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dazzling diversity:
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Bat

Tessa Laird

REAKTION BOOKS

1 Dazzling Diversity: The Biology of Chiroptera

The scientific classification for bats is Chiroptera, and it is one of the most diverse orders of mammalia on the planet, comprising over 1,331 species.[1] Rodents are the only mammalian order boasting more species than bats, but they are arguably less thrilling than their winged cousins, who range from monster-sized fruit eaters with a wingspan the length of an adult human to tiny insectivores weighing little more than a bumblebee. The success of such diverse chiropterans can be attributed to evolutionary developments dating back more than 50 million years, the most obvious being that bats are the only mammals that are capable of true flight. Additionally, most bats can echolocate, emitting high-pitched sonic pulses whose echoes they interpret to build up a picture of their surroundings and their prey.[2] These, along with several other 'superpowers', demonstrate not only the dazzling diversity of Chiroptera but their intrinsic role in the maintenance of healthy ecosystems. Such mysterious powers may also offer a clue as to why bats are so commonly feared. Their association with evil, magic and madness finds them most often in the company of filmic and literary villains. Occasionally, however, their superpowers inspire superheroes.

The habitats, diets and physical characteristics of bats differ so vastly that Richard Dawkins said that to speak of bats as though they were all the same would be 'to speak of dogs, lions, weasels,

Two grey-headed flying foxes hanging out together.

Some of the first known images of bats can be found in the ancient Egyptian tomb paintings at Beni Hasan, Twelfth Dynasty, about 2000 BCE. Here a bat with wings spread wide can just be made out beneath a palimpsest of hieroglyphs and Coptic inscriptions.

bears, hyenas, pandas and otters all in one breath, just because they are all carnivores'.[3] Yet bats persist in the popular imagination as a rather generic type: small, black, squeaky and leathery. They are largely ignored except for their regular appearances in Halloween decorations, horror films and virus outbreaks. Meanwhile, climate change and habitat loss are depleting global bat populations at an alarming rate, making it more important than ever that we understand the biology and behaviour of these fascinating and varied creatures. As the great American modernist poet Marianne Moore put it, when describing a bat, 'we / do not admire what / we cannot understand'.[4]

Chiroptera is a compound of two Greek words, *chier* meaning hand and *pteron* meaning wing. Bats have very short upper arms while their forearms are greatly elongated, their fingers even more so. Each 'spoke' of their webbed wings (which somewhat resemble black umbrellas) is actually a finger, and the tiny hook at the top of each wing is equivalent to a human thumb. Recent research emphasizes the sensitivity of bats' wings, which, like human hands, are full of sensory receptors. This sense of touch makes bats'

wings superbly adapted for flight, but they can equally be used to scoop insects or cradle a baby.[5] Bats also use their leathery appendages as raincoats or sleeping bags; many bats sleep hanging upside down from trees, wrapped in their own wings. Bats' legs, however, are comparatively short and stumpy, and their clawed feet resemble our hands. They use these claws like grappling hooks (one of Batman's favourite tools) with which to hang upside down without effort – attested to by the fact that dead bats are often found still dangling by a vice-like grip. A fruit bat can hang comfortably from one leg, and looks in this posture like a piece of furry fruit, a veritable 'animated pear', as one bat researcher put it.[6] As if constant inversion wasn't strange enough, bats are unique among mammals for having knees that point outwards rather than forwards, an attribute that facilitates steering during flight and helps them crawl across surfaces such as the interiors of caves. In this posture, they look something like giant furry crickets.

For a long time the order Chiroptera was divided into two suborders: Microchiroptera and Megachiroptera, often simply called microbats and megabats, or, in German, the dainty *Fledermaus* versus the hefty *Flughund*. While the two suborders have been recently revised, they are still useful for distinguishing broadly between two very different types of bat. The former are

Unknown artist, detail from the Aberdeen Bestiary, *c.* 1200, folio 51v.

Centurio senex, or wrinkle-faced bat, from Belize.

predominantly small insect-eaters who use echolocation for navigation, and comprise a vast array of species with bizarre, fleshy facial ornaments, which the eighteenth-century French naturalist the Comte de Buffon described as 'a kind of pudding above the lips'.[7] (Perhaps this says more about the comestibles of Buffon's era than it does about bats' faces.) The latter are the larger fruit-eaters whose common name 'flying fox' gives a good indication of their endearingly dog-like faces, with large eyes, twitching ears, long snouts and lolling tongues. These fruit bats are restricted to mostly tropical regions – Africa, parts of Asia and Indo-Australasia – and constitute a single family, the Pteropodidae. Microbats, on the other hand, can be found on every continent except Antarctica, and comprise eighteen different families.[8] In order to cope with a vast range of climatic conditions, bats that live in colder locations have developed the ability to

hibernate; in hibernation their hearts, which run to around 400 beats per minute while awake, drop to a mere 25 beats.[9]

Even those living in warmer climates can use torpor, a drop in body temperature and metabolic rate, as a flexible energy-saving strategy, not unlike a hybrid car.[10] Nevertheless, the vast majority (over 80 per cent) of all bat species live in tropical climes, leading biologists to suspect that bats evolved in tropical regions.[11]

A recent reclassification of bats, still in two camps, uses modern genetic sequencing and puts some of the microbats into the mega category, now known as Yinpterochiroptera, while the rest of the microbats are accounted for under the subordinal heading of Yangochiroptera. That this system recalls the Chinese symbol of yin-yang – opposites that mingle and flux – is apposite given the Chinese love of bats as being symbolic of good luck. The newly delineated categories contain a big surprise: the superfamily Rhinolophoidea, which includes horseshoe bats, leaf-nosed bats and ghost bats, is more closely related to the Pteropodidae or fruit bat family than to microbats. This is remarkable because the Rhinolophoidea are the most complex and sophisticated echolocators – they are able to alter their calls subtly to compensate for error due to the Doppler effect, that is, the changing frequencies caused by the shifting positions of both predator and prey – while most flying foxes don't echolocate at all.[12]

