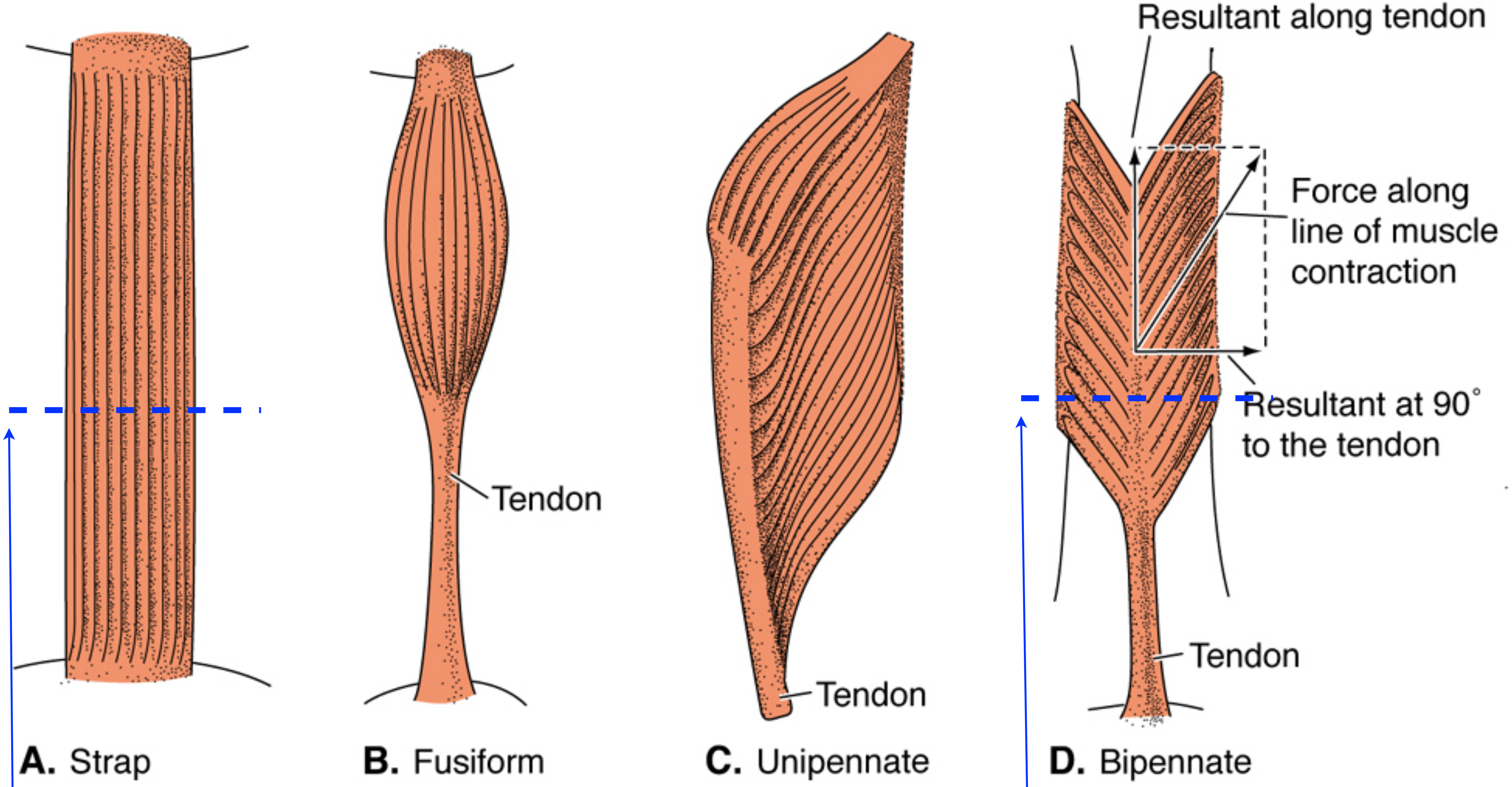
Muscle Architecture: Force vs. Speed

Force produced is proportional to # cross-bridges involved

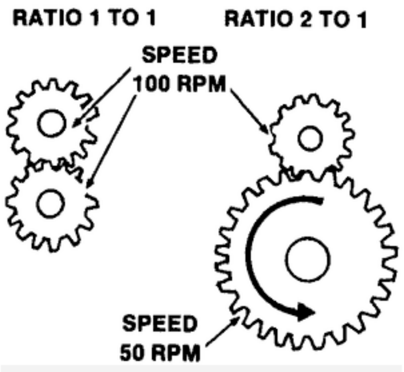


A. Strap **B.** Fusiform **C.** Unipennate **D.** Bipennate

Lower Force: Fewer cross-bridges per cross-sectional area
Speed: Many Sarcomeres in series, Shortens a lot

