats because they share a similar environment across all latitudes and all macroclimates. While some bats with a very restricted distribution such as Kitti's hog-nosed bat (*Craseonycteris thonglongyai*) are found only in karstic caves, others, such as many European species, are found equally in caves, disused mines, railway tunnels, wartime fortifications, churches and domestic roof spaces. Beyond local variations, temperature is the most basic physical factor distinguishing abiotic environments in tropical versus temperate caves (Deharveng and Bedos 2012). In temperate regions, caves provide roosting sites for hibernation and for some species, breeding in summer, and in tropical regions, where bats do not hibernate, they support very large colonies and high bat diversity (Rodriguez-Durán and Lewis 1987; Monadjem et al. 2010; Furey et al. 2011).

The majority of temperate zone bat species hibernate in caves, and a few taxa continue to roost there throughout the year including the summer period of reproduction (Dietz et al. 2009; Nagy and Postawa 2010). In early autumn, thousands of bats swarm at the entrances of caves each night, flying in and out, although most leave before dawn. The sex ratio of swarming bats is heavily skewed towards males and it is thought that mating occurs, and since the swarming bats come from many different colonies, that this provides an opportunity for gene flow and also for mothers to show their young where to hibernate (Parsons and Jones 2003; Parsons et al. 2003a, b). Bats are also attracted to potential hibernacula by the echolocation calls of conspecifics (Avery et al. 1984). In temperate regions, the mating that began at swarming continues in some species until spring. During hibernation, males often arouse and copulate with torpid females (Thomas et al. 1979). Analysis of the ambient temperature records at which bats were found torpid in the wild reveal that these range from −10 to 21 °C, with a mode of 6 °C for vespertilionid bats ($n = 29$ species) and 11 °C for rhinolophids ($n = 5$ species) (Webb et al. 1995).

In Europe, bats make extensive use of subterranean fortifications, such as those of the Maginot line constructed between France and Germany before World War 1 and the 30 km of underground tunnels built at Nietoperek in eastern Poland during World War 2 on the strategic route from Warsaw to Berlin. The integral drainage system of the latter was subsequently vandalized so parts of the system are now flooded and there is a range of humidities and airflows. Annual hibernation counts are carried out and 37,000 bats of eight species were recorded in 2013, making this the most important hibernaculum in Central Europe, with comparable numbers of bats to many natural European caves (Kokurewicz et al. 2013). Use of wartime structures by bats is also common in the Netherlands and de Boer et al. (2013) found that internal size-related variables had the greatest positive effect on hibernation site suitability. Of the 45 bat species in North America, 28 roost in old mines, which are the only known roosts of the Curacaoan long-nosed bat (*Leptonycteris curasoae*) in the USA (Pierson 1998). With over 300,000 abandoned mines in the state of Nevada alone, guidelines were required for their evaluation as a conservation resource and to resolve potential conflicts (Riddle 1995), and these have been adapted for wider use by Bat Conservation International (Tuttle and Taylor 1994).

In contrast to temperate regions, cave environments in the tropics are typically more stable and uniformly inhabited (Brosset 1966). Though species diversity and population sizes in a cave can fluctuate between different seasons, many tropical bat species roost in caves throughout the year so that reproduction occurs there (McWilliam 1982; McDonald et al. 1990; Siles et al. 2007; Rodriguez-Durán 2009; Monadjem et al. 2010; Furey et al. 2011). Studies of their social organization have revealed that males defend groups of females in erosion domes in the ceilings of karstic caves in several species including the greater spear-nosed bat (*Phyllostomus hastatus*) in the Neotropics (McCracken and Bradbury 1981) and Hildegarde's tomb bat (*Taphozous hildegardeae*) in coastal limestone caves in Kenya (McWilliam 1988). Recent evidence also suggests that *E. spelaea* may adopt a similar harem social organisation in Thailand (Bumrungsri et al. 2013). The abundance of crevices and cavities in caves is believed to facilitate population substructuring and the defense of these roosts by harem males, with clear benefits for both sexes since males achieve most copulations in a cluster they protect, and females gain protection for themselves and their offspring (Bradbury 1977; McCracken and Bradbury 1981). McCracken (1993) has shown how lactating female *T. brasiliensis* in huge maternity colonies locate their own young on cave walls by spatial memory, together with the sound and scent of their young.

A defining characteristic of karst areas—the abundance of calcium as the cation of calcium carbonate—has been suggested as a driver of the use of karstic caves by insectivorous bats. Insects are a poor source of calcium and several studies have shown that calcium levels in the bones of female bats are lowest during lactation, as calcium is mobilized and transferred to the young in milk (Kwiecinski et al. 1987; Booher and Hood 2010). This led Barclay (1994, 1995) to suggest that shortage of calcium may be a greater constraint on reproduction than meeting its energy demands and that one of the reasons that bats roost in karst caves is that they acquire calcium by licking the walls, which is a common observation (Codd et al. 1999). There has been only one study to test this hypothesis, which was not supported by the evidence, since bats were distributed across all underground sites in a wide range of geological formations and were not concentrated in karst landscapes (Bernard and Davison 1996). Nevertheless, the fact that Adams et al. (2003) captured more female and juvenile bats over water holes with harder water (indicating higher calcium levels) suggests that environmental calcium is important, particularly for reproducing females and their young.

15.3.1 Cave Selection

The numbers and diversity of bats found in caves are influenced by their dimensions, structural complexity and microclimate, the availability of food in the surrounding landscape, parasite and predation pressure, human disturbance, historical use by bats, their maneuverabilty in flight and interactions between species. Considering how important caves are for global and local bat biodiversity, there have been relatively few studies of these factors. For instance, half of the bat species known from a 155 km^2 karst reserve in North Vietnam (21/42) used a single large cave over a 23 month period (Furey et al. 2011), whereas in Malaysia, Struebig et al. (2009) found that a single area of karst caves had a dominant influence on bat assemblage composition at non-karst sites up to 11 km away through the presence of two cave-dwelling species.

Brunet and Medellin (2001) revealed a positive relationship between species richness and cave surface area in central Mexico. Roost site diversity as indicated by spatial variation in relative humidity and the presence of erosion domes in cave ceilings (Fig. 15.3) was associated with this species-area relationship. Consistent with this, Arita (1996) found that the largest caves in the northern Yucatan Peninsula of Mexico harbored the most diverse assemblages and largest populations, including several species of conservation concern. At a national level however, Arita (1993b) found that few of the vulnerable species of Mexican bats roost in caves with high species richness or large populations, suggesting that conservation plans based solely on diversity would not adequately protect the country's cave bat fauna. Non-random associations are also common among bats roosting in the hot caves of Puerto Rico and Rodriguez-Durán (1998) speculated that interspecific variation in peak emergence times associated with temporal differences in foraging patterns might allow these caves to support more bats than would be possible in a monospecific colony or random assemblage of species.

Fig. 15.3 Cave roost of *Taphozous melanopogon* in an erosion dome in Thailand (single bat to left of the main group is *Eonycteris spelaea* (© Pipat Soisook)

In a study of the cave complex in Ankarana National Park in the limestone massif of northern Madagascar, Cardiff (2006) found that longer caves, more complex caves, those with larger entrances or with entrances at lower elevation and those with less temporal variation in ambient temperature all had significantly higher bat species richness. In a similar study in the karstic Bemaraha National Park in western Madagascar, Kofoky et al. (2007) found that species richness and abundance was low in all but one of 16 caves—Anjohikinakina, which contained five species and over 9000 individuals of one. This cave was difficult to access and, unlike some of the others in the national park, was seldom visited by tourists.

These findings are broadly reflected in East Asia. In a study of 255 subterranean sites in central and eastern China, Luo et al. (2013) found that bat species richness was positively correlated with cave size and negatively correlated with human disturbance. The incidence of nationally threatened and endemic species was also positively correlated with species richness, which was greater in caves formerly used for tourism than in abandoned mines. In a study of 25 subterranean sites in Funiu Mountain (eastern China), Niu et al. (2007) similarly found that bat species distributions were highly dependent on the type and size of roost, with large caves supporting unusually high species richness and abundances. Over 80 % of the bats recorded were located on the southern side of the mountain which was attributed to climatic differences (higher annual rainfall and average temperatures) and the higher incidence of large caves there.

Nagy and Postawa (2010) further explored the relationship between cave variables and bat occupancy during the hibernation and breeding seasons in 79 caves in mountainous areas of Romania. Maternity colonies were divided between species that select either high or low temperatures, whereas winter aggregations were divided across three groups: (i) species that prefer high temperatures and hibernate at low altitudes, (ii) species preferring mid- to high elevations and low temperatures, and, (iii) species that hibernate in large, cold cave systems with permanent water flow. Piksa et al. (2013) also found that the species richness and assemblage structure of hibernating bats varied altitudinally across 70 caves in the nearby Carpathian mountains of southern Poland, such that stepped changes occurred in assemblage structure that reflected zones observed in vegetation. Geographical location and temperature were found to be the most important factors influencing overall species occurrence by Nagy and Postawa (2010) and their results support Brunet and Medellin's (2001) conclusion that high cave densities provide suitable conditions for large populations of different bat species.

The influence of external environment or "ecological context" on cave selection by bats appears little studied, particularly in terms of access to factors such as food and water. Nevertheless, there seems little doubt that, as in foliage-roosting species, persistent degradation and loss of foraging habitats is likely to threaten the viability of cave-dwelling populations as a result of increased nightly commuting costs and poorer foraging conditions reducing individual fitness (Kingston 2013). For instance, in a comparative study of pristine and modified forests in Vietnamese karst, Furey et al. (2010) found that although species richness was only slightly reduced, the abundance of cave-dwelling rhinolophids and hipposiderids in disturbed and degraded forests was less than a third of that in primary forest, despite comparable sampling effort and availability of caves. In addition, as cave-dwelling species in Asia differ considerably in their wing morphology and thus vagility (Furey 2009), it would appear likely that progressive isolation of cave roosts in anthropogenic landscapes will differentially affect species with weaker dispersal abilities (Fig. 15.4). However, these potential population and species losses may be mitigated to some extent by increases in the abundance of species that use human-made habitats (Mendenhall et al. 2014).

15.3.2 Influence of Cave Microclimate

There are several microclimatic factors which may determine the selection of caves and the location of roost sites within them—temperature, relative humidity and airflow, which are interrelated, and, light intensity. There have been several studies investigating the importance of cave temperature, but the most instructive, extending over 15 years, took place in the Guelhemergroeve mines in South Limburg, Netherlands, where limestone has been mined since the Middle Ages (Daan and Wichers 1968). Nine species of vespertilionid and rhinolophid bats are found there. Two, which approach the northern border of their distribution in South Limburg (Geoffroy's myotis *Myotis emarginatus* and lesser horseshoe bat *Rhinolophus hipposideros*) arrive early and hibernate in the warmer distal end of

Fig. 15.4 Forested karst hills surrounded by wet rice cultivation in North Vietnam (© Neil Furey)

the tunnel system all winter, until late spring (Fig. 15.5a). Three species (the barbastelle *Barbastella barbastellus*, Natterer's bat *M. nattereri* and long-eared bats *Plecotus auritus*) are found in small numbers in protected positions in the mine entrance and stay for the shortest periods, with frequent arrivals and departures (Fig. 15.5b). The four remaining species (the pond bat *M. dasycneme*, the mouse-eared bat *M. myotis*, Daubenton's bat *M. daubentonii* and the whiskered bat *M. mystacinus*) which comprise 80 % of the bats occupying the mines in winter and whose distribution extends further north in Europe, arrive late, in November and December. They hibernate initially in the warmer distal end of the tunnel system where they hang in exposed situations, but as winter progresses, they arouse and move progressively closer to the cold entrance, where they hibernate in crevices, presumably to avoid air currents (Fig. 15.5c). This movement, which has been termed 'internal migration', reflects a preference for lower temperature as winter progresses. So why don't these bats hibernate at the entrance at the beginning of winter? This may reflect selection for higher relative humidity which maintains the condition of the bats' delicate wing membranes but which decreases as temperature increases. At the beginning of the winter, the entrance is relatively warm and humidity is lower than at the distal end of the cave. As the winter gets colder, bats move to take advantage of the rising humidity at the entrance. The arousals and movements which characterize internal migration would also appear to reflect the fact that the fat is metabolized at a faster rate in the warmer distal end of the tunnel system, and that the same amount of fat will last longer if the metabolic rate of the bats is lower at the colder entrance (Daan and Wichers 1968). In the UK, Ransome (1968, 1971) has also shown that the greater horseshoe bat (*Rhinolophus ferrumequinum*) requires a series of hibernacula providing a range of airflow patterns and temperature regimes.