Up until 2008 a controversy raged among evolutionary biologists as to whether flying foxes shared any common ancestry with echolocating microbats. The Australian neuroscientist Jack Pettigrew argued against bat monophyly (descent from a single common ancestor) and promoted the idea of convergent evolution – two separate groups of mammals that evolved flight independently of each other. He even went so far as to suggest that flying foxes were descended from a kind of 'flying primate'. Pettigrew deployed many compelling arguments to prove his

point, including aspects of the flying foxes' reproductive cycle. For example, foraging microbats leave their young at home in communal 'nurseries', while megabats carry their young with them just as primates do.[13] Megabats have a recognizable menstrual cycle, which is a feature common to primates, and extraordinarily uncommon in the vast majority of all other animal species. Defecation also provides clues: fruit bats reverse position, dangling upright by their hooked 'thumbs' (as does the colugo, a gliding mammal from Southeast Asia, to which Pettigrew believed that fruit bats were connected). In contrast, microbats defecate while dangling upside down, and simply arch their backs to avoid soiling their fur.[14] But the key piece of evidence that started Pettigrew on his voyage of discovery in the first place is that megabats' eyes, as well as the wiring of their optic nerves, conform to the primate model and are totally different to those of microbats.[15]

Pettigrew's hypothesis was always speculative, and he himself said, perhaps in honour of his frugivorous subjects, that even if proven wrong, it would remain a 'most fruitful, wrong hypothesis'.[16] DNA experiments ultimately appeared to disprove Pettigrew's hypothesis, but led to the new 'yin-yang' system of classification. The current consensus is that bats *are* monophyletic, that is, descended from a common ancestor, and that megabats evolved from microbats, although gaps in the fossil record have had some scientists argue that the reverse might be the case. In a rather fruity train of thought, Glover Morrill Allen, an American zoologist working in the early twentieth century, pondered whether vampire bats might first have been fruit-juice drinkers who later learned to puncture the skins of animals 'to secure their juices'.[17] The prevailing scientific thinking, however, suggests that fruit-eating megabats were indeed descended from echolocating, insect-eating microbats. Not only have megabats lost the ability to echolocate, but they have lost the very anatomy required to do so.[18] It may be

that echolocation limits the size of bats, since calls are coupled to respiratory and wingbeat cycles. As bats get bigger and wingbeat frequency drops, call emission frequency also falls, and this would reduce the rate of information reception, making it a less viable option for larger bats, although *Vampyrum spectrum*, with a wingspan of nearly 1 metre, manages to echolocate despite its large size.[19]

Whatever the scientific truth, Pettigrew's opinion that 'some bats are much less like mice or birds than they are like people' allows for a charmingly empathetic engagement with a group of animals that have hitherto been thought of as bestial, devilish and 'other'.[20] Pettigrew even included something he called the 'fallen angel' hypothesis in his theory of convergent evolution, 'for poetic and logical completeness only', in which winged primates evolve first, but later some branches of the family lose their airborne appendages.[21] Taking this hypothesis to its 'poetic and logical' extreme would make us humans a kind of 'flightless bat'.

Genetic relationships between humans and bats may sound far-fetched, but in parts of Australia and Papua New Guinea kinship between these two groups is revered in myths and song cycles. Even the great eighteenth-century taxonomist Carl von Linnaeus placed bats close to humans in his first attempt at an evolutionary

'Spectre Bat', now known as the spectral bat or *Vampyrum spectrum*, in J. Johnson's *The Natural History of Quadrupeds (after Linnaeus)* (1801). The mammal's mammaries are rather prominent, following Linnaeus's coinage of the class of Mammalia after the Latin word for breast.

Ectophylla alba, Honduran white bats, making their home in a leaf tent in Costa Rica. The bats have cut the midribs of the leaf to form a tent.

classification system, noting that only primates, elephants and bats possess a single pair of nipples for suckling their young.[22] Linnaeus coined the name of the entire class of mammalia from the Latin word for 'breast', since mammals are all suckled on their mothers' milk. It was Linnaeus' focus on the breasts of mammals (rather than his later categorization by teeth) which had us briefly occupy the same taxonomic category as the bat. As one author put it, Linnaeus had been 'led astray by the location of the mammae', as many good men have been, before and since.[23]

To be fair, however, it is bats' differences from us, and from each other, that make them such a fascinating subject. There are tiny, furry white bats, with yellow ears and noses, that curl up in fluffy balls in 'tents' they fashion from folded leaves in the tropical forests of Honduras and Costa Rica. *Kerivoula picta*, the painted bat, is apricot buff with orange and black wings in a fetching zig-zag known as 'cryptic' patterning, so the creature can pass as a withered leaf as it hangs quietly in Asian woodlands. In 1896 the appropriately named Major S. S. Flower reported from Thailand (then Siam) that he had found a specimen of this beautiful bat

curled up in a calla lily.[24] Henry David Thoreau wrote of finding a tiny red bat hanging asleep among some ferns, and compared its rusty brown fur to the cinnamon-coloured 'wool' of the fern, as well as the 'plush of a ripe cat-tail head'.[25] The butterfly bat of Cameroon has delicately veined wings that resemble a skeletonized leaf. The spotted bat sports a black back with three white circles making a kind of face, less a death's head than a 'surprise' emoticon. This bat roosts in the Grand Canyon, and has the longest ears of any bat for its body size. The African yellow-winged bat possesses, as you might have guessed, yellow wings, as well as silvery-white fur and dramatic ears which look as if two enormous gold-plated cockroaches have burrowed into the bat's brow. Together with its sharp, triangular nose, this bat looks every bit an emissary from outer space.

