Lecture 9 - Locomotion I: Flight

I. Powered flight has evolved independently many times in animals, but only once in mammals. It always involves a flight membrane and a support structure.

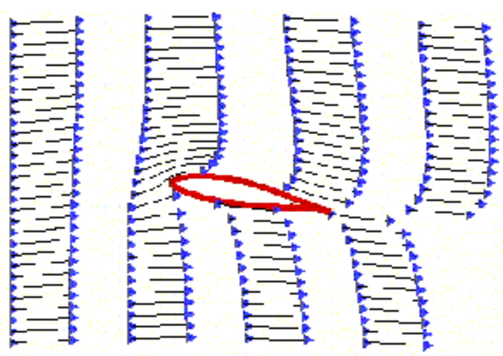
A. Insects - membranous sheets of chitin supported by veins.
B. Pterosaurs - skin membrane supported by single digit (4^{th}).
C. Birds - feathers, supported by limb bones and reduced 2^{nd} & 3^{rd} metacarpal and digit.
D. Bats - skin membrane supported by the 2^{nd} through 5^{th} digits.
Note how elongated the digits are.

II. Regardless of what the flying object is, the basic aspects of aerodynamics are the same.

A. Flight involves overcoming the force of gravity, that is **generating lift**.

Lift relies on **laminar flow**, parallel movement of air streams (as opposed to turbulent flow).

The principle is the same whether we're addressing a bat or an airplane and involves an airfoil. They are usually asymmetric in cross-section.



When the onrushing stream of air is split, some passes above and some passes below.

The air that passes over the top of the airfoil accelerates and moves faster than the air that passes across the lower surface: $V_{Upper} > V_{Lower}$. This difference in velocities is critical.

B. Bernoulli's Theorem: relates air pressure to velocity. An approximation, for our purposes, is:

$$P = C - \frac{dV^2}{2}$$

P is air pressure, *C* is a constant, *d* is the density of air, and *V* is velocity

Therefore, the higher velocity, the lower the air pressure and the fact that the airstream is moving faster across the top of the wing results in higher air pressure on the wing below than above. This differential in pressure is called lift, and when the magnitude of lift is greater than the force of gravity acting on the object, flight is achieved.

$$\text{Lift} = P_{(Lower)} - P_{(Upper)}$$

The magnitude of lift is dependent on the differential in V, the speed with which air passes along airfoil. This differential increases with flight speed, so it's more difficult to maintain flight at low speeds. For example, a plane has to accelerate to take off.

III. This difficulty to achieve lift at low flight speeds is particularly important to flight in bats because, for the most part, they're slow fliers.

There is variation in flight speed (look at 3 species we saw in lab):

Myotis lucifigus - 20 mph
Eptesicus fuscus - up to 40 mph
Tadarida brasiliensis - up to 60 mph regularly, occasionally just over 80 mph (O'mara et al. 2021 – pdf on curse website).

But most bats are slow fliers, more like *Myotis*, and slow flying is probably the ancestral condition. Bats generate lift at low flight speeds.

A. Bats deal with generating **lift at low flight speeds** in a number of ways.

1. One is to increase the curvature of the upper surface – **camber.**

The nature of the airfoil in bats is a little different than a plane; it's a thin airfoil, and the shape can be modified. The skin in the patagium is thinner than typical and has elastin bundles running along the wing and there are up to 5 intramembranous muscles (Chaney et al. 2017. J. Anatomy, 230:510).

As increase curvature → increase the differential in speed of airflow across upper surface relative to lower surface → increase lift.

2. Another is to increase the **angle of attack** - an airfoil coming at an air stream edge-on generates less lift than one that is inclined slightly. Again, this is because of the difference in distance that the split air stream travels.

3. A third relates to wing size and shape.

a. **Wing loading** - Body weight /surface area.

In general, the lower the wing loading, the easier it is to overcome the force of gravity.

Bats typically have low wing loadings

	Body Weight	Surface Area	Wing Load
House wren	11.0 g	48.4 cm^2	0.24 g/ cm^2
Glossophaga	10.6 g	99.3 cm^2	0.11 g/ cm^2
Myotis	4.2 g	67.6 cm^2	0.06 g/ cm^2

b. **Aspect ratio** - shape of the wing - length / width

Low aspect ratio wings are better for slow maneuverable flight. Remember that *Artibeus* is a phyllostomid bat that eats fruit and forages in forests.

High aspect ratio wings are better for rapid flight. *Tadarida* is a molossid bat that you saw in the lab that forages in the open.

4. Another is a phenomenon called leading-edge flaps. At low flight speeds, there is a tendency for laminar flow to break down. The next time you're on a plane check out the front of the wings on take-off. Leading-edge flaps promote laminar flow at low speeds.

Bats do all of these things. Slow flyers tend to have higher angles of attack, higher camber wings, and larger surface area wings with low aspect ratio.

B. Parts of a bat wing contribute differently to flight.

Propatagium -between shoulder and wrist
Dactylopatagium brevis - between first and second digits
D. minus - between second and third
D. longus - between third and fourth
D. latus - between 4th and 5th
Plagiopatagium - between 5th digit and the hind limb
Uropatagium - between the two hind limbs

IV. So far, we've only been talking about lift, but unlike in an aircraft, the wing also has to generate thrust.

A. Wing-beat cycle.

1. Down stroke is the power stroke. It is powered by three muscles:
pectoralis
subscapularis
serratus

2. One part of the wing in particular has been implicated in generating thrust.

Dactylopatagium longus. This is not well braced, so during the down stroke, this segment of the wing lags above the rest of the wing. As the down-stroke finishes, the front of the *D. longus* is much lower than the back; this has the effect of forcing air backwards. This is what generates thrust. It is also likely that the *D. latus* has some thrust generating function as well.

3. The function of the other portions of the wing during the down stroke.

Propatagium, *D. brevis*, and *D. minus* serve as leading edge flaps.

Plagiopatagiun is actually very well-supported by the 5th digit and the hind limb. It serves as the main airfoil.

This allows it to maintain both its camber and angle of attack throughout the downstroke and therefore it is the primary lift generator.

The Uropatagium is not present in many bats, but it serves for steering, and in many insectivorous forms, is used as a net to catch insects in while flying.

4. The upstroke is the recovery stroke.

The wing is partially closed. There are muscles that function during the upstroke, but these are greatly assisted by air pressure, so, to some degree, the upstroke is passive.

There's a great deal of variation in the manner in which the upstroke is stopped.

Shoulder-locking mechanism is formed by the greater tuberosity of the humerus.

In mollossids, the really fast fliers, the situation is as I've shown in the slide.

In vespertilionids, the greater tuberosity is also well developed, and acts as a locking mechanism.

In phyllostomids (and megabats, Pteropodids), there is only a moderate expansion of the greater tuberosity.

There are a few groups, such as the family Emballonuridae, with no expansion of the greater tuberosity, and no shoulder locking mechanism. The upstroke is stopped entirely by muscular contraction.

V. Some other skeletal adaptations to flight.

A. Many bats have a keeled sternum - manubrium, the first segment.

B. Some have axial skeleton modifications.

Natalidae - very rigid axial skeleton that is formed by

1. Compressed thoracic vertebrae - not fused, but very tightly interconnecting
2. Fused sacral vertebrae and fused lumbar vertebrae.