Higher Force: More cross-bridges per cross-sectional area
Low Speed: Doesn't shorten much

Forget 5th graders - are you smarter than an auto mechanic?



http://blog.hemmings.com/index.php/2007/11/01/a-different-kind-of-brain-teaser/

Variable gearing in pennate muscles

Emanuel Azizi*, Elizabeth L. Brainerd, and Thomas J. Roberts

Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912

Edited by Ewald R. Weibel, University of Bern, Bern, Switzerland, and approved December 3, 2007 (received for review September 27, 2007)

Muscle fiber architecture, i.e., the physical arrangement of fibers within a muscle, is an important determinant of a muscle's mechanical function. In pennate muscles, fibers are oriented at an angle to the muscle's line of action and rotate as they shorten, becoming more oblique such that the fraction of force directed along the muscle's line of action decreases throughout a contraction. Fiber rotation decreases a muscle's output force but increases output velocity by allowing the muscle to function at a higher gear ratio (muscle velocity/fiber velocity). The magnitude of fiber rotation, and therefore gear ratio, depends on how the muscle changes shape in the dimensions orthogonal to the muscle's line of action. Here, we show that gear ratio is not fixed for a given muscle but decreases significantly with the force of contraction ($P < 0.0001$). We find that dynamic muscle-shape changes promote fiber rotation at low forces and resist fiber rotation at high forces. As a result, gearing varies automatically with the load, to favor velocity output during low-load contractions and force output for contractions against high loads. Therefore, muscle-shape changes act as an automatic transmission system allowing a pennate muscle to shift from a high gear during rapid contractions to low gear during forceful contractions. These results suggest that variable gearing in pennate muscles provides a mechanism to modulate muscle performance during mechanically diverse functions.

biomechanics | force–velocity tradeoff | gear ratio | muscle architecture

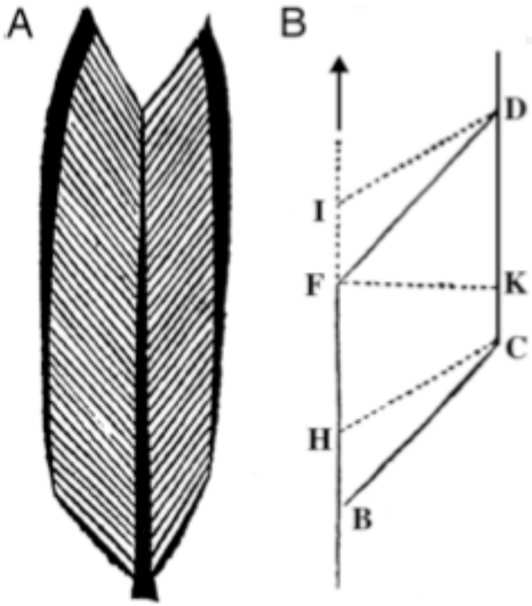
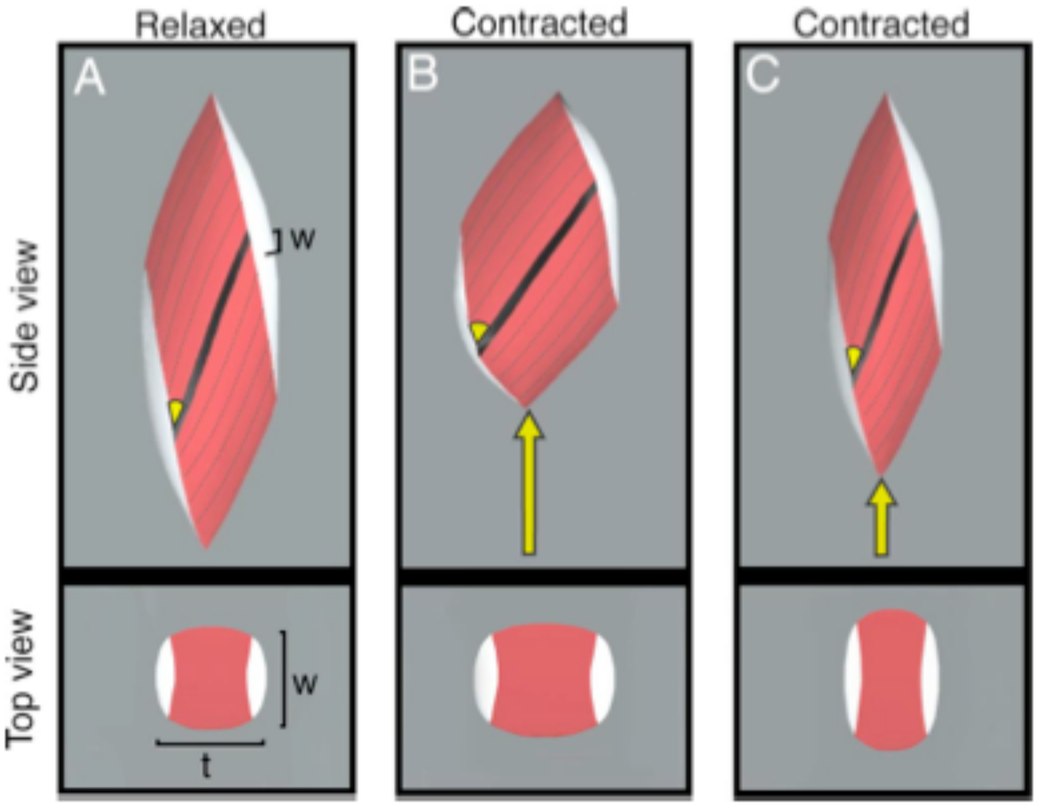