The giant golden-crowned flying fox of the Philippines is one of the largest of the megabats, reaching a wingspan of almost 180 cm, and weighing over a kilogram. These beautiful endangered creatures are hunted both for meat and for their pelts. At the other end of the scale, the lesser bamboo bat, found in South and Southeast Asia, is so diminutive that it can hide inside the hollow stems of bamboo, using tiny adhesive pads to grip the smooth interior surface. Another tiny sucker-footed bat called *Myzopoda* is found only in Madagascar; with a wise face and extravagant, upswept ears, it resembles a little brown Yoda (although the prize for looking most like Yoda, which is fiercely contested in the bat kingdom, might rather be bestowed upon the nyctimene tube-nosed fruit bat of Papua New Guinea). The smallest chiropteran of all is Kitti's hog-nosed bat of Thailand, the so-called bumblebee bat, which weighs just 2 grams. Arguably the smallest mammal on the planet, this bat is sadly vulnerable owing to habitat loss.

A list of types of bat is a veritable cascade of evolutionary variety: there are bats whose names suggest they have noses shaped like leaves, swords, horseshoes, tridents and spears. There are not

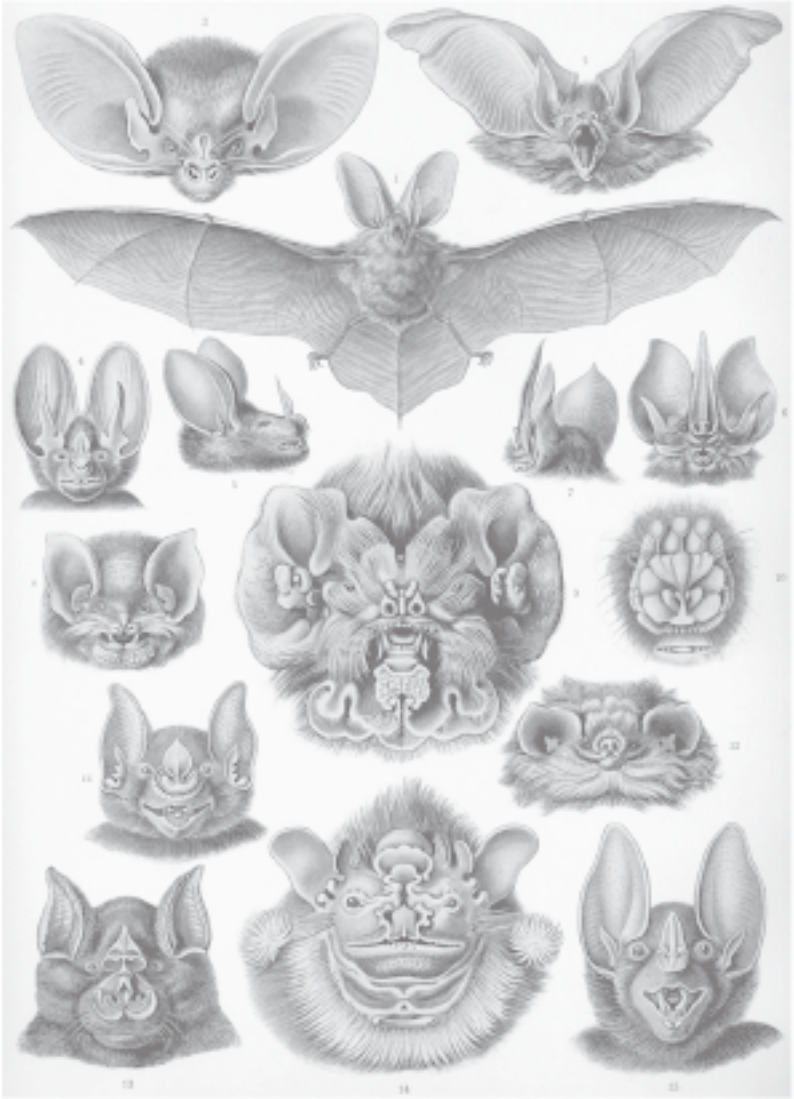
The smallest bat of all and possibly the world's smallest mammal, *Craseonycteris thonglongyai* or Kitti's hog-nosed bat.

just leaf-*nosed* bats, but leaf-*lipped* bats and leaf-*chinned* bats too; there are pallid bats, and African slit-faced bats (both of which feed on scorpions); there are well-dressed moustachioed bats and epauletted bats, and less appropriately attired naked-backed bats. There are spectral bats, ghost-faced bats and smoky bats. There are long-tongued, long-nosed and long-legged bats. There are not just flying foxes but bulldog bats and mastiff bats (although it is the wrinkle-faced bat who looks most like a squashed-nose pug). There are mouse-tailed bats, frog-eating bats, big-eared bats and little big-eared bats. There are woolly false vampire bats who, as their name suggests, don't actually feed on blood, and there are hairy-legged vampire bats who do. Perhaps the most effusive ode to the dazzling diversity of bats has been written by

the author and naturalist Diane Ackerman, who lists a veritable 'carnival of bats' in her essay 'In Praise of Bats'. She notes that the tube-nosed fruit bats' elongated nostrils look 'like party favours' and the funnel-eared bat resembles 'a golden Pekingese', while the Brazilian free-tailed bat possesses a face 'as wrinkled as a wise old extraterrestrial's might be'.[26]

