The Biology of Bats:
Characteristics, Behavior, Evolution, and Conservation

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Honors Paper

Fundamentals of Biology II

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Introduction

Of the world's 4800 or so species of mammals, almost 1000, or one in five, are bats. Because they are the only mammals capable of true flight, bats are distributed throughout most of the world. However, most people know very little about bats because of their nocturnal lifestyle and often remote homes. Everyone reacts to bats, sometimes with fascination and sometimes with fear – an emotion that has been furthered by the misconceptions in horror movies.

Bats are actually very interesting – they have a complex social life and senses that are beyond our comprehension. They are the only terrestrial mammals that use echolocation to find food. Their evolution is mostly unknown, but every known species has at least one remarkable feature associated with it, and in some cases scientists don't even know the purpose of these unique adaptations.

Bats play an important role in the ecosystem. Every night, insect-eating bats prey on huge numbers of flying insects. Some of these insects are serious pests to crops, animals, buildings, and humans. Bats who eat fruit disperse seeds over wide areas, and nectar feeders pollinate tropical trees and even help in regenerating cleared tropical forests.

The conservation of these animals is a serious issue because protecting them necessitates the protection of both the areas where they roost and where they eat. Migrating species have even more habitats that require a conservation plan. Public education and protection by law is needed to conserve the biodiversity of these important species.

Characteristics and Morphology of Bats – Order Chiroptera

After the rodents, bats are the second largest order of mammals, representing about 20% of all mammalian species (Graham, 2002, p. 8). All living bats are classified in the order Chiroptera, from the Greek words cheir, or "hand," and pteron, or "wing" (Richardson, 2011, p. 6). This order is subdivided into the two main suborders of living bats: the larger-bodied, less specialized and mostly fruit-eating Megachiroptera, and the smaller-bodied, highly specialized Microchiroptera (Tudge, 2006, p. 59).

The suborder Megachiroptera includes the various species of flying foxes, named for their fox-like faces and large eyes (Graham, 2002, p. 5). Some are called blossom bats because they feed on nectar and pollen. Most do not use echolocation, a kind of natural sonar for finding food. Megachiropteran bats are found only in the Old World, from Europe, Africa, and Asia to Australia and the Pacific Islands. There are about 170 species of Megachiroptera (Richardson, 2011, p. 39).

The Microchiroptera are usually insectivorous, using echolocation tofind prey. Microchiropteran bats are a diverse and widely distributed group (Graham, 2002, p. 5). There are about 800 species of these microbats, and they often have strange-looking noses and large ears to help with echolocation (Richardson, 2011, p. 48).

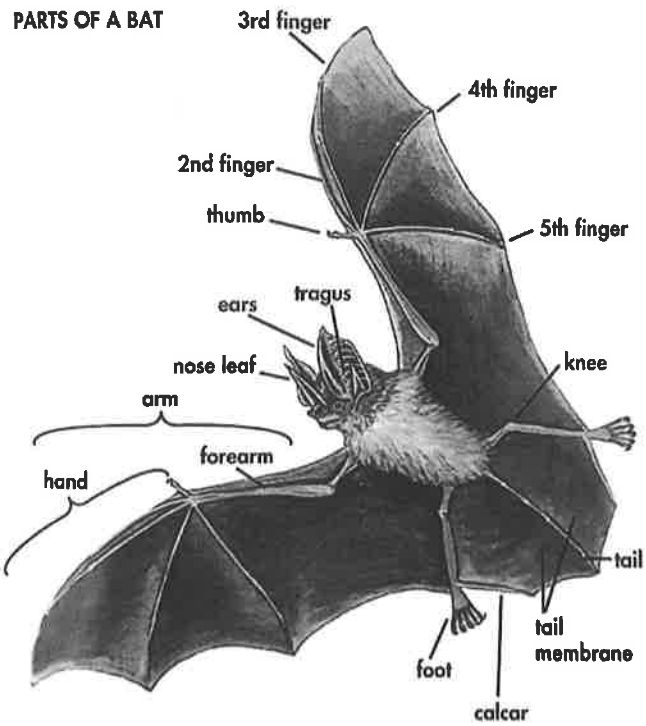

Figure 1. Parts of a Bat (Graham, 2002, p. 15).

Bats are the only mammals capable of true flight, so their wings are their most remarkable feature. The basic requirements for flight include a streamlined body, a method for keeping the body above the ground, or lift, and a means of propulsion through the air, or thrust (Graham, 2002, p. 14). Bat wings must be resistant to bending and be light in weight to keep inertial forces low (Norberg, 1998, p. 93). Both types of bats have wings made of a nearly hairless membrane that stretches from the hind legs and body to the extremely elongated hands and fingers. The thumb is not part of this membrane and has a claw that is used for crawling or hanging. The other four fingers serve as struts that strengthen and control the wing, sort of like the spokes in an umbrella (Shipman, 1999, p. 221). These fingers are clawless, very thin, and about as long as the body itself (Richardson, 2011, p. 11).

Bat muscles and tendons are arranged to give a lot of power to the wings (Norberg, 1998, p. 93). Some of the flight muscles are attached to the sternum, along with additional muscles that run along the back. The muscles run along the body rather than in the wing so that the bats can fly with less energy expenditure (Graham, 2002, p. 15). Numerous blood vessels and nerves run through the wing membrane (Simmons and Conway, 1998).

The hind legs are attached to the patagium, a membrane that runs down the sides of the body from the wings to the feet. The hind legs extend out to the sides of the body to provide the wing with additional control during flight and to allow the bat to roost upside down (Schutt, 1998, p. 157). The hind feet are clawed so that the bat can grasp the sides of trees or cave walls. The knees of the bat bend backwards and outwards – the opposite of human knees – so that the bat can move rapidly on all fours across a cave roof and squeeze into crevices to escape predators. The tail membrane moves downward when flying to help the bat catch food (Richardson, 2011, p. 12). This tail membrane is called the uropatagium, and it is contiguous with the wings. The uropatagium varies in size from species to species, and it helps to increase the total surface of the wing and can act as an air brake during flight (Shipman, 1998, p. 222).

