Lecture 8 - Locomotion I: Flight

I. Powered flight has evolved independently many times, but only once in mammals.

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 3^{rd} metacapral and digit
D. Bats - skin membrane supported by the 2^{nd} through 4^{th} digits

II. Basic aspects of aerodynamics.

A. The problem involves overcoming the force of gravity, or **generating lift**.

The principle is the same whether we're talking about a bat or an airplane.

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

Lift relies on Laminar Flow, parallel movement of air streams.

One property of laminar flow is that air stream that is split by the leading edge of the airfoil arrives at the trailing edge at the same time. So air flows faster across the top than bottom of the airfoil if there is a curvature.

B. Bernoulli's Theorem:

$$P = C - (dV^2)/2$$

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

Therefore, the higher velocity across the top of the wing results in lower air pressure on the wing above than below. 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.

$$\text{Lift} = P_{(\text{upper})} - P_{(\text{lower})}$$

Amount 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.

III. This is particularly important to flight in bats because for the most part, they're slow fliers.

There is variation in flight speed:
Myotis lucifigus - 20 mph
Eptesicus fuscus - up to 40 mph
Tadarida brasiliensis - up to 60 mph

But most bats are slow fliers, more like *Myotis*, and slow flying is the primitive condition.

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

1. One way around this 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.

   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 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, *Artebius* is a phyllostomid bat that eats fruit and forage 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.

   Page 210 in Text has good illustration of these two wings

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 behind 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 strongly-braced 5th digit and the hind limb

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 in most forms.

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 up-stroke is stopped.

Shoulder-locking mechanism - greater-tuberosity of the humerus.

In mollossids, the really fast fliers, the situation is as I've drawn on the board.

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

In phyllostomids, there is only a moderate expansion of the greater tuberosity.

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

The nature of the shoulder locking mechanism is used to divide the families of Microchiroptera into 4 superfamilies.

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.

Mammalogy Lecture 9 - Locomotion II: Functional Morphology

I. Again, we're going to be resolving force vectors to understand, from a **biomechanical** perspective, why evolution has shaped mammal limb bones the way it has.

We'll take an optimality point of view & look at morphology from an engineer's perspective

II. Limbs are a series of levers – example forelimb

A. Structure

B. Let's look at the forces generated by these muscles, and resolve those force vectors

C. Now, we need to define a few terms...

F_o = Out force - the force the limb can generate. This is the phenotype on which selection will operate.

F_i = In force - the force the muscles can generate. This is the resultant that we just defined.

L_i = In-lever - perpendicular distance between the line of action of the F_i and the fulcrum.

L_o = Out-lever - perpendicular distance between the line of action of the F_o and the fulcrum.

The relationship between F_i and F_o depends on the lever arm that each force has.

Torque is the turning force at the fulcrum

In-lever Torque = $T_i = L_iF_i$

Out-lever torque = $T_o - L_oF_o$

D. Remember , at equilibrium, all forces are equal ----> $T_o = T_i$

This means then that $F_oL_o = F_i L_i$

F_o is the parameter of interest, so we solve for F_o: $F_o = (L_iF_i)/L_o = F_i (L_i / L_o)$

We can therefore optimize the force of a limb, F_o, in two ways

1) Increase F_i --> this is determined by the number of muscle fibers.
We have a finite space, so optimizing F_o by this means is limited

2) Increase L_i / L_o

In terms of mammalian forelimb, long olecranon process & short forearm

We do see mammals that appear to optimize F_o in this manner:
1) Talpidae - mole family *Scapanus orarius*
2) Dasypodidae - Armadillo
3) Geomyidae - gopher family - *Thomomys talpoides*
4) All the myrmecophagous forms we've mentioned.

We might then ask the question why isn't F_o always optimized. That is, why don't we see a long olecranon process and short forearm in everything.

E. Of course the answer is that there's a direct trade off with velocity.

At equilibrium, $V_oL_i = V_iL_o$

V_o = velocity at the end of the out-lever; V_i = velocity at the end of the in-lever

So if we optimize the speed at which a lever works $V_o = Vi\ L_o/L_i$ or $V_i (L_o/L_i)$

Again, velocity can be optimized in two ways

1) Increase V_i --- > V_i is the velocity of muscular contraction is physiologically limited

2) Increase L_o/L_i ---> Directly opposite optimization of force.

We expect that limbs that optimize velocity to have a very short olecranon process and a very long forearm.

We actually see such limbs in:

- Cervids - Deer family - *Odocoileus*
- Bovids - Cow and goat family - *Ovis canadensis*
- Equids - Horse family - *Equus caballus*
- Leporids - Rabitt and hare family - *Lepus townsendii*
- Canids - Dog family - *Canis latrans*
- Felids - Cat family - *Puma concolor*

Selection has optimized V_o at the expense of F_o.

Most mammals have limbs that represent a compromise. Generalized limbs have a moderate capacity of generating power and moderate velocity.