There are bats that eat fish and hunt on the wing, sometimes skimming the surface of the water, and sometimes using their wings as oars as they submerge all but their heads. In New Zealand, bats are the only native land mammal and, having gone to all the evolutionary trouble of growing wings, they spend most of their time rummaging on the forest floor, using their elbows as legs. So unique and specialized is *Mystacina tuberculata* that it possesses its own personalized species of blind, wingless bat-fly, which feeds on the fungi that grow on the bat's guano (all other species of bat-fly are parasitic, feeding on their hosts' blood).[27] The New Zealand short-tail bat's closest living relative is actually the fisherman bat of South America, an example of the separation of related families in the break-up of the Gondwanaland supercontinent in the late Cretaceous era.[28] Through the fish-eaters, the insectivorous New Zealand short-tail is a distant cousin of the only other ground-crawling bat in the world: the fearsome vampire, which creeps up on its unsuspecting prey, and can also jump several times its own length by pushing downwards with its folded wings and hind feet.[29]

The vast majority of bats, however, are insect eaters, and some species are so adept that they can catch over a thousand mosquitoes or other undesirable insects in an hour. Insectivorous bats are usually classified as either 'gleaners' that echolocate softly in order to pluck their prey from foliage, or 'aerial-hawkers' whose much louder calls enable them to catch insects on the wing – otherwise differentiated as 'whisperers' and 'screamers'.[30]



Fruit-eating bats prove to be just as pivotal to healthy ecosystems as insect-eating bats, since they pollinate and disperse the seeds of beneficial plant species. The fragrant white flowers of Arizona's iconic organ pipe and saguaro cacti are sturdy enough to bear the weight of the bats who nose-dive the blooms by night, to emerge ghost-faced, as if dusted with icing sugar. Without bats to pollinate them, these cacti could become extinct. Many tropical fruits, such as mangoes, bananas and guavas, rely on bats for either pollination or seed dispersal in the wild, as does that notoriously odoriferous delicacy, the durian. Ackerman's sensuous description of bats among moonlit flowers imagines them as libidinous creatures, 'garish and available as prostitutes leaning against a streetlamp'. The co-evolved flowers have 'seductive, trumpetlike mouths' while the pollinating bat possesses a 'long, nectar-loving tongue'.[31] Indeed, the tube-lipped nectar bat of Ecuador has a tongue which, at 8.5 cm in length, is one and a half times longer than its entire body.

Bats' successful adaptations as hunters and foragers rely on one important factor – flight – and because they are nocturnal, they fulfil specific ecological niches that diurnal birds cannot. For example, rainforest birds avoid flying in open areas to avoid hawk attacks, whereas tropical fruit-eating bats cross great distances at night, passing seeds as they go. This makes bats the most valuable asset in terms of reforestation of cleared areas throughout the world's tropics.[32]

Pteropus mariannus, Mariana flying fox, pollinating a coral tree in Guam.

With scientific understatement, the University of Leeds professor of animal ecology and dedicated bat champion John Altringham notes that 'Flying is not easy.'[33] Leonardo da Vinci, the Wright Brothers and Harry Potter would surely agree. But bats have been perfecting this, their most striking superpower, for millions of years. A distinction is made between 'true' flight and gliding, since several species of mammal have the ability to glide among tree tops thanks to a membrane between their front and back limbs. These animals cannot, however, take off from the ground, maintain altitude or stay aloft for more than a few moments, compared with the ten to twelve hours of non-stop flight which has been observed in Brazilian free-tailed bats,[34]

along with prodigiously rapid wingbeats, up to twenty per second in some species.[35] Bats can migrate over distances of at least 800–1,000 km to ensure access to food sources over changing seasons.

In spite of these extraordinary feats, the Comte de Buffon, who didn't like bats' faces and didn't think much of their flying skills either, wrote: 'Their motion in the air is rather a desultory fluttering, than flying, which they execute very aukwardly.'[36] What he interpreted as erratic movement is more likely to have been the exceptionally accurate aerial acrobatics of bats hunting insects on the wing. Not only do bats possess true powered flight, but they can fly at incredible speeds through dense thickets of trees, turning tight corners again and again.[37] Donald Griffin, who discovered echolocation in bats around the time of the Second World War, wrote that the dexterity of the smaller bats, if scaled up to the dimensions of an airplane, 'would terrify even the hottest pilot'.[38] Indeed, the famous 'trench run' sequence of the original 1977 *Star Wars* film (the Rebel X-wings' attempt to detonate the Death Star while being pursued by the Empire's TIE fighters) would be a breeze for your average microbat. Unsurprisingly, in this space-age epic, it is the baddies' aircrafts – the TIE fighters – that most resemble the silhouette of a bat in flight: the advanced models are even called 'bent-wing' just like a species of bat. And who is Darth Vader, with his black cloak and bat-like face, if not a space-age Dracula?

