

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 ricochetral locomotion.

This is seen in several groups

- Macropodids
- Paremélids
- some 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*

Mirinae - 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_0 & 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 vertebrae; these function in shock absorption.

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

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

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

II. Cursorial - Adaptations 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

Digitigrade – Canids, Felids, Leporids - only digits on ground - metapodials are lengthened.

Unguligrade - Terrestrial 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 weight. 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: $V_o \text{ Total} = \text{Sum of all } V_o \text{ in limb}$
 - scapula rotating
 - inclusion of wrist/ankle associated with digitigrade/unguligrade

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

3. Decrease inertia of limb distally

- decrease the distal mass of the limb so less E is 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 - Astragalus 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 severe 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 (new world monkeys).

- 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 front limb 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 styler cartilage that extends into the wing.

The thinking had always been that these functioned to increase the surface area 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 interesting 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*, the woolly 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 on pine needles 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.

- Proportional to cross-sectional area, so a rod shape (shape is very long and thin) minimizes pressure drag.

B. Frictional Drag – Drag associated with laminar flow, created by the friction between parallel streams of water

- Proportional to the surface area, so 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, which optimizes the trade-off. Therefore we tend to see fusiform bodies.

C. Adaptations to swimming.

1. Semi-aquatic forms - shrews - *Sorex palustris*
 - mustelids (Lutrines) otters - *Lutra 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. front limbs - modified into flippers - entirely syndactylous
 - may provide thrust - Otariids (Sea lions and fur seals)
 - 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. All cervical vertebrae are present, but they're compressed and fused.
2. Fusion of atlas and axis.
3. Increase in robustness relative to terrestrial vertebrates 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 lifestyle in whales is well documented by fossil intermediates.

This was rapid, probably occurring over ca. 8 MY, but 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. It was fully aquatic, and very large

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

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