Mammalogy Lecture 11 - 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; we'll look at these specialized forms and their adaptations.

II. Saltatorial - Bipedal hopping, or ricochetal locomotion, usually is seen in prey species.

This is seen in several groups
- Macropodids (kangaroos and wallabies)
- Some primates, such as these ringtail lemurs (*Lemur catta*)

In fact, saltation has evolved at least five different times independently just in rodents.
Heteromyidae - Kangaroo rats and mice
Pedetidae - Springhares - South African family of rodents.
Twice within Mudidae
Gerbillinae – Gerbils
Mirunae – several Old-world mice are saltatorial.
Dipodidae - Old World forms such as jerboas and the local jumping mouse *Zapus*

Adaptations

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 (high gear ratio).

B. To compensate for the trade-off that this implies with power, they also have quite large hind limb musculature.

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

The front limb is almost always 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

2 - Elastic storage mechanisms save energy - Achilles tendons are elastic. At moderate constant speeds saltation is more efficient than running.

3 - Long counter-balancing tail, which is often tufted to add weight as in the banner-tailed kangaroo rat (*Dipodomys spectabilis*).

D. Advantages – Saltation enables extremely rapid acceleration. It is also very amenable to sudden changes in direction; K-rats can actually change direction in mid-air predator avoidance. It also seems to be associated with soft substrate.

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

For example, Lagomorphs, terrestrial Cetartiodactyls (giraffids, cervids, bovids, antilocaprids), perissodactyls, canids, and felids are mainly cursorial.

In general, there are **two ways** that cursorial mammals increase running speed: 1 - Increased Stride Rate; 2 - Increased Stride Length. (Often one adaptation influences both)

A. Increase stride length.

1. Typically, the distal elements of limbs are elongated; this increases stride length

2. Change in foot posture that serves to lengthen limb.

Plantigrade - Generalized (non-cursorial condition) – palm/sole on the ground (*Homo*)
Digitagrade – Canids, felids, leporids - only digits on ground - metapodials are lengthened somewhat.
Unguligrade - Terrestrial cetartiodactyls and perissodactyls - Only the hoof is on the ground.

Hoof is a modified claw or ungula.

Unguligrade posture allows for the extreme expansion of metapodials & fusion into cannon bone.

Compared to a generalized form, the cannon bone lengthens the limb.

We can see a trend in terrestrial cetartiodactyls.
Peccary - No fusion.
Camels - Fused proximally, not distally.
Cervids - Fused entirely.

In equids, we see the expansion of 3rd metapodials.

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 allows scapula to rotate during the stride.

- 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 = 68 mph

- This has a huge energetic cost because the entire body has to be lifted with each stride.

This works well for rapid bursts (i.e., sprinters) but not for cursors that are endurance runners or for large cursors with high body weight. So horses only exhibit moderate dorsoventral flexion, and the same is true for pronghorn (*Antilocapra*), which are very fast (40-45 mph), but also excellent endurance runners.

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

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

3. Decrease inertia of limb distally

- This will 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 shin and expanded metapodials & no muscular force is required.

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

So, many cursorial adaptations increase both stride rate and stride length.

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*) *Galago*
   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 (*Ateles*).

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

4. Suction cups - sucker-footed bats in the family Myzopodidae (leaf-roosting bats).
   These have cups on wrists and ankles.
   Make tents of leaves.

C. Typically have stiffened trunks to resist bending.
1. Vertebral column robust
2. Expanded ribs may 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 (i.e., *Hylobates*)

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 gliding membrane (as in bats, it's called a patagium) involves a webbing of skin between the front limb and hind limb. In dermopterans, the gliding membrane also encompasses the tail and comes up to the lower jaw.

This patagium is often extended somewhat by styliform 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 type that we'll address now 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,* three species of wooly flying squirrel. These occur in Pakistan and China and live 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 mammal can swim. Let's just consider those modified for swimming

Drag is also an issue for swimmers because water is very viscous.

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 - *Lontra canadensis*
   - Rodents - beaver, capybara, nutria, muskrats

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; these take a different approach and actually walk along the floor of the river.

2. Fully aquatic - Cetaceans, pinniped carnivorans & sirenians – all are fusiform

a. Limb modification -

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

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

2. Hind limbs vary in fully aquatic forms:

   - may be vestigial, as in cetaceans and sirenians

   - fossil cetaceans with actual hind limbs

   - may be modified into flippers

   Phocids use hind limbs to generate thrus. These forms actually can't use their hind limbs for terrestrial locomotion.

   Otariids use hind limbs as rudders and actually can use hind limbs on land.

b. Axial Skeleton modification - Especially seen in cetaceans.

1. Shortening and fusing 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. All three fully aquatic lineages evolved from terrestrial ancestors and the secondary evolution of aquatic lifestyle is well documented by fossil intermediates.

For example, we have quadrupedal ancient sireniens - *Prorastomus* (Savage et al. 1994. J. Vert. Paleont., 14:427) and *Pezosiren* (Domning. 2001. Nature, 413:625).

We also have quadrupedal early pinnipeds (e.g., *Puijila*: Rybczynski et al. 2009. Nature, 458: 1021) and transitional forms with intermediate limbs (e.g., *Enaliarctos*: Berta and Ray. 1990 - pdf on course website).

A recent phylogeny of fossil and living pinnipeds (Patterson et al. 2020 – pdf on course website) shows the positions of these taxa exactly where one would predict based on their transitional, intermediate nature.

Perhaps the evolution of cetaceans from quadrupedal ancestors is the best documented.

This was rapid, probably occurring over ca. 8 MY, but there are several transitional fossils; we'll just note a few.

Pakicetus fossils are from ca 52 MYA and had functional hind limbs (described in 1978).

Ambulocetus fossils are from 49 MYA and also had functional hind limbs but was more aquatic (described in 1994).

Basilosaurus is known from 40 MYA and has fully formed, but extremely small hind limbs. It was fully aquatic, and very large (discovered in Louisiana in 1834).

Megaptera retains vestigial pelvic bone, but limbs have been lost.

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

http://web.neomed.edu/web/anatomy/Thewissen/whale_origins/index.html

In addition, a paper was published a few years ago that addresses genomic changes associated with the secondary evolution of aquatic lifestyles in whales (Huelsmann et al. 2019 – pdf on course website).