The frequency of most sonic waves is too high for us

Bats produce echolocation sounds in their larynx, at a frequency ranging from 8-160 kHz depending on the species or genus, though most of these calls are beyond our hearing capacity. These sounds leave the bat's body through the mouth, or through the nose in the case of the horseshoe bats (Rhinolophidae). Horseshoe bats have special folds at their nose which focus the sonic waves. To receive the echo, bats are equipped with highly developed ears and large pinnae, which frequently sport a broad, movable tragus. The vertical position of the object relative to the bat is determined either by means of interference patterns created by the tragus or by independently raising and lowering their pinnae. Bats adapt their echolocation calls to the prey's distance. In order to detect prey at a long distance, they emit long, narrow-band calls of only a few frequencies. For short-distance location, on the other hand, they emit broad-band calls that span many frequencies and last less than 5 milliseconds. These calls allow them to determine the exact location of an object. Such bats are also known as FM (frequency modulated) bats. There are also bats that only produce echolocation calls with constant frequencies. These are classified as CF (constant frequency) bats.

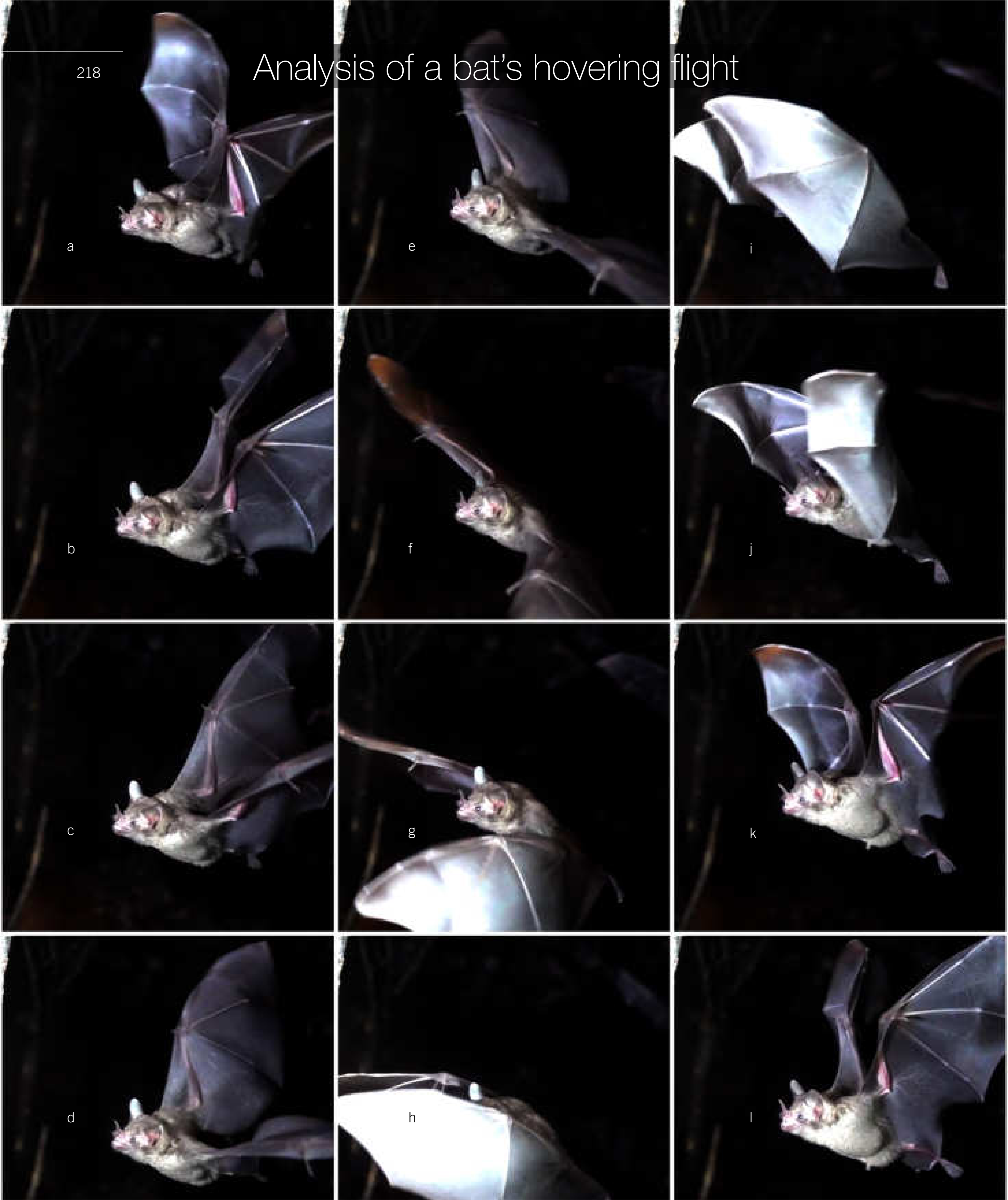
Leaf-nosed bats – from the "vampire" to the fruit eater