Fig. 1. A 17th century geometric examination of muscle architecture (5). (*A*) The adductor muscle in the claw of a lobster exemplifies bipennate architecture. (*B*) A geometric model of a unipennate muscle highlighting the orientation of fibers at rest (BC and DF) and contracted (HC and ID). This classic model predicts a change in pennation angle (i.e., fiber rotation) during contraction and assumes that muscle thickness (FK) remains constant. Arrow indicates the direction of the muscles' lines of action. Modified from reference 5.

Azizi, Brainerd, Roberts (2008) PNAS 105: 1745-50

www.pnas.org/cgi/content/full/ 0709212105/DC1.

$$\text{Anatomical Gear Ratio} = \frac{\text{Whole-Muscle Velocity}}{\text{Muscle Fiber Shortening Velocity}}$$



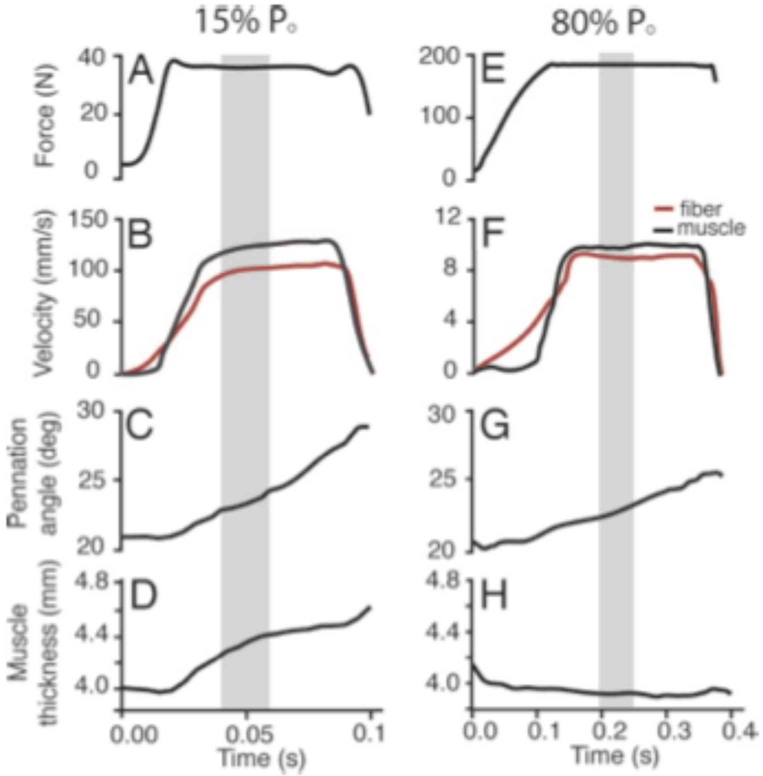
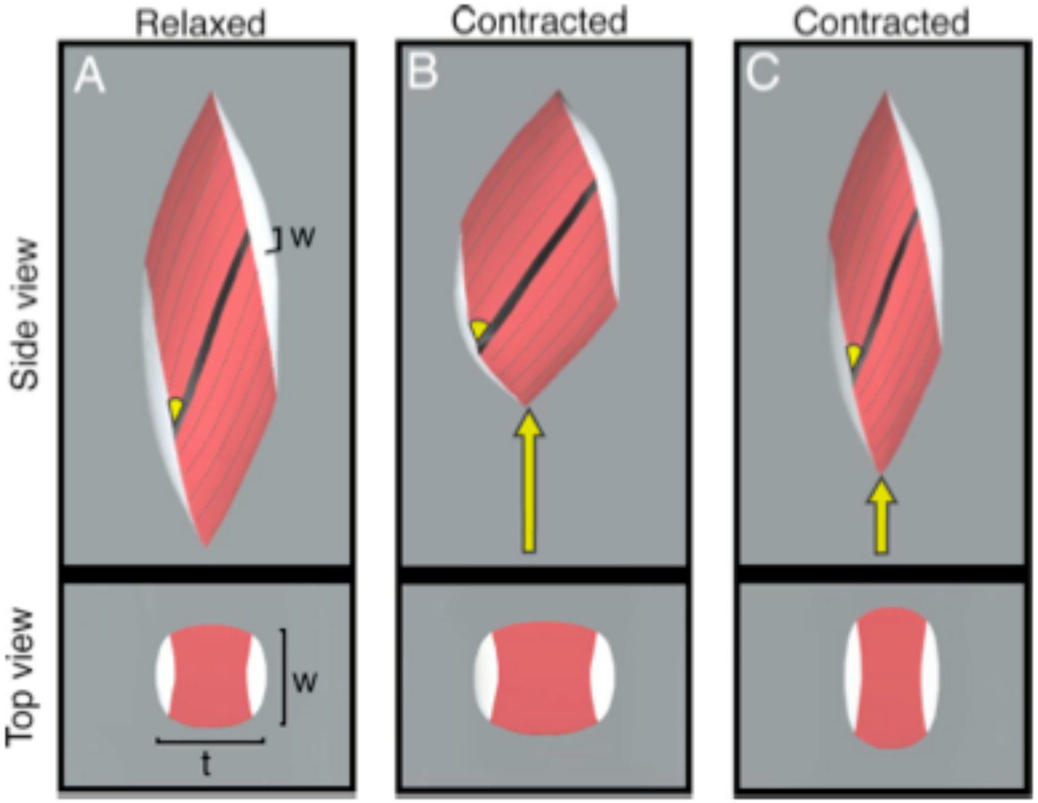
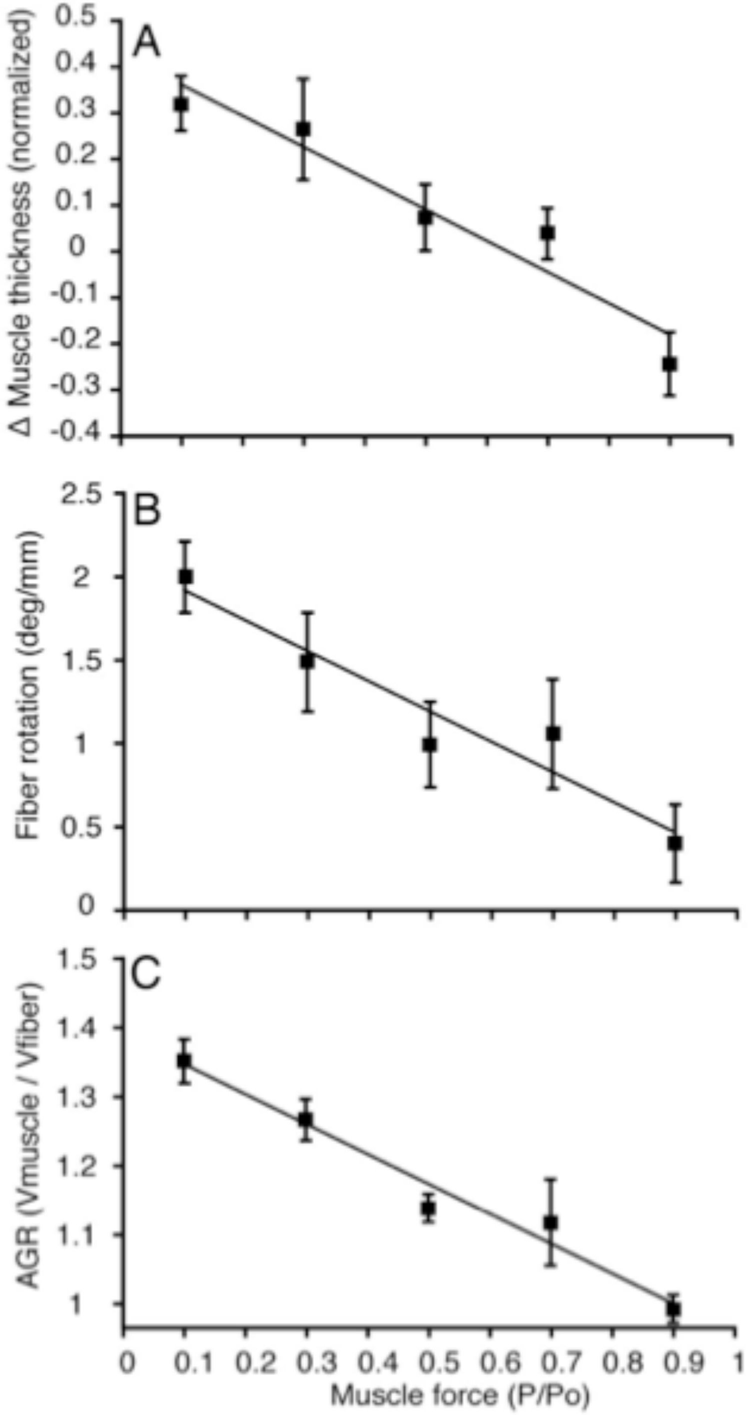


