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THE UNIQUENESS OF BATS

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1.1 INTRODUCTION

The aim of this chapter is to provide an overview of the distinctive features of bats, many of which are unique among mammals, and in particular to highlight features of their biology that may have some bearing on the high prevalence of viruses in this group (Luis *et al.*, 2013).

Bats are the only mammals with the capacity for powered flight. The associated skeletal adaptations of elongated forelimb bones were fully developed in the first fossil bat *Icaronycteris index* 50 million years ago, discovered in the Green River formation in Wyoming, USA (Jepsen, 1966, 1970). Also evident were auditory bullae at the base of the cranium, indicating the presence of large cochlea, associated with echolocation, which enabled bats to fly in darkness. Flight and echolocation allowed bats to occupy and eventually dominate the nocturnal aerial feeding niche where they are relatively free of competitors and predators. Among the exceptions are caprimulgid birds (nightjars and goatsuckers), an Old World bat hawk and a New World bat falcon. Owls cannot match the flight agility of bats, although they are opportunist predators at roosts (Fenton & Fleming, 1976).

From the same Eocene fossil beds in Wyoming, Simmons *et al.* (2008) described *Onychonycteris finneyi,* of similar age to *Icaronycteris index* but more primitive, in that its limb bones are intermediate in proportion between terrestrial mammals and other Eocene bats. The cochlea is also smaller indicating that echolocation was either less well developed or absent, supporting the view that flight evolved before echolocation. However, in the absence of a more extensive fossil record, the evolutionary history of bats from a small terrestrial shrew-like early mammal of the Triassic to the fossil bats found 150 million years later is a matter of speculation. The most plausible hypothesis is that bats evolved from a species similar to modern day tree shrews, in which the limbs and digits became connected by folds of skin and the forelimbs became elongated to form an aerofoil (Smith, 1977; Hill & Smith, 1984). Jumping from branch to branch led to gliding and eventually to flapping flight.

With 1301–1331 species (January 2014, N.B Simmons, Pers. Comm.; Simmons, 2015) bats are the second largest order of mammals, and the number of species continues to rise as new ones are described or the taxonomy of particular genera is reviewed. Nevertheless, bats continue to account for about a fifth of all mammals because the same processes are happening in the largest order of mammals, the rodents, which has about twice as many species as bats. Bats are distributed throughout the world, with the exception of some isolated oceanic islands such as Tahiti and the polar regions, although they breed inside the Arctic Circle (Rydell, 1989). However, although there are twice as many bat species in the Old as in the New World, bats achieve their greatest species richness in South America (Hutson *et al.*, 2001; Jones *et al.*, 2009). Regardless of continent or scale, latitudinal gradients of richness are qualitatively similar and species number increases with decreasing latitude and decreases with increasing elevation (Willig *et al.*, 2003). Family-level species richness varies greatly, from one and two species in the Craseonycteridae and Myzopodidae respectively to more than 300 species in the Vespertilionidae (Simmons & Conway, 2003).

Historically, bats were divided into two suborders: the Megachiroptera consisted of a single family, the Pteropodidae – Old World vegetarians with large eyes, which do not echolocate; and the Microchiroptera with 16 families of echolocating and mainly insectivorous bats. Recent phylogenetic analysis has revised the classification of bats, and two new suborders have replaced the old: The Yinpterochiroptera consisting of the Pteropodidae and five other families grouped within the superfamily Rhinolophoidea; and the Yangochiroptera, with three superfamilies – the Emballonuroidea, the Vespertilionoidea and the Noctilionoidea, comprising a total of 13 families (Teeling *et al.*, 2005).

1.2   FLIGHT

The ability to glide by extending flaps of skin between the limbs has evolved several times among mammals, in the marsupial sugar gliders and flying phalangers of Australia and New Guinea, in placental mammals like flying squirrels and colugos of Asia, and anomalures of Africa. Bats are unique, however, in their capacity for powered flight. All forelimb bones in bats are elongated, although the ulna no longer extends to the wrist and is vestigial, so pronation and supination (turning about the elbow) is no longer possible nor desirable. Digit one – the thumb – is free and clawed and is important for climbing and grooming, and in some cases for aggression. Digits two and three are

generally close together and form the rigid leading edge of the aerofoil. Digits four and five support the wing membrane or patagium, which consists of a double layer of skin, well provided with elastic tissue so that it can change shape in flight but retracts and folds at rest. The hind limbs are also elongated, attached to the patagium and involved in steering. They are generally joined to the tail by the interfemoral membrane which is sometimes used in prey capture. The overall flexibility of the wing means that some bats have a unique flying attribute – the ability to carry out stall turns – to rotate through 90° in their own body length.