Mammalogy Lecture 10 - Locomotion III: Types of Locomotion

I. In general, we can recognize several types of locomotory specializations in mammals: In addition to powered flight, we see:

a. Saltatorial - Hopping
b. Cursorial - Running
c. Scansorial - Climbing
d. Gliding
e. Swimming

Most groups are pretty generalized, but there are many specialists that do one of these particularly well.

II. Saltatorial - Bipedal hopping usually is seen in prey species, and is also known as ricochetal locomotion.

This is seen in several groups
- Macropodids
- Paremelids
- a couple of primates such as these ringtail lemurs

In fact, has evolved at least five different times independently just in rodents.

Heteromyidae - Kangaroo rats and mice
Pedetidae - Springhares - South African family of rodents
Dipodidae - Old World forms such as jerboas and the local jumping mouse *Zapus*
Mirunae - Old World mice that are saltatorial
Gerbillinae - Gerbils

A. All these forms have very long **hind** limbs. They all have responded to selection to optimize V_o & they have very long out levers on their hind limbs.

B. To compensate for the trade-off that this implies with power, they also have really large hind limb musculature - in fact it's hard to imagine more lopsided beast than a K-rat.

There often is a reduction in number of digits in the hind limb.

The forelimb is almost always very generalized, and is used in feeding grooming, etc.

C. Other adaptations:

1 - Stiffening of the spine to resist whiplash
- cervical vertebrae are often fused in saltators
- lumbar vertebrae tend to be robust
- the sacrum and pelvic girdle are strongly fused
- There are ligaments running from thoracic to cervical vertebrae and from sacral to lumbar; these function in shock absorption

2 - Long counter-balancing tail that may used to change direction in mid air, is often tufted to add weight.

3 - Use elastic storage mechanisms to save energy - hind limb ligaments are elastic. At moderate constant speeds saltation is more efficient than running.

D. Advantages – Saltation enable extremely rapid acceleration. It is also very amenable to sudden changes in direction; K-rats can actually change direction in mid-air predator avoidance.

II. Cursorial - Adaptation for running are seen in both predators and prey.

For example Lagomorphs, terrestrial Cetartiodactyls (giraffids, cervids, bovids, antilocaprids), Perissodactyls, Carnivora (canids, and felids), Thylacynids all are cursorial.

In general, there are **two ways** that cursorial mammals increase speed: Increased Stride Rate & Increased Stride Length

A. Increase stride length.

1. Typically, the distal limb bones are elongated; this increases stride length

2. Change in foot posture

Plantigrade - Generalized (non-cursorial condition) -- palm on the ground
Digitagrade – Canids, Felids, Leporids - only digits on ground - metapodials are lengthened
Unguligrade - Terrestrail Cetartiodactyls and Perissodactyls - Only the hoof on the ground.

Hoof is a modified claw or ungula.

This then allows for the extreme expansion of metapodials fusion into cannon bone

3. Loss/Reduction of clavicle allows the scapula to pivot and rotate as part of the limb as well because it does not articulate with the axial skeleton.

- Front limb is supported by a muscular sling formed by the trapezius, rhomboideus, serratus and pectoralis.

- This also acts to absorb the shock of the limb striking the ground

4. Increased dorso-ventral flexion of the spine.

   - Extreme in cheetahs - the fastest mammals have a bounding leaping run up to 110 Km/hr = 70 mph

   - This has a huge energetic cost because the entire body has to be lifted with each stride. This works well for rapid bursts but not for cursors that are endurance runners or for large cursors with high body. So horses only exhibit moderate dorsoventral flexion.

B. Increase stride rate. This is tied to optimizing V_o

1. Short in-levers and long out levers: olecranon process for front limb; calcaneum for hind limb. Thus, lengthening the distal portion of the limb has a dual advantage for cursors.

2. Increase the number of joints: V_o Total = Sum of all V_o in limb
   - scapula rotating
   - inclusion of wrist/ankle associated with digitagrade/unguligrade

$$V_{o(Total)} = V_{o(Scapula)} + V_{o(Humerus)} + V_{o(Ulna)} + V_{o(Canon\ Bone)} + V_{o(Hoof)}$$

3. Decrease inertia of limb distally

   - decrease the distal mass of the limb - less E required to move it quickly.

   - loss of peripheral digits - reduce to splints
     Terrestrial Cetartiodactyls - only the 3rd and 4th are well developed
     Perissodactyls - third digit is well developed others vestigial

   - Confining movement to a single plane -
     Ungulates - Astragulus acts as a tongue and groove system between forelimb and expanded metapodials

   - Concentration of muscles to the proximal locations - long tendons very slender limbs

III. Scansorial (Climbing)

A. There are many climbing mammals of all kinds. Climbing creates a need to move in a complex, 3 dimensional environment

- It's pretty obvious that there would be great adaptive significance of traits that reduce the likelihood of falling.

- However, the danger of falling is more sever for large bodied climbers than small because small ones have a much lower terminal velocity (maximum velocity that can be reached) This relates to surface area to volume ratio.

- Large climbers therefore tend to be slow and cautious, small ones more acrobatic.