Bats vary greatly in size. The smallest bat, *Craseonycteris thonglongyai*, weighs less than 2 grams and has a wingspan of 12-13 centimeters, while the largest bats of the genus *Pteropus* weigh up to 1.5 kilograms and have a wing span over 2 meters (Simmons and Conway, 1998). Bats are much lighter than non-flying mammals of similar size because their bones are thin and lightweight. Flight requires so much energy that weight is a huge factor in energy use and maneuverability (Richardson, 2011, p. 10). It may appear that bats are poor fliers because of their restricted size and the shape of their wings, but this is not the case. Bats fly continuously under their own power and are capable of diving, twisting, hovering, turning, and flying quickly even in congested areas. The species with sonar have a complex sensory adaptation that makes them even more effective at their type of flight. Most bat species feed while flying, and then they do little else except hang upside down to rest (Shipman, 1999, p. 241).

Microchiropteran bats spend the majority of their time hanging upside down, so they have special vertebrae that allow them to bend their necks backwards. Their heads hang straight down during roosting, and they can even arch their heads back to look around (Richardson, 2011, p. 13). Hanging upside down would normally cause blood to accumulate in the head, but bats have special veins that prevent this from happening (Graham, 2002, p. 27).

Fruit bats have flat molars to help mash fruit pulp, and insect-eating

bats have sharp, spiky edges on their teeth that act like scissors on the hard bodies of insects. Bats that use sonar have very small front teeth to prevent any interference with their echolocation pulses (Richardson, 2011, p. 13).

Bats use echolocation to orient themselves in space and to determine the size, shape, texture, distance, speed, and direction of prey or other food items. Humans cannot hear bats echolocating; any sounds that humans do hear are usually warning calls or mother bats communicating with their young. Bats produce echolocation calls, or pulses, in the larynx by forcing air past very thin vocal membranes. Most species emit sounds though their mouths, but some have a complex nose structure that directs the sound though the nostrils. Only a few Megachiropteran bats echolocate, using tongue clicks instead of vocal cords to produce sound (Graham, 2002, p. 21).

Bats use their large, funnel-shaped ears to receive the echoes of their pulses. Many species have a tragus, or vertical flap, inside each ear that helps to direct the incoming sounds. The bat eardrum is thinner and the cochlea is larger than in most other animals. The cochlea is specialized for frequencies in the ultrasonic range, and generates nerve impulses that are transported to the brain for processing (Graham, 2002, p. 21).

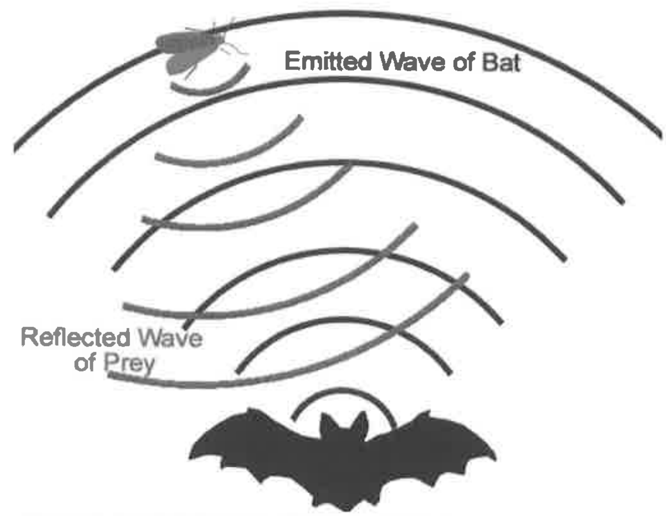

Figure 2. Bat Echolocation ("Humans," 2012).

All bats can see, but their eyes are adapted for seeing in the near dark. For example, Microchiropteran bats see objects only in black and white. These bats use their eyes only to orient themselves in space and to monitor the light level in their environment. Megachiropteran bats use vision rather than echolocation for most of their activities. Their eyes are very large and have a tapetum lucidum, which is a reflective layer under the retina. This layer is typical of most nocturnal mammals and allows more light to reflect and pass over the light-sensitive cells of the retina (Graham, 2002, p. 19).

Ecology and Behavior of Bats

Modern bats are specialized into a variety of ecological niches, which affect each species' morphology and lifestyle. However, bats are much more ecologically streamlined than birds. For example, virtually all bats are nocturnal, and most species are insectivorous. Bats probably specialized in nocturnal flying and insect catching to fill a niche that was not already utilized by birds. When bats began to evolve, birds were already competent daytime fliers that occupied many different niches. During that time period, birds may have fed in the air or perched on trees and shrubs, eating a variety of food sources such as insects or fruit. Other mammals, such as squirrels, already lived in the trees and ate mostly plant foods. This left night flying and insect eating, using echolocation rather than vision, as an evolutionary opportunity for bats. Later, some bats evolved to eat nectar, fruit, fish, rodents, and blood (Shanor, 2011, p. 256)

Bats are nocturnal for two main reasons. The first one, as stated above, is that bats faced competition from diurnal birds, who were already well-established when bats were first evolving. Second, bats probably evolved from a gliding, nocturnal ancestor. Flying at night eliminated the possibility of soaring to save energy, because there are no thermal currents at night. Therefore, bats developed true flight. The increased energy use of flight restricted bats from evolving into a larger size (Shipman, 1999, p. 239). Bat flight is very expensive in terms of energy, and bats have developed highly advanced wing adaptations for the flight patterns, speeds, and maneuvers required for survival in each particular species' niche (Norberg, 1998, p. 105).