In contrast to birds, where most power for flight comes from two muscles – the pectoralis and the supracoracoideus working antagonistically – flight in bats is powered by nine pairs of muscles, mainly abductors and adductors, concentrated towards the midline (in contrast to the situation in terrestrial mammals where the flexors and extensors of the limbs power locomotion). In birds the muscles that elevate and depress the wings are on the ventral surface, whereas in bats the elevators are dorsal and the depressors are ventral. The keel on the sternum of bats is much less prominent than in birds. The muscles responsible for opening and closing the wing are also situated in the proximal parts of the forelimb and their power is transmitted by extended tendons. The wing opens and closes in one plane and twisting is eliminated. The clavicle braces the shoulder joint against the axial skeleton, in contrast to the situation in birds where the coracoid provides a more rigid brace.

Although the hind limbs may be elongated, the pelvic girdle is reduced compared with the pectoral girdle, and the diameter of the birth canal is reduced. However, across the pubic symphysis, the interpubic ligament joins the pubic bones ventrally, and can expand to increase the diameter of the birth canal from 2 to 35 mm in *Tadarida brasiliensis*. This expansion is under the influence of the hormone relaxin (Crelin, 1969). The hind limbs have become rotated by 90° in many bats, although they have retained the ability for terrestrial locomotion, sometimes impressively so (Lawrence, 1969; Riskin *et al.*, 2006). In some groups, however, such as horseshoe bats (family Rhinolophidae), the limbs have rotated though 180° and terrestrial locomotion is no longer possible so they can only hang or fly, although some species are able to land on the ground in pursuit of prey and lift off from a stationary position.

The overall shape of the wing is an important determinant of flight capability and foraging behaviour. Wing loading refers to the weight of the bat divided by the total area of the flight membrane, so that high wing loading occurs in a large bat with relatively small wings. Aspect ratio is the square of the wingspan divided by the wing area and is low in bats with short broad wings and high in bats with long narrow ones. A principal components analysis between increasing wing loading and aspect ratio reveals four broad flight capabilities (Norberg & Rayner, 1987):

1. Slow open-air flight, long distance migration.
2. Slow maneuverable flight in cluttered environments.
3. Fast flight in cluttered environments.
4. Fast open-air hawking, short range migration.

Of particular relevance in the context of disease transmission is the migratory ability of bats which will be considered later. In addition, O'Shea *et al.* (2014) have

hypothesized that bat flight provides the selection pressure for co-existence with viruses through a daily cycle of activity that elevates metabolism and body temperature analogous to the febrile response in other mammals.

1.3   ECHOLOCATION

Although the role of the ears in enabling bats to avoid obstacles in the dark was established in the late 18th century by Spallanzani and Jurine, it was not until the mid-20th century that the use of echolocation to catch insects was revealed by Griffin and colleagues (Griffin, 1958). Echolocation involves the analysis by an animal of the echoes of its own emitted sound to gain information about its environment. Echolocation is used by most bats to detect obstacles and prey. It has also evolved in some nocturnal cave-nesting birds like swiftlets (*Collocalia*) of the Old World tropics and the South American oilbird (*Steatornis*) and among mammals in toothed whales and in some insectivores (Sales & Pye, 1974). It has, however, been best studied in bats where it has reached extraordinary levels of sophistication (Fenton, 2013).

Most bats produce their echolocation calls in the larynx, which in bats is proportionally larger, and is tensioned by well-developed cricothyroid muscles. Lips, flaps of skin and noseleafs appear to act as acoustic lenses, focussing outgoing signals. The external ears are generally large and have a cartilaginous projection or tragus at their base which may limit the receptive field to an area 30–40° either side of the midline and this may in turn affect the directionality of incoming echoes (Altringham, 2011).

Bats use a variety of echolocation calls with different combinations of signal strength, signal duration and pattern of frequency change over time. As they approach targets, they produce shorter and shorter signals to ensure the outgoing pulses do not mask returning echoes.

Echolocation calls are generally beyond the range of human hearing (and so by definition are ultrasonic) and in the frequency range 20–120 kHz. They are also of high intensity and loud enough to be uncomfortable if we could hear them. To avoid deafening themselves by their own emitted sounds, most echolocating bats separate pulse and echo in time. Furthermore, they disconnect one of the middle ear bones, the stapes, from the oval window at the entrance to the cochlea, by contracting the stapedius muscle. When foraging, bats emit pulses of ultrasound and the pulse repetition rate increases when the echoes indicate the presence of a prey item, in some cases up to 200 Hz. The stapedius muscle can operate at this frequency, one of the highest recorded in mammals (Altringham, 2011).

Horseshoe bats (Rhinolophidae), leaf-nosed bats (Phyllostomidae), and three species of moustached bats (Mormoopidae), separate pulse and echo in frequency. They do so by exploiting Doppler shifts of their outgoing signals, which are dominated by a single frequency.

High frequency sounds attenuate rapidly in air so that a bat echolocating with signals that have most energy at 30 kHz is unlikely to detect insect-sized targets beyond 40 m. The frequency of sound is inversely proportional to its wavelength and so the higher the frequency the smaller the wavelength. The best sound for detecting an object is one with a wavelength similar in length to the object, so that bats feeding on small insects tend to use high frequency short wavelength calls.