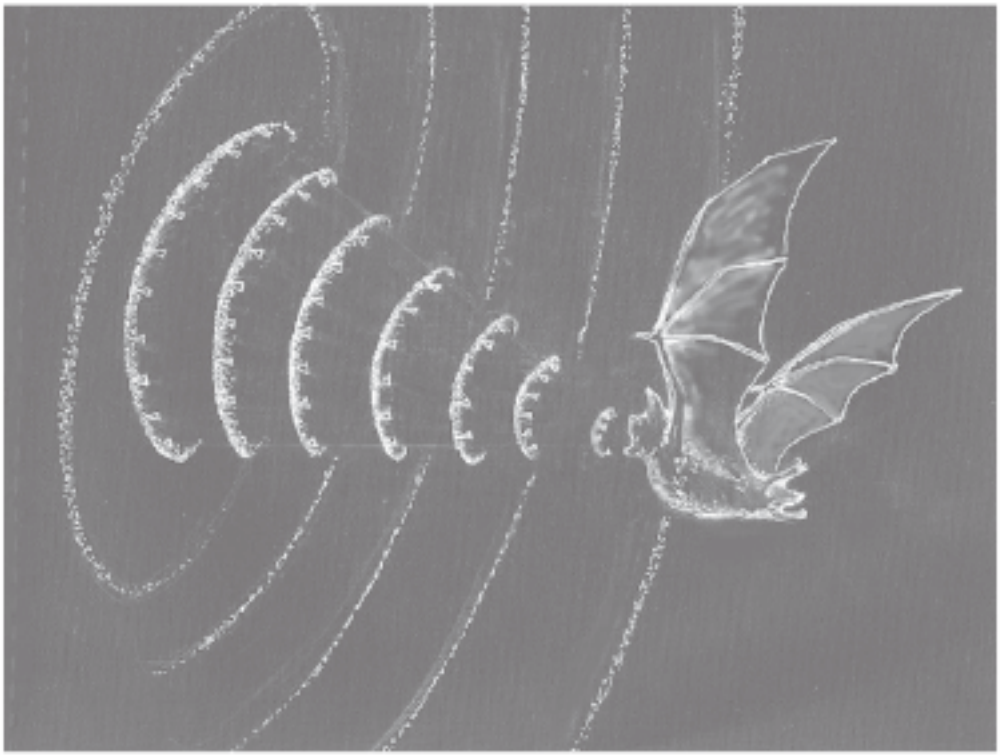
Bats offer a different model for aerodynamics because, unlike birds, they can move their wings independently and, by folding one wing, can make rapid turns.[39] Current research involves careful analysis of bat flight in order to envisage high-tech small

aircraft for the future.[40] Over five hundred years ago, Leonardo da Vinci drew countless sketches for potential flying machines which featured bat-like, rather than bird-like, wings, in which spokes or 'fingers' within the wings would allow for greater control of wing shape and thus more manoeuvrability. He recommended that flying machines imitate bats, with their flexible, super-light bones and highly elastic wings, writing in his notebook: 'Dissect the bat, and concentrate on this, and on this model arrange the machine.'[41] More than four hundred years later, in 1890, a French inventor named Clément Ader claimed he achieved manned, powered flight, albeit unsustained and uncontrolled, for 50 m, in an aircraft that looked like a large, ungainly bat.[42] This steam-powered bat-plane was criticized for its bewildering complexity of wing-movements, which 'no mortal pilot could have survived more than a few seconds.'[43] Ader's insistence on perfecting his ungainly bat-like craft long after viable aeroplanes took to the skies branded him a romantic out of tune with progressive thinking, but recent research trends may yet prove that he and Leonardo were right after all.

Clément Ader's bat-like *Avion III*, 1897, aloft in the Musée des Arts et Métiers in Paris.

Bats' wing membranes are comprised of two layers of skin sandwiching a thin layer of connective tissue and muscle fibres.[44] Like human skin, this membrane is self-repairing, so bats with wings shredded by cats or barbed-wire fences can be nursed back to health and released back into the wild. Even when at rest, bats' wings are marvels of design. Donald Griffin, who wrote *Listening in the Dark* about his discovery of echolocation in bats, observed that when folded, wings do not form large flaps like curtains, but that in fact the wing's surface turns itself into countless tiny crescent-shaped pockets which, rather fetchingly, 'fold individually like the petals of a flower'.[45]

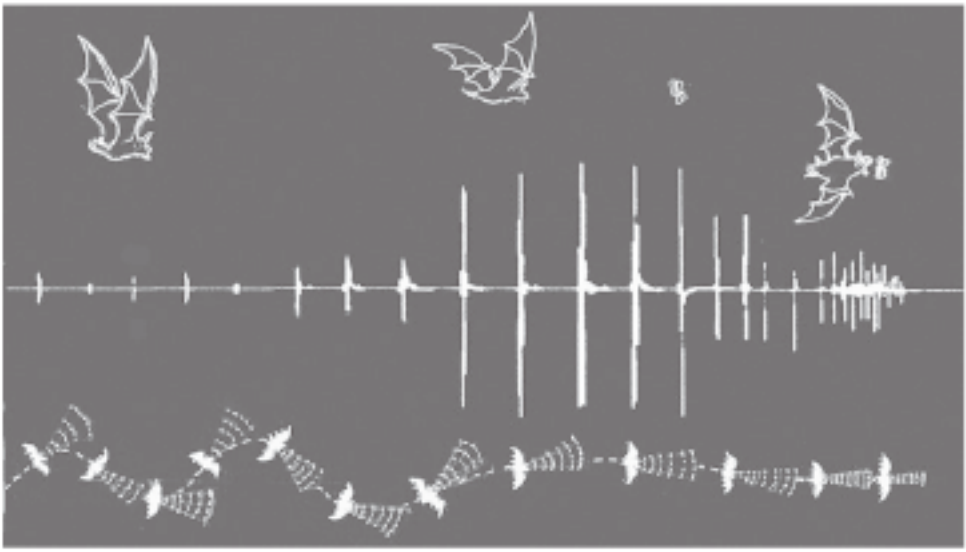
Another stunning bat superpower is echolocation, a complex navigation system made from the sound waves bats produce with



Depiction of echolocation or bat 'sonar' by Simon Crowhurst from the Department of Earth Sciences at the University of Cambridge.