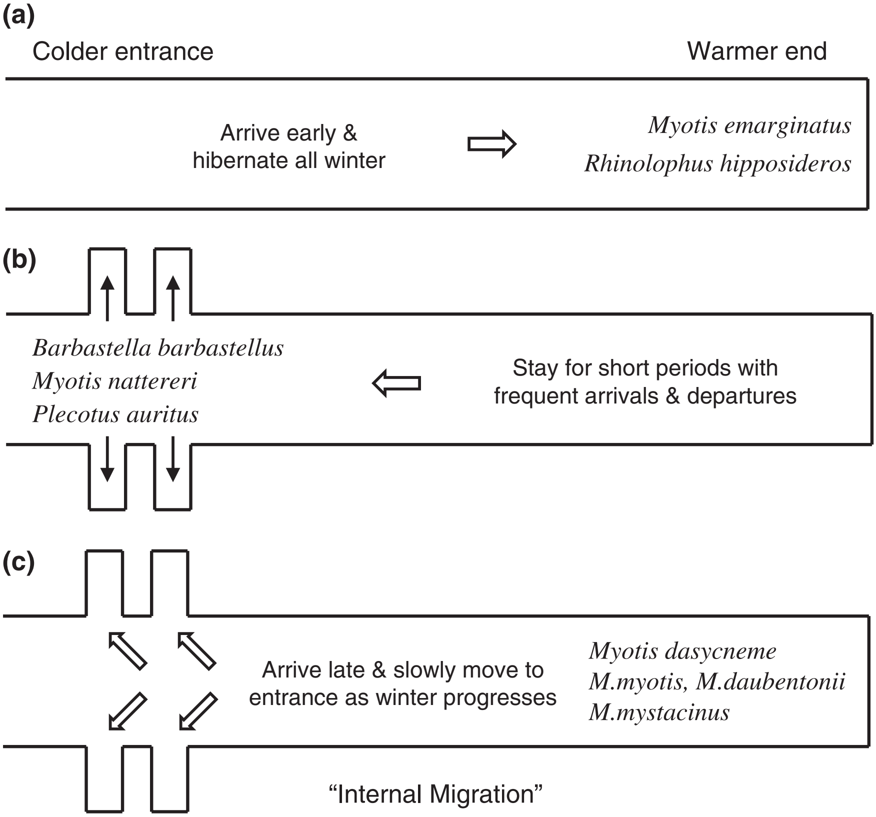

Fig. 15.5 **a–c** Differences in use of South Limburg limestone mines among nine bat species, four of which exhibit 'internal migration'. (after Daan and Wichers 1968)

In isolated mountain ranges in California, the Californian leaf-nosed bat (*Macrotus californicus*) uses geothermally heated winter roost sites in abandoned mines, with stable year round temperatures of about 29 °C, which minimizes energy expenditures. They also have an energetically frugal pattern of foraging which relies on visual prey detection. These two factors have allowed this most northerly representative of the Phyllostomidae to invade the temperate zone (Bell et al. 1986).

Although in temperate regions bats use caves mainly for hibernation, some species continue to occupy them throughout the year and young are born there. Slight differences in summer temperature between caves are important and young of the same bat species in caves with higher temperature grow faster and reach adult dimensions sooner. Growth rates of known-age young of the gray myotis (*M. grisescens*), a nationally endangered species endemic to several eastern states in the USA, were compared between a colony of 600 in a cave at 13.9 °C and a colony of 2200 at 16.4 °C. Significantly increased growth rates in the latter resulted in mean attainment of first flight at 24 days of age compared with 33 days in the former. The young reared at the higher cave temperature have an extra week to increase their foraging efficiency and their body mass before hibernation begins which may be crucial to their overwintering survival (Tuttle 1976).

These temperatures are however cool compared with the hot caves of the tropics which fall into two categories so far as bats are concerned. The first are heated by convection, with hot air rising from the plain below and entering a vertical cave at higher elevation. The endemic Australian ghost bat (*Macroderma gigas*) roosted in such caves on Mount Etna, Queensland during pregnancy and lactation, and because females experience thermoneutral conditions and do not have to expend energy to maintain a high constant body temperature, they can divert more energy to growing a foetus and producing milk (P. Racey unpublished). The second type of hot cave is heated by the bats themselves. These are characterized by a small entrance, at floor level, opening onto a series of chambers, along which a temperature gradient is established. Species with low basal metabolic rates (BMR), as measured in the laboratory (the Antillean ghost-faced bat *Mormoops blainvillei*, the sooty mustached bat *Pteronotus quadridens* and Leach's single-leaf bat *Monophyllus redmani*) selected the distal hotter end of the temperature gradient, which, at 35 °C, approached thermoneutrality. Large numbers of bats are needed to maintain such a high temperature, and in Cucaracha cave, Puerto Rico, half a million bats roost in the distal chamber (Rodriguez-Durán and Lewis 1987; Rodriguez-Durán and Soto-Centeno 2003; Rodriguez-Durán 2009; Ladle et al. 2012).

In Mexico, Avila-Flores and Medellin (2004) found that heterothermic species in the family Vespertilionidae used colder caves with the widest temperature range (1.6–29.8 °C) whereas homeothermic species in the four exclusively tropical families Emballonuridae, Mormoopidae, Phyllostomidae and Natalidae occupied warmer caves (14.5–37.5 °C). Within these caves, precise homeotherms, with a narrow range of body temperatures, occupied cooler roosts than more labile homeotherms. Body size and temperature were negatively correlated. The smallest homeothermic insectivorous species, weighing less than 10 g, consistently occupied roosts with temperatures greater than 20 °C, often 25 °C, whereas only the largest homeothermic insectivores were found in caves with temperatures as low as 16 °C. Frugivorous, nectarivorous and sanguivorous bats were found in a wide range of temperatures but often less than 20 °C. No trends could be detected so far as relative humidity was concerned, and, overall, temperature was the most important physical variable influencing roost selection.

The last physical variable is light intensity, which is also the least studied because until recently, recording it accurately has not been possible. Some insectivorous bat species are more light tolerant than others, such as the Seychelles sheath-tailed bat (*Coleura seychellensis*) which often roosts in open boulder caves (Bambini et al. 2006), although light levels in these caves are not thought to be a major factor in roost selection. In contrast, Old World fruit bats (Pteropodidae) rely on vision and those species which roost in caves, such as *E. dupreanum* in Madagascar, do so within sight of the entrance (Cardiff et al. 2009). Within this bat family, the genus *Rousettus* has evolved a form of echolocation involving clicking with its tongue and is capable of roosting deep in caves (MacKinnon et al. 2003; Waters and Vollrath 2003). Gould (1988) raised the possibility that the wing-clapping of *E. spelaea* may aid their navigation in the dark caves where they roost. Similar wing-clapping is reported in the bare-backed bat (*Dobsonia moluccensis*) which also roosts in dark caves (Churchill 2008).

15.3.3 Importance of Bats for Cave Ecosytems

Due to the absence of primary production and general scarcity of food underground, most life in caves is invertebrate and largely dependent on energy sources from the surface such as penetrating tree roots and organic debris washed in by percolating waters or floods (Gillieson 1996). While bat guano appears to be less significant for cave-restricted invertebrates (often referred to as troglobites or troglobionts) inhabiting temperate caves, a considerable proportion of the terrestrial fauna in tropical caves depends upon its continued deposition (Deharveng and Bedos 2012). The significance of this lies in the fact that subterranean invertebrates are globally diverse and caves are thought to rank among the hottest of biodiversity hotspots (*sensu* Myers et al. 2000) worldwide in terms of their levels of species endemism and threat (Gilbert and Deharveng 2002; Whitten 2009).

It has long been assumed that guano accumulations support less invertebrate diversity and few narrowly-endemic species compared to low-energy cave habitats. However, this view is challenged by the recent discovery of a huge radiation of typically guanobiotic Cambalopsid millipedes across Southeast Asia, whereby each karst area harbors one or two site-endemic species (Golovatch et al. 2011). Further, as most tropical karsts have yet to be investigated and cave-restricted species new to science continue to be discovered in virtually every survey (both troglobionts and guanobionts), the era of tropical cave biodiversity exploration has clearly only just begun. Notwithstanding this, due to the major contribution guanobionts make to overall cave diversity, disturbance to bats is increasingly regarded as one of the most serious threats to tropical cave invertebrates. Paradoxically, this concern is probably more relevant to common and widespread bat species (e.g. *C. plicatus* in Asia) than rarer or non-colonial species however, since the former produce the most guano in cave ecosystems (Deharveng and Bedos 2012).

15.4 Conservation Threats

Due to their low annual reproductive rates, bat populations take a relatively long time to recover from population losses associated with human activities (Racey and Entwistle 2000). Slow population growth rates thus exacerbate existing threats to bat populations. This poses a particular problem for cave-dwelling bats, particularly species which are gregarious and colonial, as any intrusion into the relatively small and confined spaces that caves provide tends to affect the entire aggregation (McCracken 1989). The fact that large numbers of individuals are often concentrated into only a few specific roost sites results in high potential for disturbance (Sheffield et al. 1992). It also increases the potential for Allee effects—recently redefined as a positive relationship between any component of individual fitness and either numbers or density of conspecifics (Stephens et al. 1999).

Caves have a long history of human use, with the earliest direct evidence of occupation dating back to at least 700,000 BP (from the Peking person site near Beijing, China: Gillieson 1996). Originally providing havens for prehistoric hunter-gatherers, caves across the world have since served a remarkable range of purposes. These include military fortifications and wartime refuges, horticultural uses, sanatoria for patients with respiratory and other ailments, sites for religious worship and burial, storage and dumping facilities, sources of water and fertilizer, and finally, destinations for opportunistic recreation and commercial tourism. More generally, because karst is highly porous, the integrity of caves in karst areas depends on complex interactions between hydrology, biology and geomorphology within their catchments. As the health of broader subterranean communities is strongly influenced by their surrounding environment, activities impacting cave-dwelling life consequently include those affecting the surface environment (Watson et al. 1997; Vermeulen and Whitten 1999).

15.4.1 Seasonality and Climate Change

Cave-dwelling bats are especially vulnerable to disturbance during periods of torpor and hibernation. Although hibernating bats periodically arouse, such arousals are energetically expensive and can account for 75 % of winter energy expenditure (Thomas et al. 1990). Disturbance can thus cause premature arousal which can deplete critical energy reserves to the extent that the bat is unable to survive the winter (Thomas 1995). As a result, human disturbance is widely regarded as a significant cause of over-winter mortality in temperate zone bats (Sheffield et al. 1992; Mitchell-Jones et al. 2007).