Bats emit echolocation calls in pulses either at a constant frequency (CF) or frequency modulated (FM) or a mixture of the two. FM pulses are short, typically 2–5 ms long and sometimes less than 0.2 ms. If pulses were longer, the bat would be listening to the echo before it had finished emitting the pulse and neural mechanisms of echo interpretation require that to be avoided (Altringham, 2011). According to the autocorrelation function proposed by Simmons (1971), a bat behaves as if it stored the emitted pulse (in the inferior colliculus of the midbrain) and cross-correlates it with the returning echo (Altringham, 2011).

CF calls are typically 10–50 ms in duration and often have an FM component at the end. Many species with long CF components to their calls use an auditory processing system that is tolerant of pulse-echo overlap. This is possible because bats in the families Hipposideridae and Rhinolophidae have an acoustic fovea – a region of the cochlea that is extremely sensitive to the echo frequency of their calls – so that pulse and echo are separated in frequency rather than in time (Neuweiler, 1990; Altringham, 2011).

The Pteropodidae is the only family of bats not to have evolved laryngeal echolocation and relies on sight for orientation, together with olfaction for finding food. However, one genus within the Pteropodidae, *Rousettus*, has evolved a system of echolocation by rapid tongue clicking (Holland *et al.*, 2004), and as a result can roost deep in caves. Other members of the family may also roost in caves but only within sight of the entrance.

1.4 COMMUNICATION

In addition to its role in avoidance of obstacles and detection of prey, the sounds produced by bats are also important in communication between individuals (Altringham & Fenton, 2003). Although echolocation calls may have a communication function (Möhres, 1966; Barclay, 1982), social calls have been identified which often have a lower frequency than echolocation calls and may be audible to the human ear. Examples are distress calls (Russ *et al.*, 1998), mating calls (Lundberg & Gerrell, 1986), copulation calls (Thomas *et al.*, 1979), isolation calls when young are separated from their mothers (de Fanis & Jones 1995) and, together with their scent and the spatial memory of the mothers, enable young to be located among many millions on the wall of cave roosts (Balcombe & McCracken, 1992).

1.5 FORAGING, DIET, AND ECOSYSTEM SERVICES

Although bats have evolved a wide range of diets, they have retained a relatively simple digestive system and a relatively short intestinal passage time (Tedman & Hall, 1985). The majority of bat species are insectivorous, catching their prey in free flight or in various degrees of clutter, or gleaning, in which insects are taken from substrates such as leaves, bark or the ground. Such gleaners often have particularly acute hearing (Coles *et al.*, 1989) and can detect their prey by listening to the sounds of shimmering wings, or rustling, as the insect moves (Anderson & Racey, 1981; Swift & Racey, 2002). The majority of nocturnal moths, and also green lacewings, have evolved hearing organs that detect the bats' ultrasound and enable them to take avoiding action. Some arctiid moths

have evolved organs which generate sound that cause approaching bats to abandon their attack (Jones & Rydell, 2003).

Bats in the family Pteropodidae have large eyes and good night vision and feed on fruit, flowers, nectar, pollen, and leaves. Fruit contains little or no protein but bats can extract protein from pollen and leaves (Kunz & Ingalls, 1994; Long & Racey, 2007). The New World family Phyllostomidae includes many species with a diet of fruit, nectar and pollen which also catch insects to satisfy their protein requirements. The extent to which these bats rely on echolocation when feeding on plant products is unclear. However, some New World flowers have evolved nectar guides which reflect ultrasound to attract bats and encourage their role in pollination (von Helversen & von Helversen, 1999, 2003). Although the majority of bat species are insectivorous, some have become carnivorous, taking small mammals, reptiles and amphibians from the ground (Patterson *et al.*, 2003). Even more specialized are the piscivores, which echolocate ripples on the water surface before lowering their often enlarged feet into the water to gaff small fish (Schnitzler *et al.*, 1994). Vampire bats are unique as the only mammals to subsist entirely on a diet of blood. An anticoagulant in their saliva maintains blood flow once an incision has been made by sharp incisor teeth (Hawkey, 1966; Fernandez, 1999).

At least one species of vampire bat has an infrared detector on the nose leaf to assist in the localisation of prey, which in the case of the common vampire bat *Desmodus rotundus* is commonly cattle (Kürten *et al.*, 1984). Quadripedal locomotion is also well developed in vampires, which alight on the ground near their prey and are adept at avoiding their moving hoofs. They climb up the leg to the neck, make an incision and feed by lapping the blood. Before they can fly, they must lose weight and the kidney switches to water-eliminating mode. Once back in the roost, they must digest blood with no access to drinking water, so the kidney switches to a water conserving mode more efficient than that of some desert rodents (McFarland & Wimsatt, 1965). Cattle are not, however, debilitated by the loss of blood but by the diseases transmitted by the bats, the most serious of which is rabies (see Chapter 3).