B. Usually there is some type of modification to increase friction between feet and substrate

1. Friction pads on hands, feet and digits - Primates
   Porcupine (*Erethizon dorsatum*)
   Raccoon – (*Procyon lotor*)

2. Claws for digging into the substrate - Most scansorial rodents, especially well developed in squirrels *Sciurus*

3. Prehensile organs - tail - Opossum, *Cyclopes* (Silky ant-eater), *Coendu* (Prehensile-tailed porcupine), Primate family Cebidae.

   - opposable digits – opossum, primates, and *Phascolarctos*

4. Suction cups - sucker-footed bats in the family Myzopodidae

C. Typically have stiffened trunks to resist bending.

1. Vertebral column robust
2. Expanded ribs that overlap
3. Elongated thoracic region
4. Lumbar shortening - decreases movement between pelvis and ribs

D. Typically have elongated forelimbs (opposite to saltators)

One very specialized mode of scansorial locomotion is brachiation -- Gibbons

IV. Gliding

A. Gliding has evolved several times, seemingly always from an arboreal form.

A number of marsupials - Petauridae

Rodents - At least twice - Anomalurids and Sciurids

Dermoptera - Cynocephalidae

B. In all cases, the flight membrane involves a webbing of skin between the forelimb and hind limb. In dermopterans, the flight membrane also encompasses the tail and comes up to the lower jaw.

This flight membrane is often extended somewhat by stylar cartilage that extends into the wing.

The thinking had always been that these functioned to increase the surface are of the patagium, but that's not really accurate.

Any object moving through a viscous medium (including air) experiences drag. Drag is caused by air vortices that can impede movement through the air in several ways.

One that we'll worry about is called induced drag: air vortices spilling from the wing tips, resulting in downward pressure.

These cartilages aren't directed straight out during flight; they're actually directed upwards. This has the effect of displacing the induced drag so it's no longer placing downward pressure.

C. Thus, these combine to affect a controlled fall, & animals can get from tree to tree without descending. There are fewer predators in the trees.

D. *Glaucomys* can glide up to 50 meters or more. When they land, they have a very intersting habit of always scooting around to the opposite side to the trunk - interpreted as predator avoidance -- following owls.

E. One particularly cool gliding mammal is *Eupetaurus* , Giant wooly flying squirrel. This occurs in Pakistan and China and lives in caves above tree line. At night they glide down to the forests to feed and climb back up during the night.

V. Swimming - Every of mammal can swim. Let's just consider those modified for swimming

Drag is much more of an issue for swimmers than for gliders because water is more viscous than air.

A. Pressure Drag - Drag caused by having to displace the water through which the animal is moving.

- The lower the cross sectional area, the lower the pressure drag - best shape is very long and thin.

B. Frictional Drag - laminar flow, this is the drag that is created by the friction between parallel streams of water

- This is proportional to the surface area - a sphere is the shape that minimizes surface area.

So we see again, a direct trade off -

It turns out that the shape that results in the lowest overall drag is a spindle optimizes the trade-off.

C. Adaptations to swimming.

1. Semi-aquatic forms - shrews - *Sorex palustris*
   - mustelids (Lutrines) otters - *Lontra canadensis*
   - Rodents - beaver, capybara, nutria, muskrats
   - Cetartiodactyla - *Hippopotamus*

   Usually these animals have long bodies, and swim primarily with limbs

   Almost always some type of modification of webbing to increase thrust
   Exception is the family Hippopotamidae - actually take the opposite route and actually walk along the floor of the river.

2. Fully aquatic - Cetaceans, Pinniped carnivorans & Sirenians

   a. Limb modification -

   1. fore limbs - modified into flippers - entirely syndactylous
      - may provide thrust - Otariids (Sea lions and fur seals)
        - Ornithorhynchids

- may be used as rudders – Phocids (Earless seals)
  - Cetaceans
  - Odobenids (Walrus)

2. Hind limbs

   - may be vestigial, as in cetaceans and sirenians

   - fossil cetaceans with actual hind limbs

   - may be modified into flippers for propulsion as in seals

   Phocids - these forms actually can't use their hind limbs for terrestrial locomotion.

   Otariids actually can.

b. Axial Skeleton modification - Especially seen in cetaceans

   1. Reduction of cervical vertebrae: essentially no neck. Water is a viscous medium.

   2. Fusion of atlas and axis.

   3. Increase in robustness relative to terrestrial vertebrates - not for support against gravity, but to resist compression associated with the viscous medium.

c. Flukes - Tail fins of mammals, both cetaceans and sirenians, as well as dorsal fins have no skeletal component. They are entirely fibrous connective tissue.

D, The secondary evolution of aquatic lifelstyle in whales is well documented by fossil intermediates.

This was gradual and there are several transitional fossils.

Pakicetus fossils are from ca 52 MYA and had functional hind limbs.

Ambulocetus fossils are from 49 MYA and also had functional hind limbs

Basilosaurus is known from 40 MYA and has fully formed, but extremely small hind limbs.

This research, including a discussion of the scientific controversies, is available on Dr. Hans Thewissen's web site:

http://darla.neoucom.edu/DEPTS/ANAT/Thewissen/