Chapter 15
Conservation Ecology of Cave Bats

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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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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.
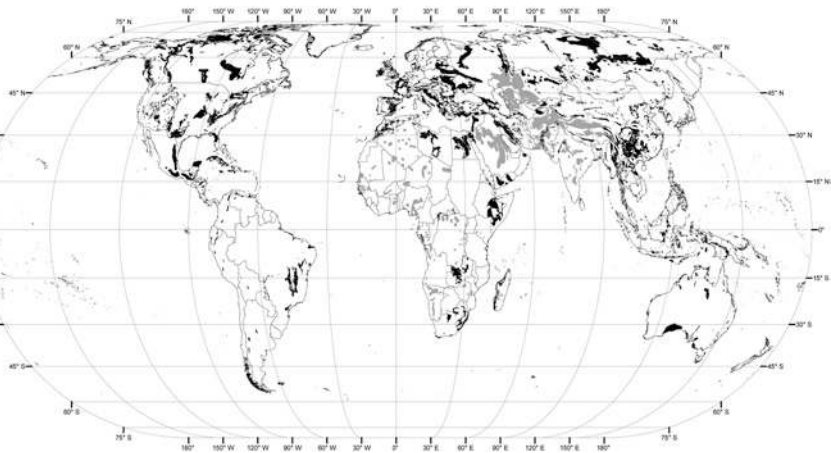
Fig. 15.1 Global distribution of carbonate rocks (© Paul Williams, University of Auckland, NZ)

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 hognosed 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.
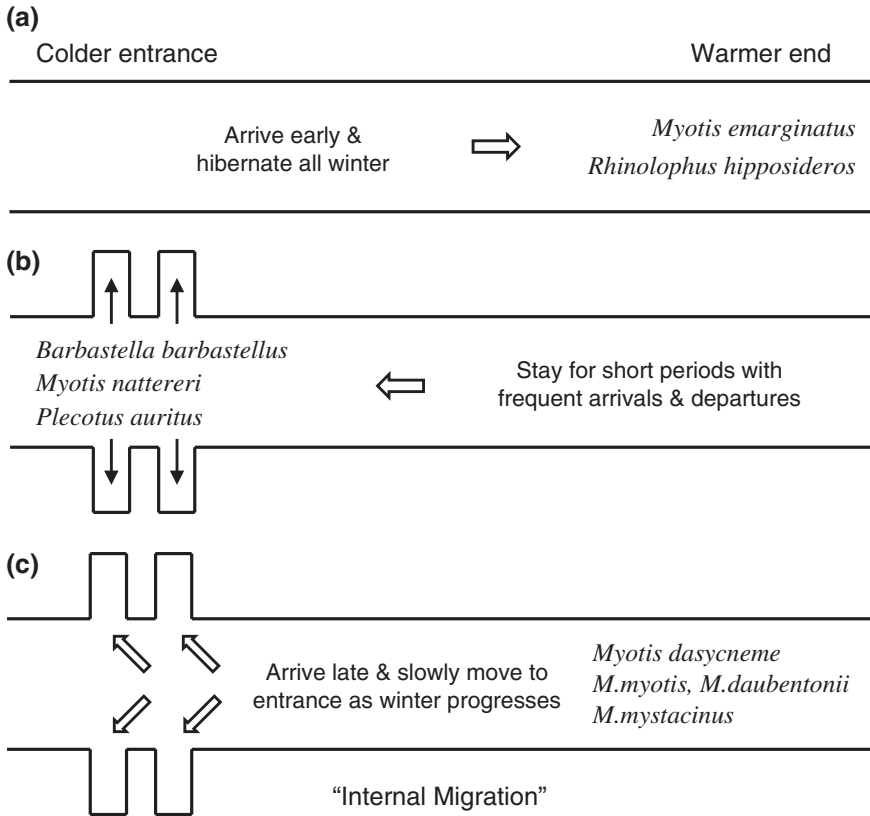
(a)

Colder entrance   Warmer end

Arrive early &   ⇒   *Myotis emarginatus*
hibernate all winter   *Rhinolophus hipposideros*

(b)

Barbastella barbastellus
Myotis nattereri   ⇐   Stay for short periods with
Plecotus auritus   frequent arrivals & departures

(c)

                        Arrive late & slowly move to   *Myotis dasycneme*
                        entrance as winter progresses   *M.myotis, M.daubentonii*
                                                             M.mystacinus

                              "Internal Migration"

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 Ecositems

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 out-standing importance for cave-dwelling bats across the European Union (known as Natura 2000) has been viewed as an important step change in European bat con-servation, 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 addi-tion to other groups dealing with related subjects such as surveillance and moni-toring 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 sev-eral cave-dwelling species, and individual states maintain their own lists of endan-gered 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 west-ern, 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 protect-ing 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 (includ-ing 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 con-troversial subject within the speleological community (Kennedy 2006), and simi-larly 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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