As knowledge of bat diets becomes more detailed, so does awareness of the eco-system services they provide (Boyles *et al.*, 2011; Kunz *et al.*, 2011). By analyzing feces, the proportion of insect pests in the diet can be determined and a monetary value placed on a colony of many millions of free-tailed bats *Tadarida brasiliensis* roosting in caves in Texas, not just in reduction of crops lost to pests but also in reducing the number of pesticide treatments the crop requires (Cleveland *et al.*, 2006). Similar ecosystem services are provided by wrinkle-lipped free-tailed bats, which act as a potential biological pest control agent through eating rice crops in Asia (Leelapaibul *et al.*, 2005). Wherever large colonies of bats roost, their guano is harvested as a fertilizer rich in nitrogen and phosphates. In many countries in the developing world, this is often the preferred fertilizer, because farmers consider that, unlike chemical fertilizers, it improves soil quality.

Fruit-eating bats disperse seeds over long distances and play an important role in forest regeneration (Lobova *et al.*, 2009; Fleming & Kress, 2013). Some plant-eating bats have become adapted to a diet of pollen and nectar and pollinate high value commercial crops such as durian in Asia (Bumrungsri *et al.*, 2009) or commonly used vegetables such as stink bean or petai (Bumrungsri *et al.*, 2008) as well as charis-matic plants, such as baobabs in Africa and Madagascar (Baum, 1995; Andriafidison *et al.*, 2006).

1.6 HETEROTHERMY, DAILY TORPOR, AND HIBERNATION

The adaptation that has enabled insectivorous bats to colonize the north and south temperate zones is the capacity for heterothermy, in which body temperature is allowed to fall, sometimes close to ambient, from which it spontaneously rewarms. This is not an intermediate state between cold-blooded vertebrates or ectotherms and warm blooded vertebrates or endotherms but is a specialised form of homeothermy. Many temperate-zone bat species make use of daily torpor, allowing their body temperature to fall to save the energy increment that would be required to maintain a high constant body temperature or homoeothermic state. In late summer, bats begin to accumulate body fat and as aerial insect density and ambient temperatures decline in autumn, the periods of daily torpor become longer and then continuous for days or weeks as the bat is hibernating. Hibernation is interrupted by spontaneous arousals, the frequency of which is related to ambient conditions. At latitudes where ambient temperatures are below freezing for long periods, arousals are less frequent than at 53°N in the UK, where over a 3-year period, pipistrelle bats *Pipistrellus pipistrellus* flew in every winter month and on a third of all winter nights (Avery, 1985). Bats will often fly when the winter temperature rises above the threshold for insect flight and winter feeding is often recorded although increases in body weight have yet to be established (Ransome, 2008). There may be other drivers of winter arousals such as the need to urinate, to drink or to check on ambient conditions, and perhaps reposition within the hibernaculum. Arousal from deep hibernation, in which the bat's body temperature is close to ambient, is energetically expensive in the amount of fat metabolized. That explains the mass winter mortality, of over six million bats of several species in North America, attributed to the cold-adapted fungus *Pseudogymnoascus destructans*. This invades the skin of the muzzle, forearm, and wing membranes, penetrating the epidermis and dermis and causing the bat to arouse repeatedly during hibernation. More fat is metabolised in doing so than will last the bat for the duration of winter and the bat starves to death (Reeder & Moore, 2013).

Although many groups of mammals (such as some carnivores and Eulipotyphla) and some birds (such as humming birds) make use of torpor, bats have taken the adaptation to extremes during pregnancy and lactation. If pregnant bats experience periods of inclement weather, so that their insect food is no longer flying, they will become torpid and the development of the fetus will be slowed or halted. Conversely, if they experience high ambient temperatures and abundant food during pregnancy, foetal development will accelerate (Racey, 1973a; Racey & Swift, 1981). Among mammals in general, the gestation period is fixed by the foetal genotype and is resistant to alteration by environmental factors (Racey, 1981). The fact that foetal development in bats may be slowed, stopped or accelerated depending on ambient temperature and food supply is unique among mammals and may be related to the fact that they have one of the slowest recorded rates of foetal growth (Racey, 1973a, 1981).

The timing of the reproductive cycle of male bats of the temperate zone is also influenced by changes in ambient temperature and food supply. Premature arousal of captive pipistrelle bats *Pipistrellus pipistrellus* from hibernation with an abundant food supply results in the initiation of spermatogenesis. Conversely, spermatogenesis is delayed in captive noctule bats *Nyctalus noctula* in which hibernation is prolonged by several months (Racey, 1971).

1.7 REPRODUCTION

Bats have unique features in their reproduction, the most significant of which is delayed fertilization associated with prolonged storage of fertile spermatozoa. All bats of the temperate zone are seasonally monestrus, and have only one birth period a year. Births occur in midsummer, and after lactation and weaning, copulation begins, so that the majority of females entering hibernation are inseminated. Spermatozoa are stored in the oviducts, in the utero-tubal junction or in the uterus, depending on the species (Racey, 1979). In the latter case, vast numbers are stored so that the uterus more closely resembles the thin-walled spermatheca, or sperm storage sac of an insect, than a mammalian uterus (Racey, 1975). After arousal from hibernation in spring, a single large follicle, which has been overwintering in the ovary, ovulates and is fertilized by one of the stored sperm, and the remainder are expelled (Potts & Racey 1971; Wimsatt *et al*., 1966; Wimsatt, 1969). Isolation experiments have demonstrated that the sperm stored by female bats can retain their fertility for as long as seven months (Racey, 1973b, 1979). Although several vertebrate and invertebrate species exceed this, among mammals it is unique.