Fig. 3. Representative isotonic contractions in the lateral gastrocnemius of the wild turkey. The muscle was maximally stimulated in a branch of the sciatic nerve. Time-series plots from two sample contractions are shown. Muscle force was allowed to increase to a preset level (15% of maximum isometric force (P_o) in *A–D* and 80% P_o in *E–H*) and was kept constant as the muscle fiber (red) and the muscle–tendon unit (black) shortened at a constant velocity. All measurements were taken during a period of constant force (gray bars) and at a similar initial pennation angle. Similar contractions were performed at varying levels of force for each muscle.

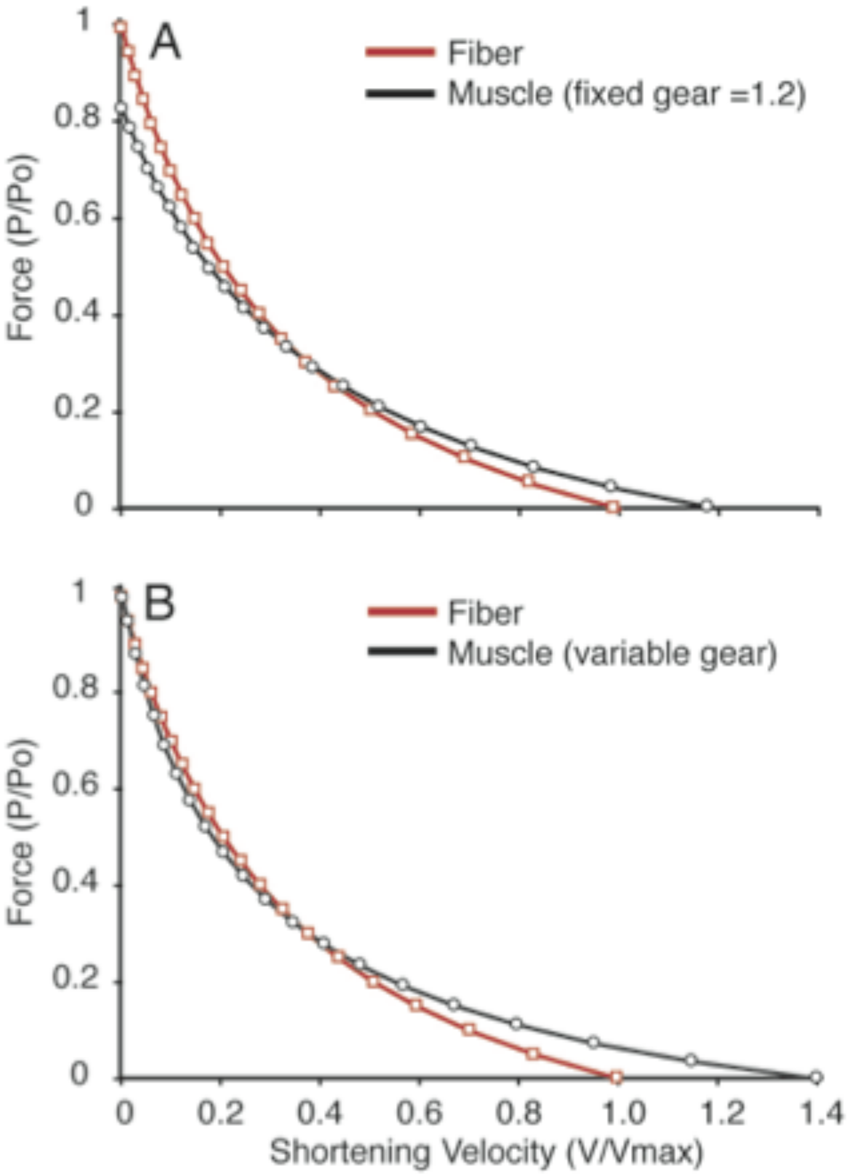
Angle changes,	Angle preserved,
Thickness ++,	Thickness --,
More rotation	No rotation,
Muscle shortens	little muscle shortening
High AGR	Low AGR
speed ++	More Force



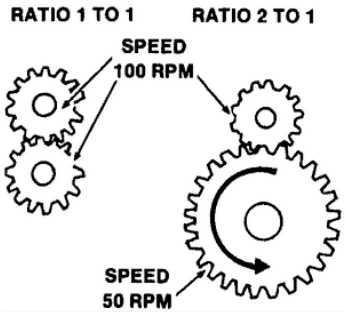


Angle changes,
Thickness ++,
More rotation
Muscle shortens
High AGR
speed ++

Angle preserved,
Thickness --,
No rotation,
little muscle shortening
Low AGR
More Force

A
Fiber
Muscle (fixed gear =1.2)
B
Fiber
Muscle (variable gear)
Force (P/Po)
1
0.8
0.6
0.4
0.2
0
Shortening Velocity (V/Vmax)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4