The lethal effects of repeated arousals during hibernation have been dramatically illustrated by the death of many millions of bats hibernating in caves in North America following infection with white-nose syndrome (*Geomyces destructans*—now renamed *Pseudogymnoascus destructans*: Minnis and Lindner 2013). This fungus invades the skin and irritates the bats, causing them to arouse repeatedly, until their stored body fat is exhausted and they starve to death (Reeder and Moore 2013). The situation regarding hibernation in the seasonal tropics is less well documented, although as many regions at higher tropical latitudes periodically experience cold winters (e.g. North Vietnam 18–23°N, lowest temperatures varying from −3.4 to 6.0 °C: Van et al. 2000), insectivorous bats inhabiting such areas are likely to undergo bouts of torpor during the coldest periods when they rely on stored body fat. Storage of spermatozoa in the reproductive tract of overwintering bats is a key reproductive adaptation of those living at temperate latitudes (Racey 1979) and the elevation of body temperature associated with frequent arousals from hibernation is thought to compromise the viability of stored sperm by encouraging their phagocytosis by leucocytes (Guthrie 1933; Racey 1975).

Disturbance during pregnancy, lactation and weaning is widely recognized as highly detrimental to recruitment in bat populations (McCracken 1989; Sheffield et al. 1992; Jubertie 2000; Mitchell-Jones et al. 2007). Protection during these periods is consequently also central to cave bat conservation. As reproduction is energetically expensive (Racey and Speakman 1987), many bat species time the event so that lactation, the most costly stage (Kurta et al. 1989), coincides with peak food availability (Racey and Entwistle 2000). This peak may also occur during weaning for many species (Bernard and Cumming 1997). In temperate zone bats, parturition and lactation occur in summer, whereas in the seasonal tropics, growing evidence suggests reproductive activity for many insectivorous, frugivorous and nectarivorous bats is associated with rainfall, with lactation occurring during the peak rainy season (Racey and Entwistle 2000).

The likelihood that reproductive cycles will be affected by global climate change warrants attention as such effects are predicted to be significant in temperate zone bats (Jones and Rebelo 2013). As with other taxa, climate change is predicted to alter the distribution of bat species (Scheel et al. 1996; La Val 2004; Rebelo et al. 2010; Hughes et al. 2012). Altered distribution patterns are also anticipated for hibernating species due to changes in energetic demands (Humphries et al. 2002). Range shifts have already been observed in the case of Kuhl's pipstrelle (*Pipistrellus kuhlii*), which has moved northwards from Mediterranean regions into Central and Eastern Europe over 15 years (Sachanowicz et al. 2006). In projecting the effects of several climate change scenarios on 171 bat species in Southeast Asia, Hughes et al. (2012) found only 1–13 % (1–22 spp.) showed no reductions in their current ranges. Though range expansions were projected for some species, it was perceived that this might challenge those with poor dispersal abilities. This could pose a particular problem for cave-dwelling bats in Asian karst areas, since widespread isolation of karst outcrops has already occurred (Struebig et al. 2009; Furey et al. 2010) (Fig. 15.6). Even species capable of shifting their ranges in response to the rapid rate of current climate change may be hampered by the limited availability of suitable caves and potential time required for suitable foraging habitats to develop (Rebelo et al. 2010).

15.4.2 Incidental Disturbance

Although intentional disturbance of cave-dwelling bats as a result of vandalism and other causes is well documented and widespread, unintentional disturbance

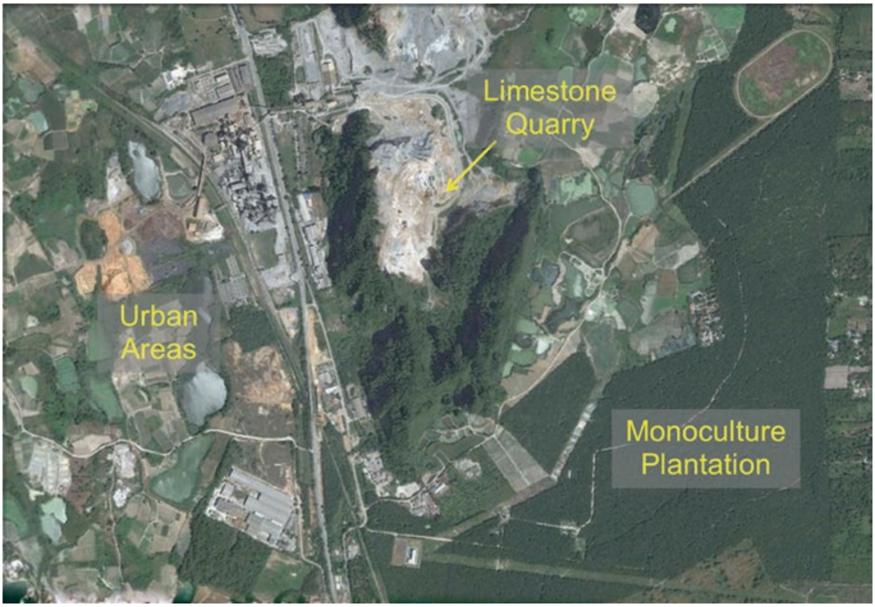

Fig. 15.6 Land use changes leading to isolation of the Gunung Kanthan karst outcrop in Ipoh, Malaysia (created by Kendra Phelps © Google Earth)

can pose an even greater threat due to the many other reasons that humans use caves (McCracken 1989) such as opportunistic recreation, camping, caving excursions, dumping refuse and use as storage facilities. For example, the importance of the Nietoperek fortifications in Western Poland as a bat hibernaculum was first brought to the attention of bat biologists outside the Iron Curtain by a Russian plan to dump radioactive waste there. The plan was shelved as a result of a successful campaign by conservationists. Throughout Poland, groups known as "bunkermen" meet socially in underground fortifications where they may disturb the bats.

Thomas (1995) showed that non-tactile disturbance from seemingly innocent cave visits during hibernation periods can cause bats to arouse and maintain significantly greater flight activity for up to eight hours afterwards. Such arousals are highly detrimental to their over-winter survival and non-tactile disturbance during other critical periods such as reproduction may lead to: (1) death of young that lose their roost-hold and fall to the cave floor, (2) females abandoning the roost for less ideal sites where prospects for reproductive success may be reduced, (3) greater energy expenditure among females and less efficient energy transfer to young (translating into slower growth of young and increased foraging demands on females), (4) reductions in the thermoregulatory benefits of a roost as a result of decreased numbers of bats frequenting the site (McCracken 1989; Sheffield et al. 1992).

As a result, uncontrolled human disturbance often leads to decreases in numbers of bats roosting in caves and mines (Tuttle 2013). For instance, disturbance in caves in West Virginia, USA, occupied by the Indiana myotis (*M. sodalis*) and Townsend's big-eared bat (*Corynorhinus townsendii*) resulted in a decline from 1137 bats to 286 in one cave and from 560 to 168 in another (Stihler and Hall 1993). Conversely, when ten caves were protected by grilling and fencing, *M. sodalis* populations increased, from 1615 to 6297 bats (290 %) and *P. townsendii* from 3455 to 7491 (117 %). Because fencing is more easily vandalized, gating is considered by many as more successful at preventing disturbance, although some bat species do not tolerate gates and it is important to establish the bat-preferred design.

15.4.3 Extractive Industries

Limestone quarrying for cement and construction materials presents a severe threat to cave-dwelling bats in karst areas as it can result in the total loss of outcrops (Fig. 15.7), leaving few options for remediation. Global demand for cement alone was projected to increase by 4.1 % per annum to 3.5 billion tons in 2013 despite the western financial crisis (Sutherland et al. 2012) (Fig. 15.8). This is believed to pose perhaps the greatest threat to cave bats in Southeast Asia, as the region has the highest annual quarrying rates in the tropics and these appear to be increasing faster than in other regions, at 5.7 % per year (Clements et al. 2006; Kingston 2010). In contrast, the impact of smaller artisanal mining operations

Fig. 15.7 Quarrying of limestone hills in southern Cambodia (© Neil Furey/Fauna & Flora International)

Fig. 15.8 Quarrying of limestone in the Petersburg mines of South Limburg, Netherlands (© Joep Orbons)

appears largely unevaluated so far, though such operations are widespread and commonly target cave sediments in countries such as Vietnam (N. Furey unpublished, Tordoff et al. 2004).

Groundwater abstraction and land cover changes in the catchments of caves can affect their environments in several ways. Though empirical data on the effects on bats appear to be few, abiotic changes include altered hydrological cycles (particularly where natural land cover is replaced with impervious surfaces such as roads) and altered cave microclimates as a result of sedimentation blocking voids for percolating water in overlying rocks (Watson et al. 1997). Removal of vegetation at cave entrances may also alter airflows and temperatures within a cave to such an extent that its habitable portions are reduced or eliminated (Sheffield et al. 1992). Conversely, alien plants may overgrow cave entrances and prevent their use as roosts (Gerlach and Taylor 2006) and other invasive species such as feral cats have been identified as predators of cave-dwelling bats (Rodriguez-Durán et al. 2010; Tuttle 2013). More dramatically, large water projects can flood caves through reservoir creation and groundwater recharge efforts. For instance, recharge efforts led to violent flooding of the Valdina Farms sinkhole in Texas in 1987, with the loss of a colony of four million *T. brasiliensis* and a rare colony of Peter's ghost-faced bat (*Mormoops megalophylla*) (Elliot 2004).

Cave-dwelling bats are especially vulnerable to harvesting for consumption and trade due to their aggregation into these confined spaces. Reviews of global patterns in bat hunting for bushmeat indicate that this is common in the Old World tropics, but with possible exceptions, does not appear to be widespread or having a significant effect in other regions (Mickleburgh et al. 2009; Mildenstein et al. 2016). Though a problem in Madagascar and in many African countries, the threat to cave-dwelling bats appears to be most widespread and acute in the Asian tropics, where bat harvesters target many species. For instance, Hall et al. (2002) reported dramatic declines in *E. spelaea* and the greater naked bat (*Cheiromeles torquatus*) during their successive surveys of Niah caves, Sarawak compared with numbers recorded in earlier surveys by Medway (1958) and attribute this to hunting for human consumption. While Asian hunters often target species that are large, colonial and/or abundant (e.g. *E. spelaea*, *Rousettus* spp., *C. torquatus*, *C. plicatus* and bent-winged bats *Miniopterus* spp.), smaller bats are also taken and harvesting activities are highly likely to negatively affect other species sharing the same caves (Hutson et al. 2001; Mickleburgh et al. 2009). Given the scale and severity of bushmeat hunting on bats, there is a pressing need for research on sustainable harvesting.

Despite its widespread occurrence, accounts of the impact of guano harvesting upon cave-dwelling bats appear to remain largely anecdotal. This may stem in part from the difficulty of accurately monitoring large bat colonies, although rates of guano accumulation and harvesting records reflect their size (Fig. 15.9).

Fig. 15.9 Entrance to Tarum Cave in western Cambodia (*main picture*) where 200–400 sacks of bat guano (*inset picture*) produced by the largest colony of *Chaerephon plicatus* in the country have been harvested every month since 1995 (© Neil Furey/Fauna & Flora International)

Fig. 15.10 Sale of decorative cave speleothems near the Vietnam-China border (© Neil Furey/ Fauna & Flora International)

It is generally acknowledged that insensitive harvesting operations can be highly detrimental to cave bat populations (Hutson et al. 2001), particularly where cave modifications are undertaken to facilitate guano extraction (Elliot 1994). Similar concerns apply to the harvesting of cave swiftlet (*Aerodramus* spp. and *Collocalia* spp.) nests in Southeast Asia (Suyanto and Struebig 2007) since trade in these has expanded greatly in recent decades, causing significant disturbance to bats sharing the same caves (Wiles and Brooke 2013). In both instances, the perceived benefits of continued harvests can encourage local communities to protect the producers (Leh and Hall 1996; Bates 2003), although research to identify and validate sustainable harvesting practices is clearly needed. Lastly, harvesting of speleothems for decorative purposes represents another widespread practice in Southeast Asia whose impacts on cave bats appear to remain largely unevaluated (Fig. 15.10).