their vocal chords in the same way we speak, only at a much higher frequency.[46] These sound waves can vary in duration from 0.3 to 300 milliseconds, and are produced up to two hundred times per second and in frequencies ranging from 8 to 210 kiloherz.[47] The bat interprets the returning echoes of these sound waves in order to build up a picture of its environment. Bats are not the only animals to use echolocation – cetaceans and cave-nesting birds do too – but some species of bat have developed echolocation to an exceptional degree of sophistication. The ancestors of bats, like some mammalian insectivores today, probably emitted ultrasonic sounds and might have possessed a simple form of echolocation. It is generally assumed that bats evolved from a small nocturnal and arboreal mammal approximately 65 million years ago, although this 'proto-bat' has yet to be identified in the fossil record. The oldest fossils of true bats have been found in Wyoming and are around 50 million years old. One of these fossils, *Icaronycteris index*, is much like a modern insectivorous bat: an enlarged cochlea (a spiral-shaped cavity in the inner ear) shows that it possessed the ability to echolocate. Another fossil of the same age, however, *Onychonycteris finneyi*, is a more primitive bat, still possessing claws at the end of each of its shorter finger bones. This bat didn't have an enlarged cochlea, so was probably not an echolocator. The temporal coexistence of these two very different specimens poses interesting questions about the sequence of events in the evolution of bats.

Echolocation would have become increasingly complex as bats became more agile flyers and entered into a co-evolutionary arms race with their prey. Insects developed their own ability to hear bats' echolocation calls, and so both hunter and hunted evolved ways to outmanoeuvre the other. Some competitive species of bat even evolved 'jamming' calls, not to confuse prey but to outfox batty brethren who became rivals at dinnertime. When these calls



This drawing demonstrates the flight path of a common pipistrelle bat (*Pipistrellus pipistrellus*) as it hunts a moth using echolocation, with changes in pitch and frequency as the bat homes in on its prey.

are translated into scientific imaging apparatus, they look very different from the ordered strokes on the oscilloscope which normal echolocation creates. Instead they resemble loops of telephone wire and sound something like sirens.[48] To avoid deafening themselves with their own calls, bats have specially insulated cochleas, and some species even have the ability to switch a kind of 'deafness' on and off at the same speed as their pulsing calls.[49] There are species able to shut out other bats' calls via a 'neural gate' which acts as a filter, while others possess their own personal call frequency.[50]

Like their flight techniques, bats developed their acoustic location technologies millions of years before *Homo sapiens*. An early form of human sonar was trialled in 1906 in order to map space underwater and thus detect icebergs, although clearly its application was not widespread: the *Titanic* disaster occurred in 1912. During the First World War, sonar technology was developed in order to detect enemy submarines; today we can map a

Icaronycteris index, an echolocating bat that lived approximately 52 million years ago. This fossil was found in the Rocky Mountain region of the United States.

human foetus in the womb. Radar, which bounces radiowaves off objects in order to determine everything from aircraft positions to meteorology (and has even been used to track the positions of bats themselves), was conceived and developed by a range of scientists and engineers working internationally and finally patented in Britain in 1935 as a system for air defence. Neither radar nor sonar, however, was inspired by bat physiology, since Donald Griffin did not confirm echolocation in bats until 1938.

Griffin's studies represented a major breakthrough, as bats' uncanny ability to navigate in the dark had perplexed scientists for centuries. The popular misnomer 'blind as a bat' probably came about because observers such as the Comte de Buffon interpreted bat flight as erratic, but only five years after Buffon's death, in 1793, the Italian biologist and Catholic priest Lazzaro Spallanzani made a startling discovery about bats' navigational skills. Unfortunately, he killed hundreds of bats in the course of his experiments, which included blinding the poor creatures with hot needles and seeing if they could still fly. They could, and this drove Spallanzani crazy as he tried to figure out what, if anything, would 'blind' the bats, including filling their mouths and ears with glue. These tests were inconclusive, while Spallanzani's contemporary Louis Jurine of Geneva achieved better success by plugging his bats' ears with dense starch. Only then did the bats exhibit signs of 'blindness'.[51] At the time, neither scientist was able to interpret these sensory data, and for more than a century their experiments were forgotten.

In 1908 the American zoologist W. L. Hahn also discovered that tightly plugging the ears of bats caused total disorientation, and concluded that 'obstacles are perceived chiefly through sense organs in the inner ear.'[52] While his hunch was correct, neither Hahn nor any other scientist of the early twentieth century could hear the bats making noises, and so the idea of echolocation was

slow to emerge. Allen, who wrote a compendium on bat biology in 1939, was aware that bats were detecting echoes reflected from objects and moving insects, but had no idea that the bats themselves were emitting high-frequency sound waves.[53] Ironically, as Allen was writing his book, Harvard undergraduate Donald Griffin had just discovered that bats produce sounds above the range of human hearing.[54] Scientists initially advanced the theory that bats might be emitting low-frequency sounds, later revising this idea to the more plausible high-frequency range. It was not until the Second World War that a sufficiently sophisticated apparatus was developed to detect sound waves above the frequency range of human hearing. Confirmation ensued: bats were indeed emitting a constant stream of sounds. Initially, it was thought that echolocation was used only to navigate, and it took some years to realize that it served a dual function as a hunting tool.