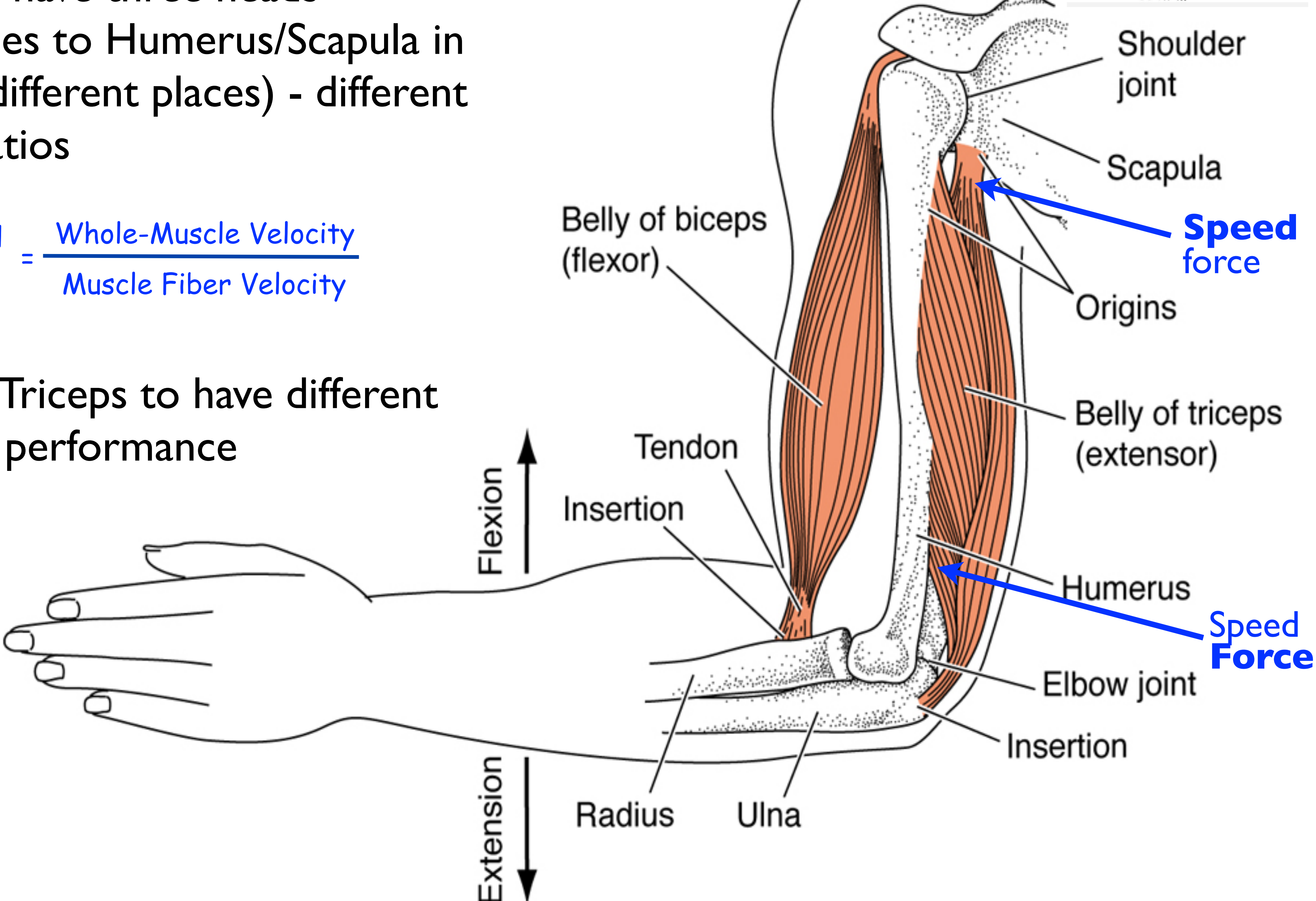
Biceps and Triceps



triceps have three heads (attaches to Humerus/Scapula in three different places) - different gear ratios

$$\text{Anatomical Gear Ratio} = \frac{\text{Whole-Muscle Velocity}}{\text{Muscle Fiber Velocity}}$$