Bats usually spend the daylight hours roosting in caves, trees, crevices, or manmade structures such as houses or bridges. Some bats are solitary, while others belong to colonies of over a million bats (Simmons and Conway, 1998). Roosts are important because bats spend over half of their lives roosting. Roosts provide protection from severe weather, temperature, and predators. They also provide sites for resting, hibernating, digesting food, exchanging information, mating, and rearing young. The number and variety of available roosts influences the diversity of bats in that area (Graham, 2002, p. 24).

Hanging upside down as a way of resting is so important that many species of bats have evolved an anatomical mechanism that locks their feet onto the perch. Their claws are highly curved and strongly compressed (Shipman, 1999, p. 192). This allows them to conserve energy while hanging, which is especially important to hibernating species on a tight energy budget (Shipman, 1999, p. 237).

Because they have such high energy needs when they are active, bats are some of the few true hibernators. Their breathing during hibernation is imperceptible, and their heartbeat drops from about 400 to 25 beats per minute. Their body temperature can drop to within a tenth of a degree of the surrounding cave walls, and a few can even survive subzero body temperatures (Tuttle, 2015, p. 9). Hibernating bat colonies cluster at different densities based upon the surrounding temperature. These clusters can vary from 300 bats per square foot in freezing temperatures to 25 per square foot at 50 degrees. They insulate themselves against cold temperatures and expose themselves for cooling in warmer areas. This reduces their metabolic needs and saves energy during hibernation (Tuttle, 2015, p. 32). Bats choose their hibernation roosts based upon the temperature of the surrounding environment, level of moisture in the air, and wind exposure (Graham, 2002, p. 25).

Several species of bat migrate, and they can spend as much energy traveling in the fall as they do during an entire winter of hibernation. Even though most bats migrate less than 200 miles, some species can travel over 2400 miles (Graham, 2002, p. 44). This means that a bat that has migrated south to its hibernation place is already low on energy, and so they need extra energy savings during hibernation. Many species live off of stored energy fats for up to six months a year (Tuttle, 2015, p. 34).

Bats can be found in almost all habitats except extremely hot deserts and the polar regions. Species are more diverse in warmer latitudes because the energy needs are lower; these species may not need to hibernate or migrate to survive. Species diversity also increases in tropical rainforest habitats and in continental areas versus islands (Graham, 2002, p. 8). Each species is restricted in its range because of its niche, depending on a specific food, temperature, and type of roosting site (Richardson, 2011, p. 10).

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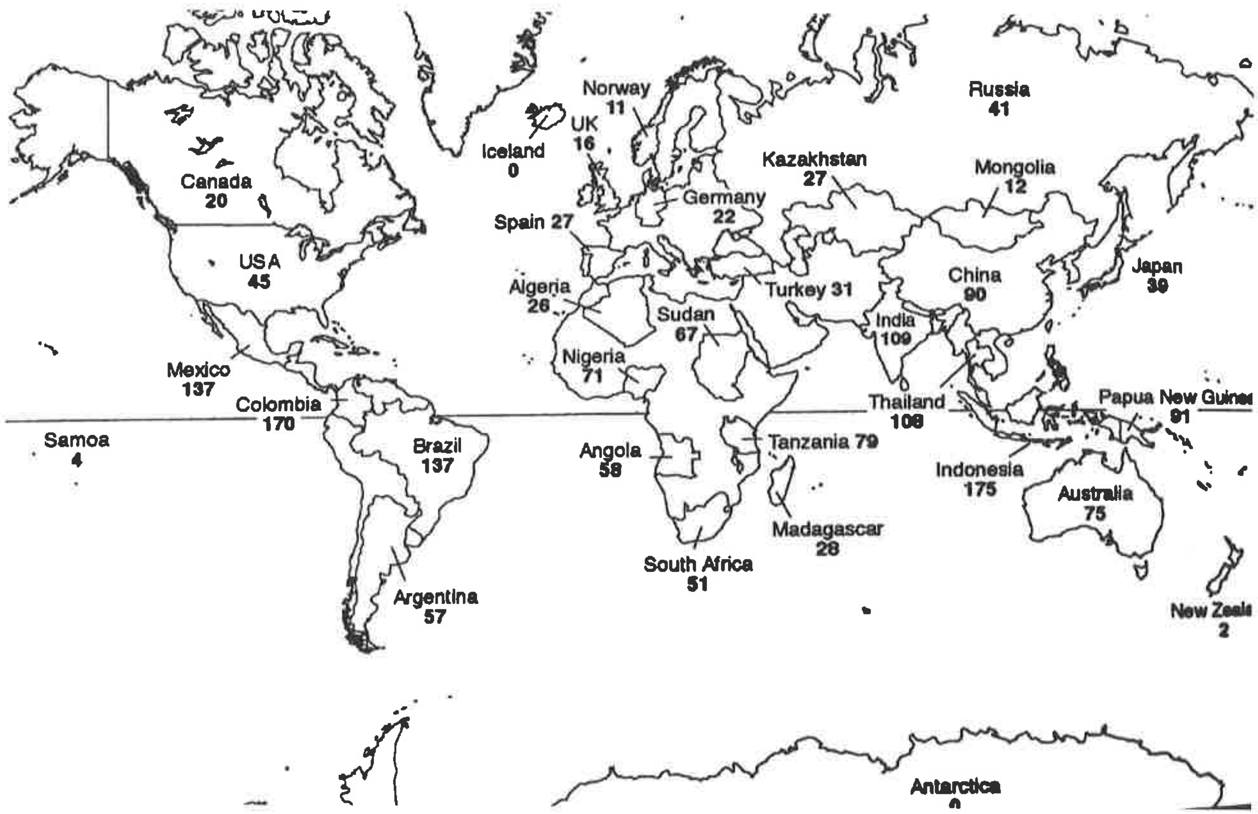

Figure 3. Distribution of Bat Species in Some Countries (Richardson, 2011, p. 10).