15.4.4 Cave Tourism

Cave tourism, which began in the late nineteenth century, has dramatically increased threats to all life in caves. Around 20 million people worldwide were estimated to visit caves recreationally each year in the mid-1990s and the industry has burgeoned in East Asia more recently (Gillieson 1996; Zhang et al. 2009; Furey et al. 2011; Luo et al. 2013) (Fig. 15.11). Development of caves for tourism typically involves the introduction of artificial lighting and physical modifications to cave substrates in the form of entrance structures, stairs, walkways, and car parks. Alongside disturbance caused by their presence, cave visitors create marked fluctuations in temperature, relative humidity and carbon dioxide concentrations, all of which can lead to roost abandonment. For instance, commercialization of Fourth Chute Cave in Quebec, Canada resulted in abandonment of the largest hibernacula of eastern small-footed myotis (*M. leibii*) known at the time in eastern North America (Mohr 1972).

Mann et al. (2002) explored behavioural responses of a maternity colony of 1000 cave myotis (*M. velifer*) by experimentally exposing the colony to cave tours. High light intensity had the most detrimental effect with bat activity levels and flight increasing with proximity to tour routes and when tour groups talked. All of these behavioural responses increased as the maternity season progressed. Consistent with this, in a review of 225 subterranean sites in China, Luo et al. (2013) showed that recreational activities had pronounced detrimental effects on the numbers of bat species and presence of species of special conservation concern. Almost 90 % of the sites were found to be disturbed and only 15 % of natural caves were unaffected by disturbance. Concerns about the impact of cave tourism on Chinese bats have also been raised by Niu et al. (2007) and Zhang et al. (2009)

Fig. 15.11 Cave visitation during the annual Tet holiday in North Vietnam (© Neil Furey)

and Olson et al. (2011) also found that numbers of hibernating bats significantly increased in Cadomin cave, Canada after restrictions on visitors were enforced. In Madagascar, associations between tourism and hunting of cave-dwelling pteropodids were noted by Cardiff et al. (2009) who speculated these might be due to improved access facilitating hunting activities when tourists are absent. Cardiff et al. (2012) also analyzed the effects of tourism on the Malagasy rousette (*Rousettus madagascariensis*) and found that maintaining a minimum distance of 12 m between tourists and roosting bats and avoiding their illumination caused the least disturbance.

One of the few detailed investigations of the effects of tourism on bat numbers has been carried out in the Dupnisa cave system in the Thrace region of Turkey, one of the largest aggregations of bats in southeast Europe with mean numbers for 15 species of 25,000 in winter and 4000 in summer (Paksuz and Özkan 2012). The maximum number of bats recorded during a single survey of the three connected caves is 56,000. The total length of the system exceeds 2.5 km and tourists are admitted to about 400 m of two hibernation caves during summer but excluded from the cave containing maternity colonies. The assertion by Paksuz and Özkan (2012) that mean bat numbers using the cave have increased, significantly so in the maternity cave, since it was opened to tourism in July 2003 has been challenged by Furman et al. (2012) who concluded that there has been a 20 and 60 % reduction in the two hibernation caves in February and March 2003–08 respectively compared with their own surveys in March 2001 and a 90 % reduction in the maternity cave in April and May 2002–07, compared with their survey in April 2001 (Furman and Özgül 2004). Furman et al. (2012) point out that the comparison made by Paksuz and Özkan (2012) is ambiguous as it contrasts the construction period (including the early days of tourism) with the later period after construction was finished and the system was opened to tourists, and they provide no data for the period before any construction work started. The only significant increase in bat numbers reported by Paksuz and Özkan (2012) was in the cave closed to tourists and bats in caves accessible to tourists may have moved to the less disturbed cave. This inconsistency is significant as the development of the Dupnisa system for tourism may be followed in other cave complexes.

15.4.5 Insights from Long Term Studies

The most distinctive feature of several European studies of bats in karst is their duration. Bats were counted in 32 limestone mines in South Limburg from 1943, yearly in half of them, to 1987 (Weinreich and Voshaar 1992). Two factors affected the caves directly over this period—the erection of grills to prevent unauthorized entry, and the cultivation of mushrooms. Intensive mushroom culture reduced the number of bats by 90 % after three years. However, extensive culture, involving much less disturbance, and the installation of grills, had no significant effect on bat numbers. Population trends for eight species for which the most complete data sets are available reveal that from 1943 until 1987, four species, *R. hipposideros*, *M. myotis*, *M. emarginatus* and *M. nattereri* showed steep declines; three *M. mystacinus/brandti*, *M. dasycneme* and *P. auritus* remained fairly stable and one, *M. daubentonii*, showed a dramatic increase. A possible explanation of this increase is the intensification of agriculture following the second world war which led to the eutrophication of fresh waters. This in turn resulted in an increase in chironomid flies on which *M. daubentonii* feeds.

The total number of bats hibernating in these 32 limestone mines decreased overall by two-thirds between 1943 and 1957. Numbers then stabilized and from 1977 returned to their former level. Although the study revealed the negative effects of intensive mushroom cultivation, other factors are implicated, in particular the cessation of banding bats during hibernation after 1957. In addition, the first decade after the second world war coincided with unlimited use of agricultural pesticides, which took its toll on many species of wildlife (Carson 1962). Restrictions were placed on the use of the most toxic and persistent of these pesticides from 1968 to 1973 and that coincides with the beginning of recovery of bat numbers (Weinreich and Voshaar 1992).

The second long running study involving both summer and winter bat populations is located in the Czech and Slovak republics. This began in 1948 and 89,000 bats of 23 species were banded in the following 52 years, approximately a third of which are found in karst caves (Gaisler et al. 2003). A regular winter census has taken place in one of the tourist caves, Sloupsko, in the Moravian karst (Zukal et al. 2003). Bats were originally banded in both summer and winter roosts but once the practice of arousing bats during hibernation to band them was abandoned, the numbers using the cave increased, as in the Dutch study. The recovery rate is remarkably high for a banding study—27 % for *M. myotis* and 18 % for *R. hipposideros*, as is the revealed longevity—37 years for the 35 g *M. myotis*.

Fifteen of the 23 bat species found in the Czech and Slovak republics are found in the Moravian karst, but the bat community in winter is dominated by *M. myotis* which accounts for about half of the bats visible during the census (Zukal et al. 2003). The numbers of *M. myotis* and *R. hipposideros,* species of conservation concern throughout their European distribution, increased dramatically in the 1990s and this is attributed to good management. Apart from the winter census, no underground activity is permitted during hibernation. Vehicular traffic on the access roads to the caves is limited throughout the year and cars and lorries are prohibited in the main valleys.

15.4.6 Declines in Cave Bats

Although the difficulties of accurate counting have confounded assessments of trends in numbers of bats using caves, most available information points to declines. Dumitresco and Orghidan (1963) reported ‘more than a hundred thousand’ common pipistrelles (*Pipistrellus pipistrellus*) in the Sura Mare cave in

Romania. Half a century later, only 34,000 individuals were recorded there, and, a total of only 150,000 individuals of 22 species in 79 caves throughout the country (Nagy and Postawa 2010). Dramatic declines have also occurred in numbers of *T. brasiliensis* in caves in the south-western USA (McCracken 2003) (Table 15.1).

The declines at Carlsbad cavern have been attributed to the use of the organochlorine insecticides DDT and dieldrin (Geluso et al. 1976, 1981), which were subsequently banned. There is no evidence however that the declines at Eagle Creek shared the same cause (McCracken, 1986). Other factors may also have contributed to these declines, such as the boring of a shaft through the main bat roosting area in Carlsbad to facilitate guano mining, which altered temperature, relative humidity and airflow within the roost (McCracken 1986). A major guano mining operation, involving the installation of electric lights, may have led to the complete abandonment of U-Bar cave, New Mexico by bats (McCracken 1986).

Equally dramatic declines have been recorded in Mexico as a result of attempts by cattle ranchers to control vampire bats by burning car tyres and dynamiting, with equally lethal effects on non-target bat species, and also mining (S. Walker pers. comm. in Hutson et al. 2001) (Table 15.2). In the intervening years however, better-targeted vampire control and other conservation initiatives in Mexico have halted or reversed these trends (Medellin 2003).

Table 15.1 Declines in cave bats in USA

Colony	Year	Estimated size
Carlsbad cavern, New Mexico	1936	8.7×10^6
	1957	4.0×10^6
	1973	218,000
Eagle Creek cave, Arizona	1963	$25–50 \times 10^6$
	1969	30,000

Table 15.2 Declines in cave bats in northern Mexico

Cave	State	Historical population	1991 population
La Ojuela	Durango	184,000	0
Tio Bartola	Nuevo Leon	4×10^6	30,000
La Boca	Nuevo Leon	Millions	100,000
Del Marviri	Sinaloa	940,000	250,000
El Omo	Tamaulipas	Millions	0
Del Guano	Tamaulipas	440,000	125,000
Quintero	Tamaulipas	567,000	30,000
La Mula	Tamaulipas	303,000	100,000

15.5 Conservation Responses

Not surprisingly, conservation responses to threats facing cave-dwelling bats are strongly linked—though by no means confined—to the growth of organizations across the world dedicated to conserving all bat species. This subject was reviewed by Racey (2013) who suggests that while bat conservation has made much progress in Europe and North America and is growing in strength in Central and South America and parts of Asia and Australasia, half of the world remains a "conservation void" so far as bats are concerned. This conservation void includes most of Africa, all of the Middle East, much of the Russian Federation and all of the former Russian republics, together with most of Asia, including China, Mongolia and Tibet.

15.5.1 National and International Initiatives for the Protection of Cave Bats

The Council of Europe reviewed underground habitats and proposed selection criteria for their protection (Jubertie 1992). This was followed by IUCN's Guidelines for Cave and Karst Protection prepared by the World Commission on Protected Areas Working Group (Watson et al. 1997), although it was realized at the time by one of the authors that more detailed treatment of biodiversity issues was required (Hamilton-Smith 2001). This was begun, but never completed. Among the many broader cave-related publications that have appeared (e.g. Gunn 2003; White and Culver 2012), the treatment of Vermeulen and Whitten (1999) for East Asia is notable in explicitly addressing the threat to cave biodiversity from tourism and exploitation of limestone for industrial purposes by providing options for impact assessment, site selection, mitigation and national management of karst areas.

National academic societies have also produced guidelines for the protection of bat roosts, particularly those in caves (e.g. Sheffield et al. 1992) and among the bat conservation NGOs, the UK's Bat Conservation Trust was among the first to produce a conservation code for cave visitors (Hutson et al. 1988). Since then, a variety of organizations have produced materials to raise public awareness of bats at karst caves around the world. In Madagascar for instance, Madagasikara Voakajy have produced guidelines in three languages (Malagasy, English and French) for tourists visiting caves in the Bemaraha karst, with clear instructions about minimizing disturbance to bats. The international speleological community has also, in general, been sensitive to the potential effects of their activities on bats and other cave fauna and codes of ethics have been published by national caving societies in several regions. An important advance within the caving community has also been the replacement of carbide lamps, the combustion products of which are toxic, with electric torches.