Sperm storage in females of the temperate zone is associated with a unique adaptation in males – extreme asynchrony between the endocrine and exocrine functions of the testis. Spermatogenesis is initiated on arousal from hibernation in spring and proceeds during summer so that sperm are released from the seminiferous tubules in July and August in the northern temperate zone and the tubules then regress, as in most seasonally breeding mammals (Racey & Tam, 1974). In bats, however, regression is complete, with the tubules in winter consisting of a single layer of spermatogonia and Sertoli cells. Copulation begins in September in the northern hemisphere (Racey, 1979) and in some bat species, continues throughout winter when males are observed in hibernacula copulating with torpid females (Wimsatt, 1945; Stebbings, 1965). It is also observed in spring (Aubert, 1963). When noctule bats (*Nyctalus noctula*) were deprived of the opportunity to copulate in autumn and introduced to females at intervals during winter they did so and females became pregnant (Racey, 1973b). This demonstrated that sperm stored for up to 7 months in the epididymis of males also retains its fertility and that the Leydig cells of the testis continue to secrete androgens during winter to maintain the integrity of the epididymis, the viability of spermatozoa and libido (Racey, 1974).

One of the advantages of prolonged sperm storage in temperate zone bats is that it avoids the necessity of finding mates and copulating when in poor body condition at the end of hibernation, and females can ovulate and pregnancy can proceed once body condition has improved (Potts & Racey, 1971). Another advantage may be that if ovulation occurs in response to increased temperature and food supply, then births will be synchronised, also at an optimal time. This may also explain the occurrence of sperm storage in some tropical bats (Racey, 1979; Racey & Entwistle, 2000).

In tropical latitudes, seasonal monestry also occurs but there is a wider range of reproductive cycles, some of which are polyestrus, so that some species have more than one young per year. Some reproductive cycles also incorporate delays in implantation and development (Racey & Entwistle, 2000).

1.8   LIFE HISTORY STRATEGIES

A striking feature of the life history characteristics of bats is the general consistency among different species, which may vary by three orders of magnitude in body mass, and occupy tropical and temperate latitudes with a wide range of diets and social systems varying from monogamous to highly polygynous (Barclay & Harder, 2003). Bats are generally monotocous and rarely have more than one young a year, after a long gestation followed by an extended lactation. The body mass of the young at birth is on average 23% that of the mother and 76% of her body mass at weaning (Barclay & Harder, 2003). Puberty seldom occurs in the year of birth but generally occurs in the following year, although in some species it may be delayed (Racey & Entwistle, 2000). A unique feature of bats, for mammals of their size, is their longevity, and Barclay and Harder (2003) give an average of 16.1 years. The average maximum recorded life span of a bat is 3.5 times that of a terrestrial placental mammal of a similar size and records of individuals surviving for more than 30 years now exist for five species (Wilkinson & South, 2002). Barclay & Harder (2003) hypothesize that low resource availability may limit reproductive output but that the overall consistency in life history characteristics reflects the evolutionary consequences of flight, which is generally associated with low extrinsic mortality (mortality associated with predators, competitors or disease) and may itself permit reduced reproductive effort per breeding event. However, such low extrinsic mortality has been challenged recently by the effects of white nose syndrome. Wilkinson and South (2002) found that life span significantly increases with hibernation and body mass and decreases with reproductive rate but is not influenced by diet or colony size. They suggested that hibernation may provide a natural example of caloric restriction which increases longevity in other mammals.

1.9   ROOSTING ECOLOGY

1.9.1   Caves

When they are not foraging, bats need shelter and are the only group of vertebrates to have successfully exploited caves as permanent daytime shelters (Kunz, 1982). In these they form some of the largest aggregations of vertebrates recorded, particularly for bats of the genus *Tadarida*, *w*ith estimates of up to 20 million *Tadarida brasiliensis* in single caves in the southern United States (Davis *et al.*, 1962; McCracken, 2003). Half a million *Hipposideros caffer* and up to 200 000 *Miniopterus schreibersii* were estimated to occupy single caves in Africa and Australia respectively (Brosset, 1966; Dwyer & Hamilton-Smith, 1965). Caves often contain several bat species and an estimated 800 000 individuals in a cave in Mexico comprised four species of mormoopid (Bateman & Vaughan, 1974) and three quarters of a million bats of three species roosted in Cucaracha cave, Puerto Rico (Rodriguez-Duran & Lewis, 1987). Although it is likely that these populations have declined in recent years (Furey & Racey, in press), the occurrence of such high densities of mammals in confined spaces is unique. Considerable effort has been expended in recent years attempting to refine methods of estimating the numbers involved (Hristov *et al.*, 2013).