Most insectivorous bats rely mainly on echolocation to locate their prey. The design of each species' echolocation calls depends upon its particular foraging requirements – such as the nature of the hunting environment, the size of the prey, the distance between the bat and the prey, and the ability of some prey to detect and avoid the bat (Francis, 1998, p. 169). All microchiropteran bats use echolocation to determine their position in their environment, and many use only echolocation to find their food. This is called active mode, and is especially utilized by bats that catch flying insects. Other bats use their senses of sight, hearing, and smell to detect their food while echolocating in passive mode. Some bats even randomly screen known feeding sites for food in random mode (Schnitzler, 1998, p. 183). Bats can alter their echolocation calls when hunting to increase their chances of success. For example, most insect-eating bats emit sounds at about 10 pulses per second when they are searching for food. Once an item is detected, they increase the rate to 25 to 50 pulses per second. During their final approach, the rate may rise to as high as 200 pulses per second. This delivers extremely precise information about the prey (Graham, 2002, p. 23).

About 70 percent of all bats eat insects as the main component of their diet. Bats capture insects by foraging while in the air, ambushing flying insects from a perch, or picking the insects off of vegetation on the ground. Some bats use their mouths to catch their prey, and others use their wing or tail membrane to trap the prey first. Most species are extremely efficient at catching insects. Because of their energy needs, they normally eat and refill stomachs several times a night. Millions of pounds of insects are eaten by bats each night. Some insects have evolved defenses to this heavy predation, such as "ears" that can hear echolocation calls or sounds that can "jam" the pulses of an approaching bat (Graham, 2002, p. 34).

Some bats eat plant parts, such as fruit, nectar, pollen, and leaves. Bats that consume mostly fruit must eat large amounts to make sure that they meet their protein needs, or they must supplement their diet with insects. Some flying foxes can chew on leaves to extract the protein, spitting out the fibrous residue. Fruit eating bats prefer ripe fruit because they are attracted to the fruit by its smell. Only a few species eat nectar and pollen, and they are very small, delicate bats that behave and look like hummingbirds (Graham, 2002, p. 36-37). Fruit trees can be scattered over a large area, and some bats protect their fruit source by giving out special shouts as warnings to other bats (Richardson, 2011, p. 37).

Carnivorous bats can capture and eat lizards, frogs, birds, rodents, fish, and other bats. Only a few of the larger species are meat eaters, and some also eat insects and fruits. Bats usually bite the head of their prey to kill it quickly. Only six species of bat eat fish. They fly low over quiet water and use echolocation to detect the fish or the ripples created by the fish swimming near the surface. They then drag their flattened talons through the water, grabbing the fish and quickly transferring it to the mouth (Graham, 2002, p. 30-32).

Sanguivory, or blood eating, bats belong to just three species. Common vampire bats feed on mammals, and the other two species feed on birds or mammals. Vampire bats are found only in the New World, from Mexico to the southern tip of South America. Vampires land on their prey and use heat-sensitive pits to locate an area of skin with a large supply of blood near the surface. They then cut a V-shaped cut with their sharp incisors, and it continues to bleed because of an anticoagulant in their saliva. Vampire bats do not suck blood but rather lick blood from the open wound, consuming about 1 ounce of blood each night. They have extra strong wings and thumbs that help them jump into the air before flying away under a heavy load. Cattle and other domestic animals are the most common victims of vampire bats. Humans are sometimes bitten, but human blood is not the preferred food of these bats (Graham, 2002, p. 33).

Courtship varies widely among bats, whose living habits range from solitary to highly gregarious. Many species have elaborate mating rituals. Some male bats keep roosting territories inside the cavities of hollow trees for groups of one to eight females. They attract females with "chirpy" songs and defend their territories by striking other male intruders with their wings. Some male fruit bats attract mates with a song and dance display, attracting females by flashing large patches of white shoulder fur at the females. Still others gather at dusk along a river, with the males spaced about 30 feet apart, singing and flapping their wings. Females fly down the line to inspect the males, hovering several times in front of a mate before landing beside him and copulating (Graham, 2002, p. 38). In some species, a single male can mate with 30 or more females, moving around a roost and mating with unsuspecting, hibernating females (Richardson, 2011, p. 33).

There is a wide variation among bat species in the timing of reproductive events. The most important factor is that the young must be weaned when food is abundant. In temperate zones this is the summer season, so bats only have one reproductive season per year. In tropical zones, bats have longer periods of food availability, so some species give birth twice a year. A few species, such as the vampire bat, have food available throughout the year, so they can give birth in any season (Graham, 2002, p. 40).

Some bats have developed exceptional strategies to the handle the timing of their reproduction. Hibernating temperate-zone bats usually mate in the fall, and the female stores the sperm, preventing fertilization from taking place until the spring. Other species can delay the implantation of a fertilized egg or the development of the embryo for three to five months (Graham, 2002, p. 41). This gives the young the best possible chance of survival and is an interesting evolutionary adaptation ("Bat Evolution").

Baby bats can weigh from 12 to 25 percent of their mothers' weight. Most species are born naked with their eyes closed and feed on milk as with all mammals. Mothers leave their babies in the roost when they feed at night. They identify their babies when they return by going to the area where they left them and then smelling and listening for the unique squeaks of their babies. Mothers are able to carry their babies on their undersides to move roosts. Many bats are fully grown and ready to fly within three weeks (Robertson, 2011, p. 35).

Bats are the world's longest living mammals for their size. Some banded bats have been recaptured over 40 years later. This longevity requires excellent hearing, mobility, and coordination well into old age, or else the bat would starve. This could be compared to a 100-year-old human running sprints on an obstacle course (Tuttle, 2015, p. 25). Even then, most bats die while still young, because bats have many natural enemies (Graham, 2002, p. 46).