The development of a network of protected areas including many sites of outstanding importance for cave-dwelling bats across the European Union (known as Natura 2000) has been viewed as an important step change in European bat conservation, although its effectiveness in protecting the foraging habitats of cave bats in the region has been questioned (Lison et al. 2013). Allied to this, the Advisory Committee of Eurobats (an intergovernmental agreement for the protection of European populations of bats) has a working group on underground sites, in addition to other groups dealing with related subjects such as surveillance and monitoring and wind farms. These have resulted in well illustrated guidelines for the protection and management of subterranean sites and lists of important sites across Europe, which are freely available from the Eurobats website (Mitchell-Jones et al. 2007).

The United States Endangered Species Act provides strong protection for several cave-dwelling species, and individual states maintain their own lists of endangered and threatened species and species of special conservation concern, as do agencies such as the Forest Service and Bureau of Land Management. Alongside four sub-national bat groups which address bat conservation issues in the western, mid-western, northeast and southeast states respectively, Bat Conservation International has mounted successful programs for bat conservation in American caves and mines, in addition to initiatives aimed at building capacity and protecting cave bats in many other countries such as the Philippines (Racey 2013).

In Central America, concerns about the plight of predominantly or wholly cave-dwelling species such as *T. brasiliensis*, *L. curasoae* and Mexican long-nosed bat (*Leptonycteris nivalis*) that migrate between Mexico and the southern United States led to the establishment in 1994 of the Program for the Conservation of Mexican Bats (PCMM: Programma para la Conservacion de los Murcielagos de Mexico). In 2007, this in turn led to the launch of the Latin American Network for Bat Conservation (RELCOM: Red Latinoamericana para la conservacion de los Murcielagos), an alliance of organizations and individuals in 22 countries (including the Caribbean) concerned with bat conservation. In South and Southeast Asia, the respective regional equivalents are Chiropteran Conservation Information Network for South Asia (CCINSA) and Southeast Asian Bat Conservation Research Unit (SEABCRU), whereas in Africa, a new network Bat Conservation Africa was formed by bat conservationists in 2013 which encompasses 19 African countries and the West Indian Ocean islands (Kingston et al. 2016).

15.5.2 Development of Gating

The large number of abandoned mines in the USA, the need to maintain public safety and to conserve resident bats has led to extensive gating of both mines and caves (Dalton and Dalton 1995; Vories et al. 2004). Gating has long been a controversial subject within the speleological community (Kennedy 2006), and similarly for bat conservationists, not least because gates installed at cave entrances from the 1950s through the early 1970s virtually always led to roost abandonment (Tuttle 1977). Much has been learnt through trial and error however, so that studies of more recently installed cave gates provide grounds for optimism (e.g. Pierson et al. 1991, Stihler and Hall 1993; Decher and Choate 1995; Fant et al. 2009). For instance, Martin et al. (2003) recorded a statistically significant increase in the numbers of *M. grisescens* from 60,130 to 70,640 bats between 1981 and 2001 in 25 gated caves in Oklahoma, USA. However, recent studies before and after gating hibernacula of *M. sodalis* reported decreased rates of growth for increasing populations and the reverse for declining populations (Crimmins et al. 2014). Berthinussen et al. (2014) summarise the mixed results of ten gating studies on three continents.

Because fencing is more easily vandalized, gating is recognized by many as more successful at preventing disturbance. However, species such as *T. brasiliensis* cannot tolerate gates due to their flight geometry and large colony sizes, and for bat species that can, it is critical to establish their preferred design. Improperly designed gates can alter cave environments by restricting air circulation, causing population declines (Richter et al. 1993). For example, *M. grisescens* requires an open flyway above gates, whereas *P. townsendii* will tolerate full gates with horizontal bars (Tuttle 1977). In the UK, Pugh and Altringham (2005) examined the effect of different sizes of horizontal gate spacings on numbers of Natterer's bats (*Myotis nattereri*) entering swarming sites in autumn and provided clear recommendations for future gate design. While a detailed treatment of the subject is beyond the scope of the present chapter, the proceedings of a multidisciplinary meeting to develop gate design provides a wide variety of well-illustrated examples of gated caves and mines (Vories et al. 2004) and similarly useful advice is given in Hildreth-Werker and Werker (2006), Mitchell-Jones et al. (2007) and Fant et al. (2009).

Nevertheless, a great deal remains to be learnt about the reactions of bats to gates, even in the USA and Canada, where most of the voluminous information available is anecdotal with few systematic studies conducted to date (Sherwin and Altenbach 2004; Spanjer and Fenton 2005). For instance, Vories et al. (2004) recommended studies of the effects of gates on cave microclimate, wind tunnel assessments of the airflow characteristics of different gate designs, the acoustic signatures of the gates and their possible interference with echolocation calls. Since gates have the potential of protecting cave bats from disturbance but little or no information exists on the responses to gating of hundreds of species across the world, clearly much research lies ahead.

15.5.3 Artificial Hibernacula and Maternity Roosts

In the UK, members of local conservation groups have constructed many artificial caves, often from a series of concrete sewer pipes to which roosting cavities are added. Unfortunately, the rate of occupancy, even over a 25 year period of monitoring, has been so low that such an approach cannot be recommended as a means of mitigating threats to cave-dwelling bats. Furthermore, Berthinussen et al. (2014) found no published evidence for the effects of providing artificial hibernacula for bats to replace sites lost to development. However, in Brittany, France and County Clare, Ireland, houses were constructed to serve as maternity roosts and hibernacula for *R. ferrumequinum* and *R. hipposideros* respectively. The former was used by over 100 individuals in summer and winter and the latter by 220 hibernating bats (Eurobats 2014).

The Combe Down stone mine complex in the UK is one of the twenty most important hibernacula in Europe. Because engineering work was required to stabilise the complex in order to protect the parts of Combe Down village that were above it, and both UK species of *Rhinolophus* roost there during summer and winter, extensive mitigation was devised by Ransome (2010). This included the construction of three incubation chambers, each inside a different mine. Each chamber was a small underground room partly maintained at ca 27 °C with a roof lined with mesh-covered plywood from which the bats could hang. Both rhinolophid species used the chambers, and subsequently gave birth and reared young there. In 2014, there were two underground breeding colonies of *R. hipposideros*, each of some 40–70 adults and 30 young and a colony of *R. ferrumequinum* with about 120 adults and a dozen pups (R. Ransome pers. comm.). This initiative stemmed from Ransome's earlier success in the improving the survivorship of young of *R. ferrumequinum* by installing electric tubular heaters in the maternity roost at his study colony in the roof of a mansion (Ransome 1998).

Some success has also been obtained in the UK by protecting sites already known to be used by bats, often by gating (S. Thompson pers. comm.; Hutson 1993). Examples are small chalk caves entered by a vertical shaft (known as dene holes in the South of England) and ice houses (brick-lined domed structures) constructed mainly underground, often on a hillside close to water. The success of concentrating conservation efforts on known roosts was exemplified recently by the massive enlargement of a small bat cave on a hillside above a much larger cave occupied by 20,000 bats which was to be inundated by the Balikesir Havran irrigation dam in Turkey. Floor material containing invertebrates and guano was transferred from the old to the new cave and up to 13,000 bats took up residence there (Irfan Albayrak and Eda Türkyiğit pers. comm.).

More generally, the survival of bats that overwinter in caves has been helped in summer by the widespread use of bat boxes of various sizes and designs. Berthinussen et al. (2014) summarise the results of 22 studies of artificial roost structures across the world. In the USA, substantial progress has been achieved and some artificial roosts now provide the only hope of recovery for local populations. For instance, two large bat houses built in 1991 and 2010 in Gainesville, Florida contained 300,000 bats in 2012 (mostly *T. brasiliensis*), more than all the natural roosts in the state combined (Tuttle 2013).

15.5.4 Recent Initiatives

Due to concerns that unsustainable guano harvesting practices are increasing and threatening millions of bats worldwide, guidelines have been prepared to help address the clear need for harvesting standards that minimize negative impacts on these and other cave-dwelling organisms. The guidelines cover generic aspects such as baseline assessments, guano extraction methods and policies for site management and monitoring, and have been adopted by the IUCN (IUCN SSC 2014).

The establishment of a new Cave Invertebrate Specialist Group within the IUCN Species Survival Commission in 2013 is also promising. Unlike cave-dwelling bats, many of the invertebrates that live permanently in caves are highly range-restricted endemics incapable of dispersing to other sites (Vermeulen and Whitten 1999). As such animals are highly susceptible to environmental change and hence extinction, many will undoubtedly qualify on distributional grounds alone as Critically Endangered or Endangered in the Red List assessments that the specialist group intends to undertake as a priority.

Given the importance of bat guano to cave biodiversity in the tropics (Deharveng and Bedos 2012), additional justifications for protection of sites inhabited by cave-dwelling bats are likely to emerge. These should in turn lead to conservation outcomes either as a result of the influence the IUCN Red List exerts on national legislation for protected areas development, wildlife protection and/or EIA processes, or by alternatively triggering the environmental safeguards of multilateral institutions such as the World Bank that commonly engage in development projects in tropical karst areas (Vermeulen and Whitten 1999). Greater cooperation between bat conservationists and invertebrate biologists is therefore clearly in the interests of conserving cave life as a whole.[1]

15.6 Future Directions

Caves and other subterranean sites are critical to the survival of hundreds of bat species worldwide. Karst caves in particular are experiencing unprecedented disturbance due to their increasingly realised potential for the construction and tourism industries. As these threats are heavily exacerbated by loss of foraging habitats, bushmeat hunting, incidental disturbance and disruptive guano harvesting, research and allied conservation actions are urgently needed to reduce the impacts of these activities. Extermination attempts due to disease fears, such as the recent depopulation of bats at Kitaka mine in Uganda are also a concern (Amman et al. 2014). Since disturbance during critical periods such as reproduction are particularly detrimental to population recruitment, studies to determine when these

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[1] The Cave Invertebrate Specialist Group can be contacted at CISG@fauna-flora.org.

occur in poorly documented regions have clear conservation relevance. Similarly, the use of gates to protect cave bat colonies is relatively untested outside Europe and North America and could do much to mitigate threats in other regions.

In recent years, some international conservation NGOs have worked with major cement manufacturers such as Holcim and Lafarge in some karstic areas to identify the most important caves so far as bat and other biodiversity is concerned and to avoid disturbing them. In other areas, multinational corporations destroy caves with impunity. There is a need therefore for international protocols that protect cave biodiversity while satisfying the demand for cement and construction materials (Whitten 2012; BirdLife et al. 2014) and it would be appropriate for the IUCN to take the lead in this respect. The priority for bat biologists is to collate and develop the existing fragmented information on caves in both the Old and New World tropics and identify sites of outstanding importance at national and international levels. These can then be protected from exploitation.