The benefits of cave roosting include environmental temperatures that approach thermoneutrality, when bats do not expend energy maintaining their body temperature, thus reducing the energy costs of homeothermy. Disbenefits include a high incidence of ectoparasites (Marshall, 1982) and possibly also of disease and increased competition for food, although these remain to be rigorously established. In the temperate zone, some insectivorous bats also roost in rock crevices, such as *Eumops perotus* in the western United States (Vaughan, 1959), and in the tropics some frugivores (fruit eaters) are also crevice roosting, such as *Eidolon dupreanum* in Madagascar (Racey *et al.*, 2009) Several thousand *Eidolon helvum* also roost on cliffs at Wli Falls, Ghana (Ottou, 2011).

1.9.2 Trees

In areas devoid of caves, tree cavities may be the only available roosts and are used by species in several bat families in both temperate and tropical zones, although the size of such cavities limits the number of occupants. Even smaller numbers roost beneath exfoliating bark (Kunz & Lumsden, 2003). A few tropical bat species, mostly members of the Emballonuridae, roost in relatively exposed situations on the sides of tree boles (Kunz & Lumsden, 2003).

1.9.3 Houses

The low conductivity of wood and its suitability as a roosting substrate, especially for homoeothermic bats of the temperate zone, may explain why bats have followed it into buildings, although in terms of the evolutionary history of bats, this must be a relatively recent occurrence. Nevertheless, some bats, especially vespertilionids of the temperate zone, are now among the most synanthropic of all vertebrates. (Synanthropes are defined as animals which live near and benefit from humans and their dwellings.) These bats frequently occupy the roof spaces of houses, churches and other buildings as maternity roosts during the summer period of pregnancy, parturition and lactation. This may bring them into conflict with the human occupants of such buildings mainly because of the smell of urine and feces, and occasionally because of associated bed bugs (Cimicidae), which feed on the blood of bats and humans (Marshall, 1982). Transmission of disease from bats roosting in houses to human occupants is, however, seldom recorded and none of the five deaths from European bat lyssavirus recorded among the 590 million people in Greater Europe in the last 30 years was attributed to bats roosting in the victims' houses (Racey *et al.*, 2012).

1.9.4 Foliage

The largest bats, members of the family Pteropodidae found in the Old World tropics, roost in trees and are typically observed hanging from branches. Although the roosts of *Pteropus* were historically huge, extending over 13 square kilometres, with estimates of 30 million occupants (Ratclife, 1932), they are now much reduced in size and numbers as a result of loss of habitat, hunting for food (Mickleburgh *et al.*, 2009) or persecution by fruit farmers because of crop raiding (Furey & Racey, in press). Today, the largest recorded aggregation of fruit bats is found roosting in a small area of swamp forest in Kasanka National Park in northern Zambia where an estimated eight million

Eidolon helvum begin to arrive in October each year, to feed on wild fruit in miombo woodlands, increase in numbers to a peak in November and depart in late December (Racey, 2004). In the temperate zone, day roosting in foliage is confined to individuals or small family groups of the North American genus *Lasiurus* (Kunz & Lumsden, 2003).

Some foliage-roosting bats occupy unfurling leaves in both New and Old World habitats, and have specialised wrist and foot pads to enable them to cling to the smooth leaf surfaces (Kunz & Lumsden, 2003). Thus disc-winged bats of the genus *Thyroptera* occupy the unfurling leaves of *Heliconia* and *Calathea* in the New World (Findley & Wilson, 1974) and in Madagascar the endemic sucker-footed bat *Myzopoda aurita* roosts in the semi-unfurled central leaf of the Traveller's tree *Ravenala madagascariensis* (Ralisata *et al.*, 2010). All these roosts are highly ephemeral and the bats must find a new one when the leaf unfurls. More permanent than unfurling leaves are tents, made by 19 species in both Old and New Worlds, often by biting the leaf veins and ridges of a wide range of plant species (Kunz & Lumsden, 2003).

1.9.5   Roosts of other species

A few bat species roost in abandoned arboreal ant and termite nests which they are thought to excavate (Kunz & Lumsden, 2003). In Australia, the golden-tipped bat *Phoniscus papuensis* roosts in bird nests which it also modifies (Schulz, 2000).

1.9.6   Roost fidelity

Many bat species, especially insectivorous bats of the temperate zone, are characterized by high roost fidelity, as revealed by long-term banding studies for bats in buildings (Ransome, 2008) and caves (Gaisler *et al.*, 2003). The roosts of many fruit bats in the tropics, such as those of *Eidolon helvum* in African cities such as Accra, Dar-es-Salaam, and Kampala, and *Pteropus rufus* in Berenty National Park, Madagascar (Long & Racey, 2007) have existed for as long as local people can remember. However, in all these situations, the composition of the roosting groups is not constant and roosting groups may fragment and reform in what has been termed fission-fusion behaviour (Kerth & König, 1999).