While humans require external hardware – machines that go *ping* – to map space with ultrasonic frequencies, bats do it all via intricate internal sensory systems, including their enlarged cochlea, and in many cases, an external tragus, a cartilaginous projection at the base of the ear which operates as a kind of receiver. Those bats that have developed noseleaves echolocate through their noses rather than their mouths. The leafy protuberance serves as an acoustic lens which focuses the nasally emitted echolocation pulses, allowing the bat to simultaneously eat or drink.[55] Calls are usually synched to wingbeats, increasing in speed as bats home in on prey, with different sizes of insects requiring different frequencies. Some bats even use harmonics, like Tibetan throat singers, creating sympathetic vibrations that increase the complexity of information the bat receives, turning hunting into a high art form.[56]

Echolocation isn't only used for guidance or catching insects. Some bats echolocate to recognize the unique petal shapes of

specific nectar-bearing flowers.[57] The neotropical vine *Mucuna holtonii*, which has co-evolved with echolocating bats, has a concave petal which stands erect and acts as an acoustic mirror for reflecting a bat's calls.[58] And while bats are definitively not blind, different species possess different capabilities when it comes to visual range. All bats have well-developed rod photoreceptors for night vision, and, while it was previously assumed that bats had no cone photoreceptors (those needed for daylight and colour vision) at all, many bat species show one or two types of cones (humans possess three), thus the range of vision of Chiroptera is broader than once thought.[59] Bats that hunt for night-blooming flowers are sensitive to the ultraviolet spectrum, which humans can't see at all. Even those bats that don't see colour are finely tuned to spectral changes in the echoes bouncing off moving targets. Biologist John Altringham describes the way bats might perceive such phenomena metaphorically, as 'a change in the colour composition', emphasizing the complexity and artistry of bat senses.[60]

Herein lies a paradox for bat fanciers. One of bats' key attractions is their air of mystery, as they dart, black-clad and ninja-like, in and out of the shadows. And yet, the bats themselves live in a world of constant commotion. Naturalist, illustrator and author Russell Peterson called his charming and witty 1964 handbook of bats *Silently, by Night*, but he admitted in his preface that the title was erroneous, because 'bats are actually shouting their heads off'.[61] Diane Ackerman finds this an eerie thought as she stands in a 'seemingly silent' bat-filled grove, nevertheless pondering that bats 'spend their whole lives yelling at the world and each other. They yell at their loved ones, they yell at their enemies, they yell at their dinner, they yell at the big bustling world. Some yell fast, some slow, some loud, some soft.'[62] In *The Blind Watchmaker*, Richard Dawkins considers our inability to hear bats'

The tiny Hardwicke's woolly bat, *Kerivoula hardwickii*, can be found roosting in pitcher plants in Borneo. In this co-evolutionary arrangement, the plant offers the bat shelter while it feeds on nitrogen from the bat's droppings. The bat gets a handy bedside commode, but must be sure to stay above the pitcher's digestive juices.

calls fortunate, as they would be deafeningly loud and impossible to sleep through.[63] Every bat has its own unique signature call, but if humans want to be privy to this vocalizing, they have to resort to 'bat detectors', which reduce the frequencies of bat calls so that they are within the audible range for humans. Translating the very noisy worlds of supposedly stealthy creatures for human ears, bat detectors emit sounds something like those of a Geiger counter or, in moments of batty excitement, a string of firecrackers exploding.

Surprisingly for these fast-moving, fast-talking animals, bats are the slowest-reproducing mammals in the world for their body size. Relatively speaking, they have a slow development to sexual maturity and long pregnancies, with most species producing only

one young annually, although occasionally twins, and even quadruplets, occur. Unfortunately for mother bats, young can range from 25 to 30 per cent of the mother's body weight.[64] The slow breeding of bats is compensated for by their long lifespans: they are the longest-lived mammals for their size, frequently achieving ages of between twenty and thirty years, while the lifespan of the Brandt's myotis, a common vesper bat of Europe and Asia, can exceed forty years.[65]

Because of the wide diversity in bat species, there are all kinds of approaches to mating and reproduction. There are bats that are all-out promiscuous, bats that are monogamous and bats that are polygynous, having more than one 'wife' at a time. Cory Toth, a researcher of *Mystacina tuberculata*, New Zealand's lesser short-tailed bat, claimed to have witnessed a batty 'threesome' but was too much of a gentleman to divulge the details.[66] He did note, however, that the short-tailed bats have a 'lekking' system, where males perform to attract passing females by singing and wearing 'aftershave' made of their own urine. Some males sing their hearts out, with no luck. The more successful singers have bigger bodies, and therefore deeper voices; they are the Barry Whites of the *Mystacina* world.[67] The only other bat species known to use a lekking system is Africa's hammer-headed fruit bat: bulbous-nosed males generate spectacular hoots with their huge larynxes to attract passing females.[68] In contrast to such macho displays, the male *Myotis grisescens* or 'gray bat' of the

southeastern United States has been known to occasionally forego sex for babysitting.[69]

A few years ago, bats made the headlines for being one of the only species apart from humans to perform oral sex. Researchers in China had observed female fruit bats licking their partners' penises during the act of coupling in order to prolong the act, whether for pleasure or in order to increase the chances of pregnancy, we can only guess. The paper 'Fellatio by Fruit Bats Prolongs Copulation Time' caused much hilarity in the media, and even sparked a sexual harassment scandal in an Irish university when a male academic suggested to a female colleague that they discuss the paper's findings.[70] More recently, Indian researchers have noted that it's not just boy bats that have all the fun, publishing a paper titled 'Cunnilingus Apparently Increases Duration of Copulation in the Indian Flying Fox, *Pteropus giganteus*'.[71]

Mating and reproducing might be a saucy affair in warmer climates, but for temperate bats, hibernation poses serious problems, as during winter pregnancies cannot grow, and nor can sperm be produced. For this reason, reproductive cycles are split over two seasons. What is known as 'spermatogenesis' takes place in spring and summer, and mating follows in autumn (it may even continue during hibernation, when there's not much else to do). Although no new sperm is being produced during this time, there is enough stored sperm to mean that male bats can keep at it, even in winter. The foetus will not grow in the hibernating female, however, so some bat species have developed sperm storage in the female; fertilization takes place as soon as ovulation occurs in the spring. Other bat species have it figured out differently – fertilization occurs after mating in autumn and the fertilized egg develops into what is known as a blastocyst, a pre-embryonic structure, held in the uterus through hibernation, which can start growing again in the spring.[72] In some species, if energy needs

cannot be met during pregnancy, a mother may actually reabsorb her embryo.[73] But perhaps the strangest of all the stories about bats and reproduction are the reports that, among a certain species of Malaysian fruit bat, males can lactate as well as females. Aside from freak mutations, this happens nowhere else in the mammalian world.