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Evolution and Phylogentics of Bats

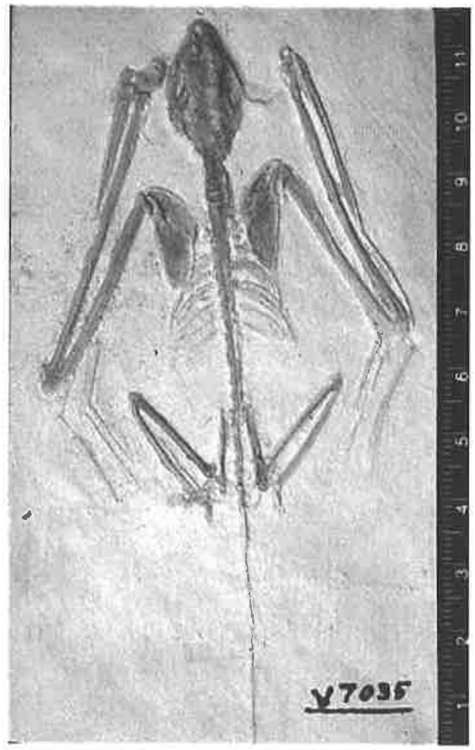


Figure 4. NEED CITATION

Mammals have existed for over 200 million years, but they really increased in diversity around 65 million years ago. There were many factors that influenced this diversification. Flowering plants diversified between 70 and 100 million years ago, providing new foods for insects and other animals. Also, the last of the dinosaurs became extinct around 65 million yeast ago, leaving new niches to fill (Richardson, 2011, p. 5).

Unfortunately, bats have left a very poor fossil record. Because bats are light-boned, their remains do not fossilize well. The earliest known bat fossil is a complete skeleton of a 52-million-year-old bat called *Icaronycteris* from the Green River Formation of Wyoming ("Bat Evolution"). It is generally identified as a member of Microchiroptera – it is clearly capable of flight and its skull is adapted for echolocation (Shipman, 1999, p. 237).

Since the only known bat fossil had already evolved flight, the evolutionary transition from a flightless mammal to flight in bats is completely undocumented in the fossil record. The major part of the bats' evolution probably occurred 70 or more million years ago. (Richardson, 2011, p. 5). There are no clues to guide scientists other than the characteristics of the living forms and the ecology of the species ("Bat Evolution").

There is indirect, physiological evidence that microchiropteran bats evolved from a shrew-like mammal that climbed trees (Graham, 2002, p. 11). In gliding mammals, all four legs are attached to the patagium, just like in bats. Both bats and gliding mammals have four elongated legs to support their bodies, although bats have taken this process further than gliders. Also, gliding mammals are often small and nocturnal like bats. Some scientists believe that the closest living group to bats is Dermoptera, the group that contains the colugo, or "flying lemur," a mammal that does not fly and is not related to the lemur. Colugos are gliders that also hang upside down when not flying. Hanging as a means of resting may be a shared adaptation derived from a common ancestor of bats and other gliders (Shipman, 1999, p. 237).

There is a lot of debate about the origins of the bats in the Microchiroptera versus the Megachiroptera suborders. The earliest known fossil of a fruit bat is 35 million years old. Fruit bats appear similar to insect-eating bats, but differ in many ways, such as the shape of their skulls, teeth, neck vertebrae, and hands (Richardson, 2011, p. 5). The fruit bats also do not echolocate using their larynx, leading some scientists to question the close relationship between the two suborders (Graham 2002, p. 11). Even then, the traditional division of fruit bats and insect-eating bats into two suborders of the order Chiroptera recognizes that both groups evolved from a common ancestor already capable of flight. Most molecular evidence does support this hypothesis that all bats are in one monophyletic group (Simmons, 2008, p. 819).

However, one popular hypothesis from the late 20th century states that Megachiroptera evolved along a completely different line from Microchiroptera. The Pettigrew or "flying primate" hypothesis proposes that fruit bats have branched off from the primate family, and could be distantly related to humans (Richardson, 2011, p. 5). This is because Megachiroptera share some anatomical features with primates, such as advanced brain characteristics. This hypothesis implies that mammalian flight evolved twice with two different evolutionary groups. Even though recent genetic studies support the monophyletic hypothesis, scientists are still debating the phylogeny of bats today (Pettigrew, 2008, p. 228).

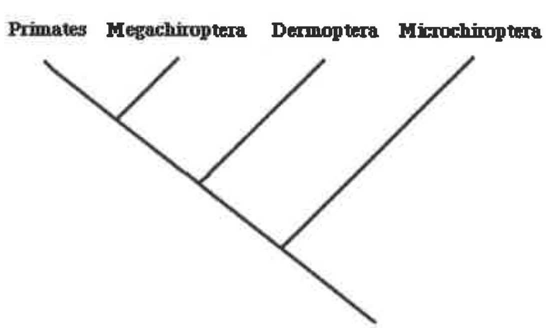


Figure 5. Anatomical (Pettigrew) Hypothesis ("Bats").

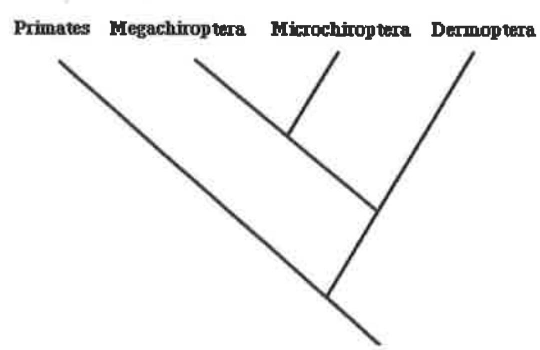


Figure 6. Genetic/Morphological Hypothesis ("Bats").