1.10   MIGRATION

Less than 7% of bats are known or suspected migrants (Krauel & McCracken, 2013) compared with 40% of birds, but migrate for similar reasons – to experience more favorable climatic conditions and feeding opportunities. Some bat species that give birth and suckle their young in the higher latitudes of the temperate zone migrate nearly 2000 km to lower latitudes and hibernate where the climate is not so severe (Hutterer *et al.*, 2005). Of the approximately 45 bat species in Europe, only six are such long-distance migrants (Fleming & Eby, 2003). A dozen are regional migrants that may move several hundred kilometres, and the remainder are so-called stationary or sedentary species that move tens of kilometres between summer and winter roosts, but rarely disperse more than 100 km (Hutterer *et al.*, 2005). The cave-roosting bent-winged bat *Miniopterus schreibersii* is one of the best studied regional migrants and also the most widespread,

ranging from Europe through Africa to Australia. In Portugal it shows strong philopatry, or loyalty to maternity roosts following weaning. Mating occurs in hibernacula which are also the colony's maternity roosts (Rodrigues & Palmeirim, 2008). As a result of this strict philopatry to maternity roosts, all gene flow is male-induced during regional migrations (Rodrigues *et al.*, 2010).

Like birds, bats may be facultative or obligate migrants. One of the best examples of the latter is the tree-roosting hoary bat *Lasiurus cinereus* which migrates long distances in a north–south direction in North America. Individuals move through New Mexico in spring (Valdez & Cryan, 2009) and are found in Alberta, Canada in July (Baerwald & Barclay, 2011). Regional migrants show more varied directions of movement and may radiate from a common hibernaculum in a star-shaped pattern in spring.

Migratory patterns of the free-tailed bat *Tadarida brasiliensis* are more difficult to characterise, because they are panmictic (mate randomly) and populations show no genetic structure (Russell *et al.*, 2005). The species appears to include facultative, partial and long distance migrants (Krauel & McCracken, 2013). In the south-eastern United States, the bats appear to be sedentary and become torpid during cold spells in winter (Cockrum, 1969; La Val, 1973). In the mid-continent, a large part of the population migrates long distances between Mexico and the USA (Cockrum, 1969) and includes one of the longest recorded insectivorous bat migrations of 1840 km (Glass, 1982).

Less is known about migration in Old World fruit bats than for insectivorous species, although in Australia radio-tracking has revealed that nomadic populations of the grey-headed flying fox *Pteropus poliocephalus* track patchy resources and migrate hundreds of kilometres between successive pulses of *Eucalyptus* flowering (Fleming & Eby, 2003). The larger size of these bats means that recent advances in satellite tracking, particularly reduction in mass of the transmitter package, has allowed its deployment. It has been inferred for some time that the largest of the African pteropodids, the straw-coloured fruit bat *Eidolon helvum*, which is widely distributed across the central belt of the continent, migrated north and south seasonally in search of food (Kingdon, 1974). Four individuals were tracked up to 2518 km from Kasanka National Park in northern Zambia to the Democratic Republic of Congo over 149 days. They travelled in a north-westerly direction at an average speed of 90 km/day (Richter & Cumming, 2006). Satellite tracking has also revealed foraging flights of 130 km in two hours as well as inter-roost movements of *Pteropus poliocephalus* of several hundred kilometres, often between different countries of South East Asia (Epstein *et al.*, 2009). The longest recorded distance travelled for a pteropodid bat appears to be 3000 km for *Pteropus alecto* (Breed *et al.*, 2010).

1.11   CLIMATE CHANGE

Bats are important indicators of climate change (Jones *et al.*, 2009). The effects of changes in temperature and food supply on the initiation of pregnancy and spermatogenesis in bats has already been described and although the studies concerned were carried out mainly on captive bats, their effects on the gestation length of *Pipistrellus pipistrellus* were confirmed in the field (Racey & Swift, 1981). In *Rhinolphus ferrumequinum*, the timing of births in midsummer was significantly advanced in warmer springs, by 18 days, when spring temperatures were elevated by 2°C (Ransome & McOwat, 1994).

More extreme disruption was reported in the mouse-eared bat *Myotis myotis* in southern Spain, where pregnancies and births occurred in December, 6 months before the usual time for this species (Ibañez, 1977).

Climate change is likely to affect the energy budgets of hibernating bats whose fat reserves must last the winter, and this in turn is likely to affect their distribution, as they seek colder temperatures in which to maintain torpor (Humphries *et al.*, 2002). Changes in elevational distribution have been described for 24 bat species previously associated with lowlands in Costa Rica, which over a 27-year period moved higher up the mountains, an effect which was at least partly ascribed to climate change (La Val, 2004). A Mediterranean species, *Pipistrellus kuhlii*, has undergone a substantial northward range expansion over the last 15 years and is now found in parts of Central and Eastern Europe (Sachanowicz *et al.*, 2006), an effect which may also be explained, at least in part, by climate change. A similar western range expansion has been recorded for *Pipistrellus nathusii* (Lundy *et al.*, 2010).