The bats pictured on this page belong to the family of leaf-nosed bats (Phyllostomidae), which are only found in the south of the USA and in Central and South America. They are a diverse family of many species, ranging from bats feeding on insects to astonishingly large predators hunting for small mammals, such as the spectral bat *Vampyrum spectrum* with a wing span of 1 m. This species is the largest bat. Only some species of flying foxes endemic to Africa and South Asia, such as the Indian flying fox with a wingspan of almost 170 cm, can grow to become larger than that. In addition to those leaf-nosed bats feeding on insects or small mammals, there are also species that have specialized in hunting fish (*Noctilio*), species that suck blood (*Desmodus*), and species feeding on fruits or the nectar of flowers (Glossophaginae).

Evolutionary adaptation of plants and insects

The precise spatial orientation and object recognition of bats is quite astonishing to us human beings. The family of leaf-nosed bats also includes species that hover in front of flowers while feeding like hummingbirds. They detect their flowers not only by their particular scent but also by using echolocation. For this purpose, some flowers have developed special ultrasound reflectors, which make it easier for bats to detect them. Some insects that are frequently hunted by bats have evolved adaptations that allow them to detect the ultrasonic calls of bats to let themselves drop to the ground quickly and escape their predators. These include many moth species that have developed special tympanal organs acting as "ears" to hear the calls of bats.

Analysis of a bat's hovering flight



Both image series show a complete wingbeat cycle (1/11 second) of a leaf-nosed bat *Carollia perspicillata* flying freely in hovering flight. The images were successively shot from the side (left-hand side) and from the front (right-hand side). The wings beat from the top back to the bottom front, and then move back in a different configuration. The image labels refer to the left-hand series, but to a large extent they can also be applied to the image series to the right. At 120 frames per second, a wingbeat lasts $11/120 \approx 1/11$ s. A small bird hovering in front of a feeding dish reaches a wingbeat frequency that is about twice as high; the wingbeat frequency of small hummingbirds with their robust wings is even five times higher. A bat's delicate flying membrane with its fairly low wing loading makes up for the low wingbeat frequency by having a large surface.

From the upper reversal point into the downstroke

Images a and b show the beginning of the upper reversal phase, and image l shows the end. The wing is here brought into a downstroke position, namely in a way that enables the wing to generate good lift forces right from the beginning of the downstroke. The downstroke is captured by images c to h. The upstroke begins with image i and ends approximately with image l. That is, the upstroke is slightly shorter than the downstroke. Moreover, the movement of the wings on the upstroke clearly differs from their movement on the downstroke.

The downstroke is easy to understand

As one would expect, the airflow during the downstroke works against the morphological underside of the wing. Pressure that is exerted on the wing from below causes the membranes between the fingers to bulge, first only slightly, but soon to their full extension, and in this configuration, the wings nearly hit each other at the bottom front – but only nearly so, they do not actually touch each other. The highest lift is produced at the middle of each stroke, when the wings extend vertically from the bat's trunk. They are slightly curved to the top towards the tip, which are most strongly affected by the aerodynamic forces.