The early evolution of bat flight is relatively unknown, but the fossilized *Icaronycteris* can be compared with modern day bats to study the last 55 million years of the bats' evolution. The early fossils show five claws on each wing, while most species today have only one or two. Modern bats have shorter hind legs and longer fore legs than ancient bats. It is still a mystery as to why the leg lengths evolved, but it may have been for better balance and control during flight ("Bat Evolution"). Another theory suggests that the femur may have undergone a weight reduction as an adaptation for early flight (Schutt, 1998, p. 158). Because of their shorter wings, early bats could not fly as quickly as those today. It is possible that they did not fly nearly as frequently millions of years ago as they do today, and this may have been an adaptation to a changing environment that encouraged more flight for survival ("Bat Evolution").

One of the most significant forms of evolution for the bat is the way in which it navigates. The inner ear that makes echolocation possible was much more primitive in the earliest bats. This is method of survival evolved and developed over time in order for the bats to be able to have the best opportunity for survival ("Bat Evolution").

Another evolutionary adaptation in bats is that the females can delay the interaction of sperm from the male to her eggs. Some species mate in the spring, but the female prevents the sperm from meeting the eggs until fall. This gives the young the best chance of survival, which is the basis for the evolutionary process (Graham, 2002, p. 41).

With almost 1000 different identified species, there are a lot of unknowns when it comes to the process of evolution for bats. Each of the various species branched off of the evolutionary tree at a different time due to its location, habitat, and feeding habits. This specialization helped some species to survive, while others became extinct. The specifics of the bat family tree are still up for much debate in the scientific community. Molecular techniques have dramatically improved, and information from mitochondrial and nuclear genes is now used in systematic studies (Simmons & Hand, 1998, p. 2). Scientists are hopeful that more bat fossils are discovered so that they can use a "total evidence" analysis of morphological and molecular data to fill in some of the knowledge gaps (Simmons, 1998, p. 3).

Convergent Evolution of Flying Vertebrates

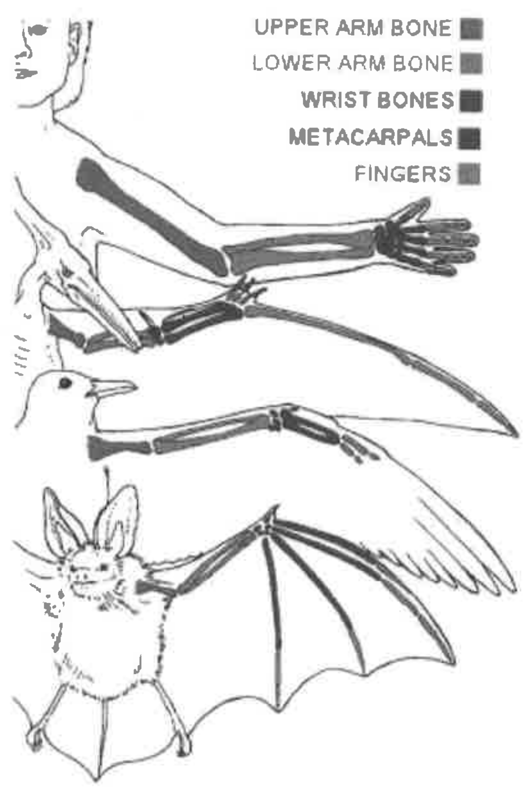
Other than bats, birds and pterosaurs are the only vertebrates that have ever evolved flight. True, sustained flight allows access to additional food resources as well as new roosting and nesting sites. Flight makes long-distance migrations possible and allows flying animals to get by physical barriers, such as cliffs and bodies of water, that are difficult for terrestrial animals. It is also an effective way to escape from most predators. Flight has been one of the main factors in the evolutionary success of both birds and bats, but the many complex specializations required for flight have probably prevented other vertebrates from evolving in the same way (Graham, 2002, p. 14).

The three airborne vertebrate groups share some important primitive ancestral features that gave them similar starting points for evolving flight. Their ancestors all had a head, body, tail, two front legs, two hind legs, and ten fingers and toes. They also had similar body systems for circulation, respiration, and digestion that had to integrate with the flight muscles that each species developed (Shipman, 1999, p. 219). Thus they all had similar biomechanical constraints. Each group's evolution toward flight is a classic example of macroevolution – the fossil record shows that once powered flight is achieved, the flying lineages evolve quickly and radiate into diverse niches ("Vertebrate Flight").

Even though bats, birds, and pterosaurs shared a similar body anatomy, they each found their own method of flight – evolving independently from different ancestors at different times. The pterosaur evolved first, with a fossil record that extends from 225 million to 65 million years ago. During this time, the pterosaur diversified into a wide range of sizes and shapes with different adaptations. Birds evolved next, with the earliest *Archaeopteryx* fossil dating back to 150 million years ago. Birds and pterosaurs coexisted for millions of years until the pterosaurs became extinct. After the pterosaurs disappeared, birds began to speciate in size, shape, and environmental preference. Subsequently, bats appeared in the fossil record about 50 million years ago. Because these first fossils are already highly adapted for flight, scientists think that their lineage might have evolved as early as 60 million years ago (Shipman, 1999, p. 220).

Because pterosaurs existed millions of years before the first birds evolved, the pterosaurs were already well-adapted for flight. Early birds had to compete with pterosaurs for resources as they evolved flight. The pterosaurs' habitat, flight methods, and feeding habits might have limited the options available to birds as they evolved. In the same way, birds contributed to the ecological context of bats as they evolved flight millions of years later (Shipman, 1998, p. 221).

Pterosaurs, birds, and bats come from very different ancestries and did not evolve flight in the same way. There are great differences in the wing structures of these three animals. Pterosaurs have narrow "finger wings" made of a thick membrane. They have three parts: the first is the shortest and attaches to the torso and the elbow, the second is longer and attaches to the elbow and wrist, and the third is the longest and runs from the wrist along the elongated fourth finger. The wing segments get longer and longer as they extend from the body of the pterosaur. The first, second, and third fingers are not part of the wing, and the fifth finger has disappeared completely (Shipman, 1998, p. 221).