The most extreme effects of climatic changes have been recorded in Australia, where severe drought and cold in 2006 caused the deaths of several hundred pups of the southern bent-winged bat *Miniopterus schreibersii bassani*. Such mortality is likely to have had a significant effect on the population which had already declined dramatically since the 1960s (Bourne & Hamilton-Smith, 2007). In contrast, extreme heat, with ambient temperatures in excess of 42°C, caused the deaths of over 3500 individuals in mixed species colonies of *Pteropus alecto* and *Pteropus poliocephalus* in January 2002 in northern New South Wales. This event led to the documentation of similar occurrences and it transpired that over 30 000 *Pteropus* spp., mainly *Pteropus poliocephalus*, had died during 19 similar temperature extremes (Welbergen *et al.*, 2008).

The increased incidence of extreme weather events is likely to have serious effects on populations of tree-roosting bats, particularly endemic species on tropical islands. The population of *Pteropus rodricensis* in the Mascarene Islands was halved by a single cyclone (Carroll, 1988) and in the Samoan Islands populations of *Pteropus samoensis* were reduced by about 90% by a cyclone in the early 1990s (Craig *et al.*, 1994).

More recently, statistical approaches have been used to predict the effect of different climate change scenarios on the distribution of bat species in Europe (Rebelo *et al.*, 2010) and SE Asia (Hughes *et al.*, 2012).

1.12 DISEASE-RELATED MORTALITY

In view of the prevalence of viruses in bats (Messenger *et al.*, 2002; Calisher *et al.*, 2006, 2008) it is surprising that there are so few recorded instances of virus-related mortality, in contrast to the devastating effects of the cold-adapted fungus *Pseudogymnoascus destructans*, known as white nose syndrome (Reeder & Moore, 2013). Even in this case, it is not the fungus itself which is the direct cause of mortality but starvation caused by frequent arousals from hibernation and consequent depletion of fat reserves (Reeder & Moore, 2013). Several thousand *Tadarida brasiliensis* died in Carlsbad cavern, New Mexico in 1955 and 1956, and the fact that half of the 20 individuals sampled were rabies-positive suggested that rabies was the overall cause of death (Burns *et al.*, 1956), although Constantine (1967) later implicated inclement weather conditions during migration in 1956. The only other mass mortality attributed to rabies

was several hundred *Epomops dobsoni* in southern Africa, of which 10–15% were found to be infected with Lagos bat virus (King *et al.*, 1994).

Pierson & Rainey (1992) described apparent epidemic disease in *Pteropus mariannus* in Micronesia in the 1930s, involving mass die-offs at the same time as measles affected the human population. An epidemic of unknown etiology was also suspected of reducing populations of *Pteropus tonganus* in Fiji during the 1940s. More recently, in 1985, many dead *Pteropus neohibernicus* were found on the Admiralty Islands (Flannery, 1989) and a similar incident involved *Pteropus rayneri* on the Solomon Islands.

Mass die-offs of *Miniopterus schreibersii* were reported in caves across southern France, extending into Spain and Portugal in 2002, which reduced the population by 60–65%. Although the cause was unclear, herpes virus was isolated from bat lungs. Other bat species roosting in the caves were apparently unaffected (Roué & Nemoz, 2004). Other than with white nose syndrome, the causal relationships of the other death events were never conclusively established.

1.13   CONSERVATION AND DISEASE SURVEILLANCE

About a quarter of all bat species are globally threatened (Mickleburgh *et al.*, 2002), mainly as a result of habitat fragmentation or loss, as well as loss of roosts. They generally have a negative public image that influences the response to outbreaks of disease and sometimes results in calls for culls, although recent studies have highlighted the need to avoid disturbances that may precipitate viral spillovers (Peel *et al.*, 2013). Loss of native fruits in the tropics often leads to increased dependency on farmed fruits, which brings bats into conflict with fruit farmers (Abdul-Aziz *et al.*, in press). In the Old World tropics, both insectivorous and frugivorous bats are hunted for food, generally unsustainably, so that their populations are becoming depleted (Mickleburgh *et al.*, 2009). Hunters and others handling dead bats may succumb to zoonotic disease such as Ebola (Leroy *et al.*, 2009). The identification of such diseases in bats, which has gathered momentum in recent years, has led to a global hunt for more bat viruses, driven by generous funding. A dichotomy has arisen in the approaches adopted. Most investigations have followed non-destructive blood-sampling protocols recommended by the Food and Agriculture Organization of the United Nations (2011). Others have involved killing large numbers of bats (Sasaki *et al*., 2012), some species of which are of conservation concern. Others have involved moving large numbers of bats across international boundaries with no acknowledged authorisation (He *et al*., 2013). Bat biologists and conservationists are keen to work with virologists and public health officials to protect the public and reduce the risks posed by zoonoses, but in a way that also minimises the impact on bat populations (Racey *et al.*, 2012) and follows widely accepted protocols for the use of animals in research, such as those of Sikes *et al.* (2011). Such an approach has proved successful in dealing with European bat lyssavirus and has been widely adopted by global organizations such as EcoHealth Alliance.

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