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References

Adams RA, Pedersen SC, Thibault KM et al (2003) Calcium as a limiting resource to insectivorous bats: can water holes provide a supplemental mineral source? J Zool (London) 260:184–189

Altringham JD (2011) Bats: from evolution to conservation. Oxford University Press, Oxford

Amman BR, Nyakarahuka L, McElroy AK et al (2014) Marburgivirus resurgence in Kitaka mine bat population after extermination attempts, Uganda. Emerg Infect Dis 20:1761–1764

Arita HT (1993a) Rarity in neotropical bats: correlations with phylogeny, diet and body mass. Ecol Appl 3:506–517

Arita HT (1993b) Conservation biology of the cave bats of Mexico. J Mamm 74:693–702

Arita HT (1996) The conservation of cave-roosting bats in Yucatan, Mexico. Biol Conserv 76:177–185

Avery MI, Racey PA, Fenton MB (1984) Short distance location of hibernaculum by little brown bats (*Myotis lucifugus*). J Zool (London) 204:588–590

Avila-Flores R, Medellin RA (2004) Ecological, taxonomical and physiological correlates of cave use by Mexican bats. J Mammal 85:675–687

Aye NN (2006) Ecology and economic importance of *Tadarida plicata* (Buchannan, 1800), free-tailed bat in some areas of Myanmar. Dissertation, University of Yangon

Bambini L, Blyth A, Bradford T et al (2006) Another Seychelles endemic close to extinction: the emballonurid bat *Coleura seychellensis*. Oryx 40:310–318

Barbu P, Sin G (1968) Observatii asupra hibernarii speciei *Nyctalus noctula* (Schreiber 1774) in faleza lacului Razelm - Capel Dolosman - Dobrogea. St Si Cerc Biol Seria Zooloogie T 20 NR. 3 P 291–297. (in Romanian - English summary)

Barclay RMR (1994) Constraint on reproduction by flying vertebrates: energy and calcium. Am Nat 144:1021–1031

Barclay RMR (1995) Does energy or calcium availability constrain reproduction in bats? In: Racey PA, Swift SM (eds) Ecology, evolution, and behaviour of bats. Clarendon Press, Oxford, pp 245–258

Bates PJJ (2003) Conservation status of the bat and bird fauna of the limestone karst areas of Mon and Kayin States, Myanmar (Burma). Unpublished report for Fauna & Flora International 100 % fund, Fauna & Flora International, Cambridge

Bell GP, Bartholomew GA, Nagy KA (1986) The role of energetics, water economy, foraging behavior and geothermal refugia in the distribution of the bat *Macrotus californicus*. J Comp Physiol B 156:441–450

Bernard RTF, Cumming GS (1997) African bats: evolution of reproductive patterns and delays. Q Rev Biol 72:253–274

Bernard RTF, Davison A (1996) Does calcium constrain reproductive activity in insectivorous bats? Some empirical evidence for Schreiber's long fingered bat (*Miniopterus schreibersii*). S Afr J Zool 31:218–220

Berthinussen A, Richardson OC, Altringham J (2014) Bat conservation: global evidence for the effects of interventions. Synyopses of conservation evidence, Pelagic Publishing Ltd

Betke M, Hirsh DE, Makris NC et al (2008) Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. J Mammal 89:18–24

BirdLife, FFI, IUCN et al (2014) Joint briefing paper on extraction and biodiversity in limestone areas. Cambridge

Booher CM, Hood WR (2010) Calcium utilisation during reproduction in big brown bats (*Eptesicus fuscus*). J Mammal 91:952–959

Boyles JG, Cryan PM, McCracken GF et al (2011) Economic importance of bats in agriculture. Science 332:41–42

Bradbury JW (1977) Social organization and communication. In: Wimsatt WA (ed) Biology of bats, vol 3. Academic Press, New York, pp 1–72

Brosset A (1966) La biologie des Chiropteres. Masson, Paris

Brunet AK, Medellin RA (2001) The species-area relationship in bat assemblages of tropical caves. J Mammal 82:1114–1122

Bumrungsri S, Harbit A, Benzie C et al (2008) The pollination ecology of two species of *Parkia* in southern Thailand. J Trop Ecol 24:467–475

Bumrungsri S, Sripaoraya E, Chongsiri T et al (2009) The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. J Trop Ecol 25:85–92

Bumrungsri S, Lang D, Harrower C et al (2013) The dawn bat, *Eonycteris spelaea* Dobson (Chiroptera: Pteropodidae) feeds mainly on pollen of economically important food plants in Thailand. Acta Chiropt 15:95–104

Cardiff SG (2006) Bat cave selection and conservation in Ankarana, northern Madagascar. Dissertation, Columbia University, Columbia

Cardiff SG, Ratrimomanarivo FH, Rembert G et al (2009) Hunting, disturbance and roost persistence of bats in caves at Ankarana, northern Madagascar. Afr J Ecol 47:640–649

Cardiff SG, Ratrimomanarivo FH, Goodman SG (2012) The effect of tourist visits on the behaviour of *Rousettus madagascariensis* (Chiroptera: Pteropodidae) in the caves of Ankarana, northern Madagascar. Acta Chiropt 14:479–490

Carson R (1962) Silent spring. Houghton Mifflin, Boston

Churchill SK (2008) Australian bats. Allen and Unwin, Sydney

Clements R, Sodhi NS, Schilthuizen M et al (2006) Limestone karsts of Southeast Asia: imperiled arks of biodiversity. Bioscience 56:733–742

Cleveland CJ, Betke M, Federico P et al (2006) Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. Front Ecol Environ 4:238–243

Codd J, Clark B, Sanderson K (1999) Drinking by the common bent-winged bat *Miniopterus schreibersii* and calcium in cave water. Bat Res News 40:9–10

Crimmins SM, McKann PC, Szymanski JA et al (2014) Effects of cave gating on population trends at individual hibernacula of the Indiana bat (*Myotis sodalis*). Acta Chiropt 16:129–137

Daan S, Wichers HJ (1968) Habitat selection of bats hibernating in a limestone cave. Sonderdruck aus Z f Säugetierkunde Bd 33:262–287

Dalton DC, Dalton VM (1995) Mine closure methods including a recommended gate design. In: Riddle BR (ed) Inactive mines as bat habitat: guidelines for research, survey, monitoring and mine management in Nevada. Biological Resources Research Centre, University of Nevada, Reno, pp 130–135

de Boer WF, van de Koppel S, de Knegt HJ et al (2013) Hibernation site requirements of bats in man-made hibernacula in a spatial context. Ecol Appl 23:502–514

Decher J, Choate JR (1995) *Myotis grisescens*. Mamm Species 510:1–7

Deharveng L, Bedos A (2012) Diversity patterns in the tropics. In: White WB, Culver DC (eds) Encyclopedia of caves. Academic Press, Chennai, pp 238–250

Dietz C, von Helversen O, Nill D (2009) Bats of Britain. Europe and Northwest Africa. A & C Black, London

Dumitresco M, Orghidan T (1963) Contribution a la connaissnace de la biologie de *Pipistrellus pipistrellus* Schreiber. Annales de Spéléol. 18:511–517

Elliot WR (1994) Conservation of Texas caves and karst. In: Elliot WR, Veni G (eds) The caves and karst of Texas. Convention Guidebook, National Speleological Society, Alabama, pp 85–97

Elliot WR (2004) Protecting caves and cave life. In: Culver DC, White WB (eds) Encyclopedia of caves. Elsevier, Amsterdam, pp 458–467

Eurobats (2014) Report of the inter-sessional working group on man-made purpose-built bat roosts. Doc.EUROBATS.StC9-AC19.34

Fant J, Kennedy J, Powers R et al (2009) Agency guide to cave and mine gates. American Cave Conservation Association, Bat Conservation International and Missouri Department of Conservation, USA

Furey NM (2009) Bat assemblages in Vietnamese karst: diversity, reproduction, echolocation and ecomorphology. Dissertation, Aberdeen University

Furey NM, Mackie IJ, Racey PA (2010) Bat diversity in Vietnamese limestone karst areas and the implications of forest degradation. Biodivers Conserv 19:1821–1838

Furey NM, Mackie IJ, Racey PA (2011) Reproductive phenology of bat assemblages in Vietnamese karst and its conservation implications. Acta Chiropt 13:341–354

Furman A, Özgül A (2004) The distribution of cave-dwelling bats and conservation status of underground habitats in Northwestern Turkey. Biol Cons 120:243–248

Furman A, Coraman E, Bilgin R (2012) Bats and tourism: a response to Paksuz and Ozkan. Oryx 46:330

Gaisler J, Hanak V, Hanzal V et al (2003) Results of bat banding in the Czech and Slovak Republics (1948–2000). (in Czech with English summary) Vespertilio 7:3–61

Geluso KN, Altenbach JS, Wilson DE (1976) Bat mortality: pesticide poisoning and migratory stress. Science 194:184–186

Geluso KN, Altenbach JS, Wilson DE (1981) Organochlorine residues in young Mexican free-tailed bats from several roosts. Amer Midl Nat 105:249–257

Gerlach J, Taylor M (2006) Habitat use, roost characteristics and diet of the Seychelles sheath-tailed bat *Coleura seychellensis*. Acta Chiropt 8:129–139

Gilbert J, Deharveng L (2002) Subterranean ecosystems: a truncated functional biodiversity. Bioscience 52:473–481

Gillieson D (1996) Caves: processes, development and management. Blackwell publishers, UK

Golovatch SI, Geoffrey JJ, Mauries JP et al (2011) New species of the millipede genus *Glyphiulus* Gervais, 1847 from the *granulatus*-group (Diplopoda: Spirostreptida: Cambalopsidae. Arthropoda Selecta 20:65–114

Gould E (1988) Wing-clapping sounds of *Eonycteris spelaea* (Pteropodidae) in Malaysia. J Mammal 69:378–379

Gunn J (2003) Climate of caves. In: Gunn J (ed) Encyclopedia of caves and karst science. Fitzroy Dearborn, Routledge, New York, pp 228–230

Guthrie MJ (1933) Notes on the seasonal movements and habits of some cave bats. J Mammal 14:1–19

Hall LS, Richards G, Abdullah MT (2002) The bats of Niah national park, Sarawak. Sarawak Museum Journal 57:28–255

Hamilton-Smith E (2001) Current initiatives in the protection of karst biodiversity. Natura Croatica 10:229–242

Hildreth-Werker V, Werker JC (2006) Cave conservation and restoration. National Speleological Society, Alabama

Horn JW, Kunz TH (2008) Analyzing NEXRAD doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (*Tadarida brasiliensis*). Integr Comp Biol 48:24–39

Hughes AC, Satasook C, Bates PJJ et al (2012) The projected effects of climatic and vegetation changes on the distribution and diversity of Southeast Asian bats. Glob Change Biol 18:1854–1865

Humphries MM, Thomas DW, Speakman JR (2002) Climate-mediated energetic constraints on the distribution of hibernating animals. Nature 418:313–316

Hutson AM (1993) Action plan for the conservation of bats in the United Kingdom. The Bat Conservation Trust, London

Hutson AM, Mickleburgh SP, Racey PA (comp.) (2001) Microchiropteran bats: global status survey and conservation action plan. IUCN/SSC Chiroptera Specialist Group. IUCN, Gland, Switzerland, and Cambridge, UK

Hutson AM, Mickleburgh SP, Mitchell-Jones AJ (1988) Bats underground, a conservation code. Fauna and Flora Preservation Society, Nature Conservancy Council and the Vincent Wildlife Trust, UK

IUCN SSC (2014) IUCN SSC guidelines for minimizing the negative impact to bats and other cave organisms from guano harvesting. Ver. 1.0. IUCN, Gland

Jones G, Rebelo H (2013) Responses of bats to climate change: learning from the past and predicting the future. In: Adams RA, Pedersen SC (eds) Bat evolution, ecology, and conservation. Springer, New York, pp 457–478

Jubertie C (1992) Underground habitats and their protection. Convention on the conservation of European wildlife and natural habitats, standing committee, Council of Europe

Jubertie C (2000) Conservation of subterranean habitats and species. In: Wilkens H, Culver DC, Humphreys WF (eds) Ecosystems of the World: subterranean ecosystems. Elsevier, Amsterdam, pp 691–700

Kennedy J (2006) On cave gates. In: Hildreth V, Werker JC (eds) Cave conservation and restoration. National Speleological Society, Alabama, pp 147–165

Kingston T (2010) Research priorities for bat conservation in Southeast Asia: a consensus approach. Biodivers Conserv 19:471–484

Kingston T (2013) Response of bat diversity to forest disturbance in Southeast Asia: insights from long-term research in Malaysia. In: Adams RA, Pedersen SC (eds) Bat evolution, ecology, and conservation. Springer, New York, pp 169–185