Alternatively, birds have "arm wings" made of feathers inserted into the bones of the arm (Simmons and Conway, 1998). The wing is separated into three parts just like in the pterosaur, but the segments are much different. The first segment is made of the humerus, the second contains the radius, ulna, and wrist bones, and the third section covers the fused metacarpals of the hand. The fingers are greatly reduced or missing because they are not needed in the wing. The bird's wing consists of a long center section and shorter first and third segments (Shipman, 1998, p. 222).

Bats have a membranous wing like pterosaurs, but it is anchored to the arms and all of the elongated fingers, comprising "hand wings." Unlike birds and pterosaurs, who have bones only at the leading edges of their wings, bats have a bony arm bone with a several spokes extending from their palms. Their wings also have three parts, with the first and second equal in length and outermost segment the longest. Bats keep all five fingers to help control their flight, and the trailing edge of their wing membrane is attached to their ankles and sometimes their tail (Shipman, 1999, p. 222). Bats' flight muscles are located throughout their bodies, with down stroke muscles in their chests and upstroke muscles in their backs. This contrasts with the flight system of birds, where all of the muscles are located in the chest (Simmons and Conway, 1998). Since bats use more than chest muscles to fly, their shoulder girdles have a well-developed and very movable scapula and clavicle that is attached to the sternum. Unlike birds and pterosaurs, the bat scapula has three facets used as attachment points for flight muscles (Norberg, 1998, p. 97).

In birds, bats, and pterosaurs, the pectoral muscle is the main adductor (depressor) and usually a pronator (nose-down rotator) of the wing. The upstroke in bats is controlled by the deltoids and trapezius muscles, and several muscles in the system are bifunctional. This complex wing system in bats, unlike in birds, reflects the use of the forelimbs in climbing and terrestrial locomotion in the earliest bats as well as current bat species (Norberg, 1998, p. 94).

The size of the sternum is associated with the size of the pectoral muscle and thus the ability to fly. Pterosaurs do not have a well-developed sternal ridge for the attachment of pectoral muscles, leading scientists to think that pterosaurs could not produce a down stroke as strong as that of the birds. Some bats have well developed sternal ridges and some do not. However, this does not affect their flight because these bats have a ligamentous sheet that anchors the pectoral muscles instead of a sternal ridge. Because ligamentous sheets do not fossilize, it is unknown if pterosaurs had the same ligamentous sheet design as bats (Norberg, 1998, p. 97).

Bats, birds, and pterosaurs have (or had) short, streamlined, and stiff trunks. The vertebrae are fused in different regions; in bats fusion is common between adjacent trunk vertebrae. If not fused, they are shaped to limit or prevent movement. The ribs are flattened to provide and origin area for the flight muscles. (Norberg, 1998, p. 96).

The three convergent flying species also have different approaches to moving while not in the air. Terrestrial locomotion is important to birds, and they usual have strong mobile legs that can used for walking, running, and swimming (Shipman, 1998, p. 241). Some species have further evolved to give up flight altogether, such as ostriches that only walk or penguins that only swim. These birds can then take advantage of a greater range of environmental niches, further diversifying into eight times more species than that of bats (Graham, 2002, p. 8).

Bats, however, have a different approach. Their wings are attached to their legs and tail, causing them to be clumsy and slow on the ground. The ball-and-socket joint at the head of the femur orients the bat's leg to the side of the body, in the same plane as the forelimb. This arrangement and the helps to control the tension and angle of the wings, greatly increasing maneuverability during flight. Because this ability is so important to the bat's survival, they have sacrificed much of their terrestrial movement. The femurs are weak when in the weight-bearing position and cannot effectively support the body when the bat is walking on all fours (Shipman, 1999, p. 228).

Evolutionary biologists are not all in agreement about the pterosaurs' walking ability. However, their femurs resemble those of birds, and were most likely used for walking or running, paralleling the evolution of birds (Shipman, 1999, p. 228). Pterosaurs probably had an intermediate approach, with legs that weren't as strong as those of birds but more mobile than those of bats. Pterosaurs most likely caught their prey in the air and may have eaten it there, also. However, the largest of the pterosaurs probably also spent time walking on the ground to conserve energy (Shipman, 1999, p. 241).

Flapping flight requires a lot of energy. Birds and bats are endotherms with high metabolic rates and a steady internal temperature. Some evolutionary biologists argue that pterosaurs may have been endothermic, also, but this is a still a contested theory (Shipman, 1999, p. 223).

Both have thin, hollow bones, which saves weight for flying. Birds have cavities inside the bones that are filled with specialized air sacs connected to the respiratory system through openings in the bones. The air sacs help with heat regulation for birds, which is needed for the muscular activity needed for flight. The air sacs increase the surface area of the respiratory system to dissipate heat quickly. They also increase the efficiency of the respiratory system, increasing oxygen intake and carbon dioxide release. Birds can actually extract oxygen from the air almost twice as fast as mammals. This enhanced respiratory system is an important part of the bird's endothermic adaptation to a flight metabolism (Shipman, 1999, p. 230).

Like birds, pterosaurs had thin, hollow bones with openings that may have been used in an air sac cooling arrangement. Their keeled sternums could have been used to keep intramuscular air sacs from collapsing while flying. Fossilized pterosaur bones have a cellular structure typical to animals that grow rapidly, which is another trait associated with endothermy. Pterosaurs' body and wings seem to have been furred, which is common characteristic of mammals (Shipman, 1999, p. 230). However, the debate over the evolution of flight in pterosaurs as well as whether they were flapping endotherms or soaring ectotherms is still ongoing (Shipman, 1999, p. 236).

Unlike birds and pterosaurs, bats have not developed hollow bones or an air sac cooling system. Bats do not need an enhanced respiratory system for cooling because they fly almost exclusively at night, when air temperatures are usually lower than body temperature. Heat is removed from the muscles through the bloodstream and carried to the wings by convection (Shipman, 1999, p. 77). Air flow over their wings is enough to dissipate the heat produced by flapping. Because bats evolved from a mammalian glider, that ancestor was already endothermic and capable of strenuous activity. Thus the evolution of flight from this ancestor did not require a change to the respiratory system (Shipman, 1999, p. 237).