As already noted, bats subsist on a huge variety of food types. Most species are exclusively insectivorous, but others eat fruit, flowers, nectar, pollen, leaves, amphibians, fish, smaller bats and other small mammals. Some are very specific in their diet: for example, the Carolliinae family show a preference for the fruit of the pepper (*Piperaceae*) family, which they eat 'corn-on-the-cob' style. These bats can defecate more than 3,000 seeds a night,[74] a fantastic service to rainforest regeneration, particularly given that seeds that have passed through a bat's digestive tract are far more likely to germinate. Others bats are more catholic in their taste: Allen noted of a leaf-nosed bat he kept in captivity over a six-month period that it ate 25 house mice, thirteen bats and three birds, 'as well as a considerable ration of banana'.[75] According to Allen, South America is a hotbed of banana-crazy Chiroptera: ripening bananas are attacked by 'hordes of hungry bats' who will even squeeze through crevices in mud huts to get at the fruit.[76]

Of all 1,331 species of bats, however, it is the three who dine solely on the blood of other animals that people find most fascinating. They are *Desmodus*, *Diphylla* and *Diaemus*: the vampires. Especially sensitive to breathing noises, vampire bats also have heat sensors in their noses for locating capillary-rich areas of skin, and enlarged, sharp-edged canines and incisors that lack enamel, to enable self-sharpening.[77] These are the bats' precision tools for clipping the fur of their intended victims and painlessly opening a shallow wound. Anticoagulant in the bats' saliva prevents the blood clotting and a grooved tongue helps

Carollia perspicillata, Seba's short-tailed bat, happily feeding on a banana.

to convey blood rapidly into the mouth.[78] This anticoagulant has been named Draculin and is being studied in relation to human blood thinning for stroke and heart attack victims. Success in this field might go some way to ameliorating the routinely bad press these bats attract.

Vampire bats are frequently portrayed as nature's villains, although unlike carnivores, they rarely kill the animals whose blood they steal. It is important to remember that vampire bats are small – only around 9 cm long – and they take just a tablespoon of blood per night, not enough to seriously harm cattle.[79] They behave like little more than outsize mosquitoes, yet hyperbolic language is routinely employed when describing vampire bats. They are accused of possessing 'uncanny watchfulness' and

A bat sucking blood from a guinea pig, from Jean Painlevé's film *Le Vampire* (1945).

of 'deliberately' stalking their 'victims'; they 'gouge' and 'attack'; they 'gorge' and 'feast'.[80]

There is no doubting the sinister air of the vampire bat caught by the French scientist and film-maker Jean Painlevé's sensitive if somewhat surreal camera. Painlevé's nine-minute *Le Vampire* (1945) intercuts sequences from F. W. Murnau's 1922 classic *Nosferatu* with footage of a vampire bat bestowing its 'deadly kiss' upon an awake but impassive guinea pig, 'which it slyly approaches like a coquettish Quasimoto'.[81] The film is excruciating as viewers hope the gormless guinea pig will shake off the pint-sized bully, but the vampire feasts on the passive vegetarian, to the unlikely strains of Duke Ellington. Apparently Painlevé saw affinities between the parasitic bat and the 'brown pest' of Nazism which had overrun his native France at the time of filming, comparing the way the postprandial bat extended its wing before going to sleep to a Nazi salute.[82] Critic Ralph Rugoff wrote that Painlevé delighted in presenting his subjects as 'uncanny hybrids that, for all their

foreignness, call to mind things close to home'.[83] Here, Painlevé suspends his usual empathetic sensibility towards traditionally unlovely creatures in order to make a metaphoric statement about the plight of France. Rugoff notes that Painlevé's films operate on an 'alternating rhythm of seduction and repulsion' and the same might be said of the human response to bats in general, not just the notorious vampires.[84]

The details of vampire bats' feeding habits make them difficult to champion: they drink up to 60 per cent of their own body-weight in a meal, and often begin to urinate while they are still feeding, since, with all that extra baggage, a return flight to the roost would be an impossible feat. *Desmodus* achieves flight via the ability to perform a kind of 'super push-up' – creepily, this bat can jump from the ground to a height of 90 cm.[85] An engorged belly during feeding is doubtless the origin of this bat's full name: *Desmodus rotundus*. Unsurprisingly, but disappointingly, this is a detail of vampiric physiology that has been overlooked in vampire fiction; imagine a Dracula who began peeing in the midst of a bloodsucking frenzy, or a *Twilight* in which the vampires were tubby overeaters who frequently soaked their designer jeans. Instead, the vampires in the *Twilight* saga are heroin-chic thin, and have skin that glitters like diamonds in the sunlight. Vampire bats might not have shiny skin, but many insectivorous bats have an almost equally glamorous attribute: sparkly poo, owing to the high percentage of shiny wings and carapaces that they chew and excrete.[86]

Whether sparkly or not, and fertilizing properties aside, going into a bat cave can be 'like going into an ice factory in which an ammonia pipe has burst'.[87] Bats can survive in an atmosphere that would be lethal to humans by lowering their metabolic rates. Carbon dioxide accumulates in the bats' blood and in respiratory mucus, and this neutralizes the ammonia and protects the

lungs.[88] It may not be a glamorous superpower, but it is another extraordinary adaptation. Wherever bats thrive, their diversity continues to amaze. But more often than not, as we shall see in the next chapter, the dazzling differences between bats and us make them unfairly reviled and unnecessarily feared.

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