Kingston T, Aguirre L, Armstrong K et al (2016) Networking networks for global bat conservation. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 539–566

Kofoky AF, Andriafidison D, Ratrimomanarivo F et al (2007) Habitat use, roost selection and conservation of bats in Tsingy de Bemaraha National Park, Madagascar. Biodivers Conserv 16:1039–1053

Kokurewicz T, Rusiński M, Weigle A (2013) 12th International winter bat census in Natura 2000 site "Nietoperek" (PLH080003) (Lubuskie County)—12th January 2013. Report from the census and the results. National Foundation for Environmental Protection, Warszawa, Wrocław 20th May 2013 (in Polish)

Kunz TH (1982) Roosting ecology. In: Kunz TH (ed) Ecology of bats. Plenum, New York, pp 1–55

Kunz TH, de Torrez EB, Bauer D et al (2011) Ecosystem services provided by bats. Ann NY Acad Sci 1223:1–38

Kurta A, Bell GP, Nagy KA et al (1989) Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). Physiol Zool 62:804–818

Kwiecinski GG, Krook L, Wimsatt WA (1987) Annual skeletal changes in the little brown bat *Myotis lucifugus lucufugus* with particular reference to pregnancy and lactation. Am J Anat 178:410–420

La Val RK (2004) Impact of global warming and locally changing climate on tropical cloud forest bats. J Mammal 85:237–244

Ladle RJ, Firmino JVL, Malhado ACM et al (2012) Unexplored diversity and conservation potential of neotropical hot caves. Conserv Biol 26:978–982

Leelapaibul W, Bumrungsri S, Pattanawiboon A (2005) Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. Acta Chiropt 7:111–119

Leh C, Hall LS (1996) Preliminary studies on the production of guano and the socioeconomics of guano collection in Niah Cave, Sarawak. Sarawak Mus J 71:25–38

Lewis SA (1995) Roost fidelity of bats: a review. J Mammal 76:481–496

Lison F, Palazon JA, Calvo JF (2013) Effectiveness of the Natura 2000 Network for the conservation of cave-dwelling bats in a Mediterranean region. Anim Conserv 16:528–537

Medway L (1958) 300,000 bats. Sarawak Mus J 8:667–679

Luo J, Jiang T, Lu G et al (2013) Bat conservation in China: should protection of subterranean habitats be a priority? Oryx 47:526–531

MacKinnon JL, Hawkins CE, Racey PA (2003) Pteropodidae. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. The University of Chicago Press, Chicago and London, pp 1299–1302

Mann SL, Steidl RJ, Dalton VM (2002) Effects of cave tours on breeding *Myotis velifer*. J Wildl Manage 66:618–624

Martin KW, Leslie DM, Payton ME et al (2003) Internal cave gating for protection of colonies of the endangered gray bat (*Myotis grisescens*). Acta Chiropt 5:143–150

McCracken GF (1986) Why are we losing our Mexican free-tailed bats? Bats 3:1–4

McCracken GF (1989) Cave conservation: special problems of bats. Am Nat Speleol Soc Bull 51:47–51

McCracken GF (1993) Locational memory and female-pup reunions in Mexican free-tailed bat maternity colonies. Anim Behav 45:811–813

McCracken GF (2003) Estimates of population sizes in summer colonies of Brazilian free-tailed bats (*Tadarida brasiliensis*). In: O'Shea TJ, Bogan MA (eds) Monitoring trends in bat populations in the United States and territories: problems and prospects. Geolological Survey, US, pp 21–30

McCracken GF, Bradbury JW (1981) Social organisation and kinship in the polygynous bat *Phyllostomus hastatus*. Behav Ecol Sociobiol 8:11–34

McDonald JT, Rautenbach IL, Nel JAJ (1990) Roosting requirements of five bat species at De Hoop Guano Cave, southern Cape Province of South Africa. S Afr J Wildl Res 20:157–161

McWilliam AN (1982) Adaptive responses to seasonality in four species of Microchiroptera in coastal Kenya. Dissertation, University of Aberdeen

McWilliam AN (1988) The reproductive cycle of male tomb bats, *Taphozous hildegardeae* (Chiroptera: Emballonuridae), in a seasonal environment of the African tropics. J Zool (London) 215:433–442

Medellin RA (2003) Diversity and conservation of bats in Mexico: research priorities, strategies and Actions. Wildl Soc B 31:87–97

Mendenhall CD, Karp DS, Meyer CFJ et al (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509:213–217

Mickleburgh SP, Hutson AM, Racey PA (2002) A review of the global conservation status of bats. Oryx 36:18–34

Mickleburgh SP, Waylen K, Racey PA (2009) Bats as bushmeat: a global review. Oryx 43:217–234

Mildenstein T, Tanshi I, Racey PA (2016) Exploitation of bats for bushmeat and medicine. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer International AG, Cham, pp 325–363

Minnis AM, Lindner DL (2013) Phylogenetic evaluation of *Geomyces* and allies reveals no close relatives of *Pseudogymnoascus destructans* comb.nov. in bat hibernacula of eastern North America. Fungal Biol. doi:10.1016/j.funbio.2013.07.001

Mitchell-Jones AJ, Bihari Z, Masing M et al. (2007) Protecting and managing underground sites for bats. EUROBATS Publication series No. 2. UNEP/EUROBATS Secretariat, Bonn, Germany

Mohr CE (1972) The status of threatened species of cave-dwelling bats. Bull Nat Speleol Soc 34:33–47

Monadjem A, Taylor PJ, Cotterill FPD et al (2010) Bats of Southern and Central Africa—a biogeographic and taxonomic synthesis. Wits University Press, Johannesburg

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nagy ZL, Postawa T (2010) Seasonal and geographical distribution of cave-dwelling bats in Romania: implications for conservation. Anim Conserv 14:74–86

Niu H, Wang N, Zhao L et al (2007) Distribution and underground habitats of cave-dwelling bats in China. Anim Conserv 10:470–477

Olson CR, Hobson DP, Pybus MJ (2011) Changes in population size of bats at a hibernaculum in Alberta, Canada, in relation to cave disturbance and access restrictions. Northwestern Naturalist 92:224–230

Paksuz S, Özkan B (2012) The protection of the cave bat community in the Dupnisa cave system, Turkey, following opening for tourism. Oryx 46:130–136

Parsons KN, Jones G (2003) Dispersion and habitat use by *Myotis daubentonii* and *Myotis nattereri* during the swarming season: implications for conservation. Anim Conserv 6:283–290

Parsons KN, Jones G, Greenaway F (2003a) Swarming activity of temperate zone microchiropteran bats: effects of season, time of night and weather conditions. J Zool (London) 261:257–264

Parsons KN, Jones G, Davidson-Watts I et al (2003b) Visitation of underground sites by bats during late summer and autumn: implications for conservation. Biol Conserv 111:63–70

Pierson ED (1998) Tall trees, deep holes and scarred landscapes—conservation biology of North American bats. In: Kunz TH, Racey PA (eds) Bat biology and conservation. Smithsonian Institution Press, Washington, pp 309–325

Pierson ED, Rainey WE, Koontz DM (1991) Bats and mines: experimental mitigation for Townsend's big-eared bat at the McLaughlin Mine in California. Thorne ecological institute proceedings V: issues and technology in the management of impacted wildlife. Thorne Ecological Institute, Boulder, pp 31–42

Piksa K, Nowak J, Zmihorski M et al (2013) Nonlinear distribution pattern of hibernating bats in caves along an elevational gradient in mountain (Carpathians, southern Poland). PLOSone 8:e68066

Pugh M, Altringham JD (2005) The effect of gates on cave entry by swarming bats. Acta Chiropt 7:293–299

Racey PA (1975) The prolonged survival of spermatozoa in bats. In: Duckett JC, Racey PA (eds) The biology of the male gamete. Biol J Linn Soc 7(Suppl 1):385–416

Racey PA (1979) The prolonged storage and survival of spermatozoa in Chiroptera. In: Comparative aspects of reproduction in chiroptera. J Reprod Fertil 56:391–402

Racey PA (2004) 8,000,000 fruit bats, Africa's best kept wildlife secret. BATS 1:1–5

Racey PA (2013) Bat conservation: past, present and future. In: Adams RA, Pedersen SC (eds) Bat evolution, ecology, and conservation. Springer, New York, pp 517–532

Racey PA, Entwistle AE (2000) Life history and reproductive strategies of bats. In: Crichton EG, Krutzsch PH (eds) Reproductive biology of bats. Academic Press, San Diego, pp 363–468

Racey PA, Speakman JR (1987) The energy costs of pregnancy and lactation in heterothermic bats. Symp Zool Soc Lond 57:107–125

Ransome RD (1968) The distribution of the greater horseshoe bat, *Rhinolophus ferrumequinum*, in relation to environmental factors. J Zool 154:77–112

Ransome RD (1971) The effect of ambient temperature on the arousal frequency of the hibernating greater horseshoe bat, *Rhinophus ferrumequinum*, in relation to site selection and the hibernation state. J Zool 164:357–371

Ransome RD (1998) The impact of maternity roost conditions on populations of greater horseshoe bats. Engl Nat Res Rep 292:1–80

Ransome RD (2010) Environment and Ecology. In: Lord F (ed) The Stabilisation of combe down stone mines: the saving of a village. Combe Down Stone Mines Project, Bath and North East Somerset Council, pp 73–77

Rebelo H, Tarroso P, Jones G et al (2010) Predicted impact of global climate change on European bats in relation to their biogeographic patterns. Glob Change Biol 16:561–576

Reeder DM, Moore MS (2013) White-Nose syndrome: a deadly emerging infectious disease of hibernating bats. In: Adams RA, Pedersen SC (eds) Bat evolution, ecology, and conservation. Springer, New York, pp 413–434

Richter AR, Humphrey SR, Cope JB et al (1993) Modified cave entrances: thermal effect on body mass and resulting decline of endangered Indiana bats (*Myotis sodalis*). Cons Biol 7:407–415

Riddle BR (ed) (1995) Inactive Mines as bat habitat: guidelines for research, survey, monitoring and mine management in Nevada. Biological Resources Research Center, University of Nevada, Reno

Rodriguez-Durán A (1998) Nonrandom aggregations and distribution of cave-dwelling bats in Puerto Rico. J Mamm 79:141–146

Rodriguez-Durán A (2009) Bat assemblages in the West Indies: the role of caves. In: Fleming TH, Racey PA (eds) Island bats: evolution, ecology, and conservation. University of Chicago Press, Chicago and London, pp 265–280

Rodriguez-Durán A, Lewis AR (1987) Patterns of population size, diet and activity time for a multispecies assemblage of bats at a cave in Puerto Rico. Carib J Sci 23:352–360

Rodriguez-Durán A, Soto-Centeno JA (2003) Temperature selection by tropical bats roosting in hot caves. J Therm Biol 28:465–468

Rodriguez-Durán A, Perez J, Montalban MA et al (2010) Predation by free-roaming cats on an insular population of bats. Acta Chiropt 12:359–362

Russell AL, McCracken GF (2006) Population genetic structure of very large populations: the Brazilian free-tailed bat *Tadarida brasiliensis*. In: Akbar Z, McCracken GF, Kunz TH (eds) Functional and evolutionary ecology of bats. Oxford University Press, Oxford, pp 225–247

Sachanowicz K, Wower A, Bashta AT (2006) Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in central and eastern Europe. Acta Chiropt 8:543–548

Scheel D, Vincent TLS, Cameron GN (1996) Global warming and the species richness of bats in Texas. Conserv Biol 10:452–464

Sheffield SR, Shaw JH, Heidt GA et al (1992) Guidelines for the protection of bat roosts. J Mammal 73:707–710