Bats have a very restricted body size because they occupy a very restricted niche. Since they are nocturnal fliers, they cannot conserve energy during flight by soaring, because there are no thermals at night. Because of their high energy flight needs, they have never evolved into a size range greater than 2 grams to 1.5 kilograms (Shipman, 1999, p. 238). Bats developed echolocation to aid in their nocturnal lifestyle. This is an adaptation evolved and developed over time in order for the bats to be able to have the best opportunity for survival ("Bat Evolution").

Modern birds that fly can range in size from the hummingbird at 1.5 gram to the condors and albatrosses that weigh up to 15 kilograms. Additionally, some extinct species had a calculated body weight of 80 kilograms. These large diurnal birds did not evolve, however, until after the pterosaurs became extinct (Shipman, 1999, p. 238).

The pterosaurs had the widest range of body sizes, from species the size of a sparrow to the largest, *Quetzalcoatlus*, that weighed about 127 kilograms. This monster flyer spent most of its time soaring on thermal currents above the waves, rather than flapping. Otherwise, it would have never had enough energy to manage its metabolic needs (Shipman, 1999, p. 239).

From an evolutionary perspective, the comparison of bats, birds, and pterosaurs is very interesting. Pterosaurs were the first to evolve flight and were able to diversify into a wider range of sizes than either bats or birds, although much of this diversity appeared after birds had evolved. Pterosaurs specialized in a narrow-wing shape and flew best in open spaces and uncluttered habitats. They were active, diurnal flyers who were most likely warm-blooded. Birds are also a diverse group of flying vertebrates, well adapted to many environments. Bats are the most specialized, taking advantage of the previously untapped resource of nocturnal flying insects and successfully diversifying into many small niches.

Bat Conservation

There is a growing international concern for the conservation status of bats. The conservation of bats presents the same kinds of problems as the conservation of other organisms (Fenton, 1998, p. 268). There are specific threats in certain countries or regions, and there are also common themes. All identified threats can be linked to human activities. As the human population expands and our technology enables us to extract resources from more remote areas, many organisms, including bats, are threatened (Pierson & Racey, 1998, p. 247).

Mobility, broad diets, and a willingness to roost in manmade structures has given at least some species of bats a buffer against the loss of natural habitat. However, human expansion has begun to cause reduced bat diversity and a shift in the population sizes of the bat populations. Several of the species with the smallest distributions and most restricted habitat requirements are now endangered or extinct as a result of human impacts. The species that are most adapted to living alongside humans are also at risk from pest control programs, vandalism, and loss of roosts. Only a few species can survive in the totally altered environments of urban areas or highly cultivated areas (Pierson & Racey, 1998, p. 247).

Habitat loss and modification due to timber production, farming, and building construction is the primary threat to the long-term survival of many bat species (Richards, 1998, p. 272). Cave-dwelling bats are put at risk by recreational caving, mining, vampire bat control, and poisoning because of misconceptions regarding disease risks. Cave-dwelling bats form large groups and are highly visible, making them especially vulnerable to human disturbance (Pierson, 1998, p. 247). Bats are also threatened by predation from humans or introduced predators such as feral cats. Environmental pollution threats include the ingestion of lead from gas fumes, absorption of fluoride from smelters, and ingestion of DDT from the food chain in areas of intense agriculture (Richards, 1998, p. 272).

There are two basic approaches to conservation – protection of each individual species and preservation of habitat. Endangered species have a small population size, evidence of population declines, limited distribution, restricted habitats, and vulnerability to human impacts. This approach is especially important in areas where bats are intensively hunted or eradicated (Wund and Myers, p. 10).

The protection of habitats or habitat features critical to the survival of bat communities is also important. Focusing only on protecting areas with high biodiversity may not be enough because bat survival depends upon the protection of both roosting and foraging areas. Roosting areas such as caverns and mature native forests must be protected as well as foraging areas such as unpolluted water sources and substantial tracts of native habitat (Pierson & Racey, 1998, p. 248). Another factor that influences the survival of migrating bats is the protection of both winter and summer roosts. Fall roosts used as mating sites or migratory rest stops can also be important (Pierson, 1998, p. 313).

One challenge for bat conservationists is public misconception. Since most bats at small and nocturnal, they are difficult to observe, and people tend to fear what they don't fully understand (Graham, 2002, p. 6). There are many misunderstandings - in North America it is the fear of rabies, in South America it is the fear of vampire bats, and in Australia it is the concern over predation in fruit orchards. The result of these misunderstandings is the same, though - bat are treated as vermin (Pierson & Racey, 1998, p. 248).

Bats are the primary predators of nocturnal insects, and this has provided an economic reason for bat preservation. Bats control populations of disease-carrying insects such as mosquitoes, feed on agricultural pests, and can limit pest outbreaks in forests. A single insect-eating bat may eat hundreds or thousands of insects a night, and there are few other nocturnal insect-eaters (Richardson, 2011, p. 98). Bats that survive on fruit and nectar depend upon native plants for food and play an important role in pollination, seed dispersal, and reforestation (Richards, 1998, p. 272). Bats also play a significant role in the nutrient transfer of natural ecosystems. Bats consume up to 100 percent of their body weight each night, producing a nutrient-rich guano that has been used by humans for centuries as fertilizer. Since bats can travel long distances between their roosts and foraging grounds, they act as "nutrient pepper shakers," redistributing nutrients over the landscape (Pierson, 1998, p. 317).

It is important to protect bats because they can protect crops from pests, they spread seeds of foods they eat, which is important in reforestation, and they help pollinate plants. By teaching people that bats are not evil creatures, it will be possible to save species of bats that are crucial to the ecosystems of the world.

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