The airflow during the upstroke is very different

because it works against the morphological upperside of the wing. The portions of the wings that are closer to the body first move at an angle to the top; the outer segments of the wing increasingly fold against the inner segments. This may look quite strange. At this point, the wing also generates lift due to its angled position. However, the "gear technology" is not as ideal as during the downstroke. This possibly explains why at some point during the upstroke, the wing relies on its tip for enhanced lift generation.

"Like a cracking whip"

The outer third of the wing, which is dragged behind relative to the remaining portion of the wing, provides enhanced lift generation. If it is positioned at an angle, it can move very quickly and since lift increases to the square of flow velocity, this configuration is very effective. It calls to mind the role of the distal portion of a bird's wing with its spread-out cascade of free primary feathers, which are struck by the airflow at an angle. This can clearly be seen when observing seagulls in slow flight (see page 56f.). They also exhibit this "whip-like unwinding." Evolution has thus produced a mechanism that seems universally applicable.

M. Prigg **Watch a fruit bat fly and a hummingbird hover: Hypnotic animations reveal exactly how different animals take to the skies**
http://www.dailymail.co.uk/sciencetech/article-2776970 (2016)

Not only at night

Flying foxes have good eyes

Flying foxes are mostly active at twilight, but they usually start their flights in search for food when there is still daylight. As opposed to purely nocturnal bats, they have large eyes, with which they orient themselves visually.

Protection against the rain

Above: Short-nosed Indian fruit bats from South-East Asia *Cynopterus sphinx*, which only reach a size of about 10 cm, typically gather into small groups for sleeping. By biting the midribs of leaves and thus causing them to collapse, they form enclosed tent-like spaces under which they can roost shelteredagainst the rain.

Living in large groups

Below: Large flying foxes (pictured here a species from the Pteropodini group) are sometimes also called fruit bats or Old World fruit bats. They spend most of the day roosting in groups on high trees, from where they take to flight to search for food.

Indian flying fox (*Pteropus giganteus*)

Very straightforward during mating
In large colonies, males tend to be very straightforward when it comes to selecting a female mating partner and copulation (see image above and 93).

Toe claw with double function
The claws on their toes are adapted for grasping branches the size of a small finger. During flight, the clawed thumbs are spread away rather than folded in. This makes the boundary layer more turbulent and thus easier to detach.

Neuweiler, G. **The Biology of Bats** *Oxford: Oxford University Press (2000)*

Tongue-clicks for echolocation

The only “barely European” flying fox

The Egyptian fruit bat *Rousettus aegyptiacus* is native to Egypt and the Arab peninsula, but it can also be found in Cyprus. With a body length of 15-17cm, it is only of moderate size compared to other flying fox species, but it is still larger than all European bats.

Click sonar similar to that of bats and dolphins

The Egyptian fruit bat has become famous for clicking its tongue inside caves as a form of echolocation. This active technique of echolocation (“click sonar”) emits sonic waves by means of subtle tongue-clicks and then processes the reflected echoes. Comparisons may be drawn to the echolocation of bats and dolphins, but these two animals use their vocal chords instead of their tongues to produce these clicking sounds. This type of spatial orientation can also be observed in blind people.

Right-hand side below: A young bat has accidentally flown to the ground and takes some time now to get back into a hanging position, which allows these animals to take to flight quickly and effortlessly. The photograph clearly shows the flying membrane between its hind legs, which is used for precise navigation during flight.

Richard A. Holland, Dean A. Waters, Jeremy M. V. Rayner **Echolocation signal structure in the Megachiropteran bat Rousettus aegyptiacus Geoffroy** *Journal of Experimental Biology 2004 207: 4361-4369; doi: 10.1242/jeb.01288 (1810)*