Sherwin RE, Altenbach JS (2004) The responses of bats to gates. In: Vories KC, Throgmorton D, Harrington A (eds) Proceedings of bat gate design: a technical interactive forum held March 4–6, 2002 at the Red Lion Hotel, Austin Texas. Office of Surface Mining, Illinois, pp 333–338

Siles L, Munoz A, Aguirre LF (2007) Bat diversity in three caves in a montane forest of Bolivia. Ecotropica 13:67–74

Spanjer GR, Fenton MB (2005) Behavioural responses of bats to gates at caves and mines. Wildl Soc Bull 33:1101–1112

Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? Oikos 87:185–190

Stihler CW, Hall JS (1993) Endangered bat populations in West Virginia caves gated or fenced to reduce human disturbance. Bat Res News 34:130

Struebig MJ, Kingston T, Zubaid A et al (2009) Conservation importance of limestone karst outcrops for Palaeotropical bats in a fragmented landscape. Biol Conserv 142:2089–2096

Sutherland WJ, Aveling R, Bennun L et al (2012) A horizon scan of global conservation issues for 2012. Trends Ecol Evol 27:12–18

Suyanto A, Struebig MJ (2007) Bats of the Sangkulirang limestone karst formations, East Kalimantan—a priority region for Bornean bat conservation. Acta Chiropt 9:67–95

Thomas DW (1995) Hibernating bats are sensitive to tactile disturbance. J Mammal 76:940–946

Thomas DW, Fenton MB, Barclay RMR (1979) Social behaviour of the little brown bat, *Myotis lucifugus* I. Mating behaviour. Behav Ecol Sociobiol 6:129–136

Thomas DW, Dorais M, Bergeron JM (1990) Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus.* I. Mating behaviour. J Mammal 71:475–479

Tordoff AW, Bao TQ, Tu ND et al (eds) (2004) Sourcebook of existing and proposed protected areas in Vietnam, 2nd edn. BirdLife International in Indochina and Ministry of Agriculture and Rural Development, Hanoi

Tuttle MD (1976) Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. Ecology 57:587–595

Tuttle MD (1977) Gating as a means of protecting cave-dwelling bats. In: Aley T, Hodes D (eds) National cave management symposium 1976. Speleobooks, Albuquerque, New Mexico, pp 77–82

Tuttle MD (2013) Threats to bats and educational challenges. In: Adams RA, Pedersen SC (eds) Bat evolution, ecology, and conservation. Springer, New York, pp 363–391

Tuttle MD, Taylor D (1994) Bats and mines. Resource Publication No 3. Bat Conservation International, Austin Texas

Van NK, Hien NT, Loc PK et al (2000) Bioclimatic diagrams of Vietnam. Vietnam National University Publishing House, Hanoi

Vermeulen JJ, Whitten AJ (1999) Biodiversity and cultural property in the management of limestone resources. The World Bank, Washington

Vories KC, Throgmorton D, Harrington A (2004) Proceedings of bat gate design: a technical interactive forum held March 4–6, 2002 at the Red Lion Hotel, Austin Texas. Office of Surface Mining, Alton, Illinois

Wanger TC, Darras K, Bumrungsri S et al (2014) Bat pest control contributes to food security in Thailand. Biol Cons 171:220–223

Waters DA, Vollrath C (2003) Echolocation performance and call structure in the megachiropteran fruit-bat *Rousettus aegyptiacus*. Acta Chiropt 2003:209–219

Watson J, Hamilton-Smith E, Gilleson D et al (eds) (1997) Guidelines for cave and karst protection. IUCN, Gland, Switzerland and Cambridge, UK

Webb PI, Speakman JR, Racey PA (1995) How hot is a hibernaculum? A review of the temperatures at which bats hibernate. Can J Zool 74:761–765

Weinreich JA, Voshaar JHO (1992) Population trends of bats hibernating in marl caves in the Netherlands (1943–1987). Myotis 30:75–84

Whitten T (2009) Applying ecology for cave management in China and neighbouring countries. J App Ecol 46:520–523

Whitten T (2012) Protecting biodiversity. International Cement Review, June 2012

Wiles GJ, Brooke AP (2013) Conservation threats to bats in the tropical pacific islands and insular Southeast Asia. In: Fleming TH, Racey PA (eds) Island bats: evolution, ecology, and conservation. University of Chicago Press, Chicago and London, pp 405–459

White WB, Culver DC (eds) (2012) Encyclopedia of caves. Academic Press, Chennai

Zhang L, Zhu G, Jones G (2009) Conservation of bats in China: problems and recommendations. Oryx 43:179–182

Zukal J, Rehak Z, Kovarik M (2003) Bats of the Sloupsko-sosuvske jeskyne cave (Moravian Karst, Central Moravia). (In Czech with English summary) Lynx (Praha) n.s. 34: 205–220

Part IV

Conservation Approaches, Educational and Outreach Programs

Chapter 16
The Roles of Taxonomy and Systematics in Bat Conservation

Susan M. Tsang, Andrea L. Cirranello, Paul J.J. Bates and Nancy B. Simmons

Abstract Taxonomy—the description, naming, and classification of organisms—and systematics—the study of the evolutionary relationships of organisms—are both crucial components in conservation, providing a necessary framework for any conservation initiative. With more than 200 new bat species identified or raised from synonymy in the past decade and additional taxa described monthly, the Age of Discovery is ongoing for bats. New taxonomic and systematic discoveries clarify the status of populations, and the recognition of distinct species and lineages allows appropriate conservation strategies to be crafted, increasing the likelihood of recovery. In addition to identifying species and specimens, taxonomists care for vouchers, provide species lists for localities, and communicate taxonomic ideas to non-experts, especially through descriptions, keys, and field guides. Taxonomists can also provide conservation planning tools such as inventory data, estimates of extinction risk and extinction rate, and information for defining protected areas. Despite the importance of taxonomy, a lack of financial and institutional support impedes the training and employment of taxonomists and such factors need to be

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S.M. Tsang (✉)
Department of Biology, City College and the Graduate Center at the City University of New York, New York, NY 10031, USA
e-mail: stsang@amnh.org

S.M. Tsang · A.L. Cirranello · N.B. Simmons
Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural History, New York, NY 10024, USA
e-mail: andreacirranello@gmail.com

N.B. Simmons
e-mail: simmons@amnh.org

P.J.J. Bates
Harrison Institute, Bowerwood House, St. Botolph's Road, Sevenoaks, Kent TN13 3AQ, UK
e-mail: pjjbates2@hotmail.com

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overcome. Taxonomic and systematic discoveries, especially those involving cryptic species and unrecognized diversity, are rapidly increasing with the advent of modern genetics. Researchers must be cautious to argue from multiple lines of evidence when naming new species and be clear about the species concept they employ, as these have wide ranging impacts beyond taxonomy. Creating new ties between taxonomists and non-experts will be crucial in conservation of a diverse range of organisms in increasingly fragile landscapes.

16.1 Introduction

Global biodiversity is being lost at an unprecedented rate as a result of environmental change and human activity. Like other organisms, bats are at risk and many populations and species are threatened. As of 2013, the International Union for Conservation of Nature and Natural Resources (IUCN) Red List recognized 81 bat species as Near Threatened, 95 as Vulnerable, 51 as Endangered, 26 as Critically Endangered, and 5 as Extinct (IUCN 2014). It is clear that decisions must be made now to combat ongoing loss of species and populations. However, appropriate management decisions cannot be made without a marriage among conservation biologists, taxonomists, and legislators. Before conservation strategies can be implemented, the species composition of a locality must be well understood; otherwise, the effectiveness of any conservation effort cannot be accurately quantified.

Clearly defining species boundaries—while often difficult—is crucial to basic research and conservation. Some level of agreement on the organisms and populations considered part of any species is necessary for studying and tracking the health of organisms and ecosystems. Taxonomy—the description, naming, and classification of organisms—provides this necessary framework. Taxonomy, along with classification, often is conflated with systematics (Schuh 2000), which is more properly defined as the study of the diversification and evolutionary relationships of organisms through time. Despite often being used interchangeably, they are distinctly different, though systematic research includes recognition of taxa (i.e., taxonomy) as a necessary ingredient to reconstructing the past. Phylogenies produced by systematists provide a crucial foundation for examining biological phenomena and hypotheses, such as adaptive radiation or biogeographic scenarios, some of which are important for informing conservation decisions. Phylogenies help predict where biodiversity hotspots may be located, inform how distinct populations may be from one another, and identify unique lineages that preserve critical genetic diversity. Without systematics, other aspects of natural history lose their historical framework; and without taxonomy, systematics loses its basic operational unit. This chapter will demonstrate the many ways in which taxonomy and systematics have contributed to past conservation efforts and how they will continue to enrich protection of bat species globally.

16.2 The Continuing Age of Discovery

Taxonomy is not a dead science; the Age of Discovery is ongoing, especially for bats (Fig. 16.1). The number of bats discovered in the last couple of decades is higher than expected when compared to other mammalian orders (Reeder et al. 2007). With each subsequent volume of *Mammal Species of the World* (Honacki et al. 1982; Wilson and Reeder 1993, 2005), the number of recognized bat species has increased dramatically, with new species described from every corner of the world. Between publication of the last edition in 2005 and the end of 2013, nearly 200 new bat species were described or resurrected from synonymy, including 120 species new to science (Table 16.1), putting the total number of bat species at just over 1300 at the time of writing of this chapter. The continuing high rate of discovery (or recognition) of new bats can be a potential impediment to conservation since it is difficult to assess the status of each newly discovered species within a short period of time, and because it is difficult to make management plans in the absence of abundance or natural history information (both of which are typically lacking for newly recognized taxa). However, new discoveries may clarify the status of isolated populations, and the recognition of these distinct species can allow appropriate conservation and management strategies to be crafted.

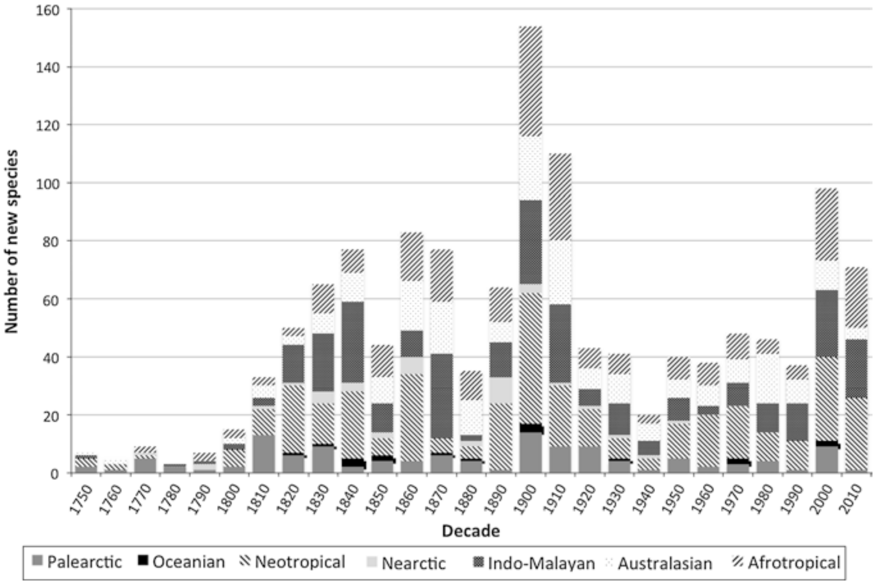

Fig. 16.1 Number of new bat species described per decade since 1750. Species were categorized to zoogeographic region (as defined by Newton 2003) of discovery according to type localities. Species since 2010 only reflect discoveries prior to the writing of this chapter (early 2014). New species are constantly being described from the tropics, with rates of discovery in the Afrotropics and Indo-Malayan regions catching up with the Neotropics