Mammalogy Lecture 10 - Locomotion II: Functional Morphology

I. We'll revisit force vectors acting at equilibrium to develop a **biomechanical** understanding of why evolution has shaped mammal limb bones the way it has.

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

II. We can think of limbs as a series of levers; we'll use the front limb as our example.

A. Structure - Muscles: two heads of triceps and anconeus.

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

Sum these:

$$T_1 + T_2 + A = \text{Resultant } (R)$$

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

F_o = Out force is the force the limb can generate. This is the phenotype on which selection will operate (force acting against ground).

F_i = In force is the force the muscles can generate. This is the resultant vector that we just defined ($F_i = R$).

The relationship between F_i and F_o depends on the length of the lever arm of each force.

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.

Torque is the turning force at the fulcrum; it's the product of the lever-arm and force.

In-lever Torque: $T_i = F_i L_i$

Out-lever torque: $T_o = F_o L_o$

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

This means then that $F_o L_o = F_i L_i$

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

We can therefore maximize 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 optimization of F_o by this means is limited

2) Increase L_i / L_o → (Leverage)

In terms of mammalian front limb, this translates to a 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) Geomyidae - gopher family - *Thomomys talpoides*
3) Dasypodidae - Armadillo
4) All the myrmecophagous forms we've mentioned.

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

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

Introduce a new velocity terms.

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

At equilibrium, $V_o L_i = V_i L_o$

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 maximized in two ways

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

2) Increase L_o / L_i (the gear ratio) → Directly opposite optimization of force; the gear ratio is the reciprocal of leverage.

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

We see such limbs, where election has optimized V_o at the expense of F_o in:

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

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