Allows Triceps to have different muscle performance

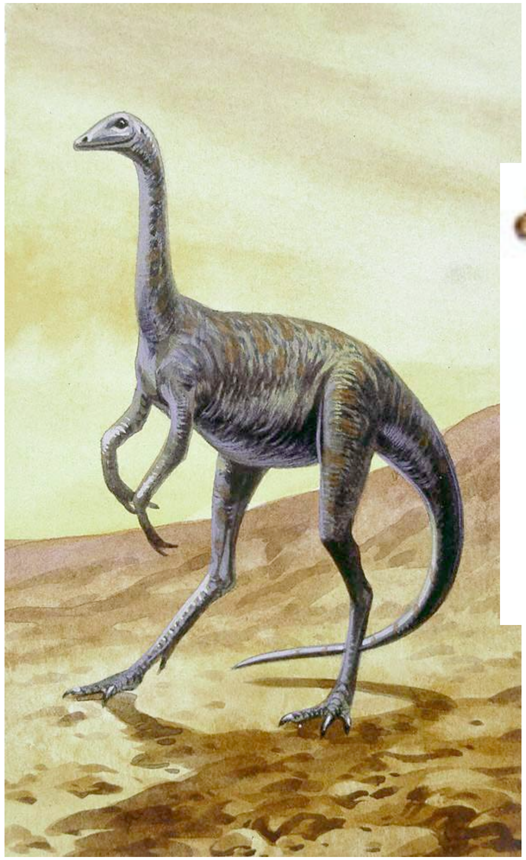


Terrestrial Locomotion

Cursorial Archosaurs

Oviraptor

Tyrannosaurian



Ornithomimid

Crocodilomorph

Bird

Cursorial lizards

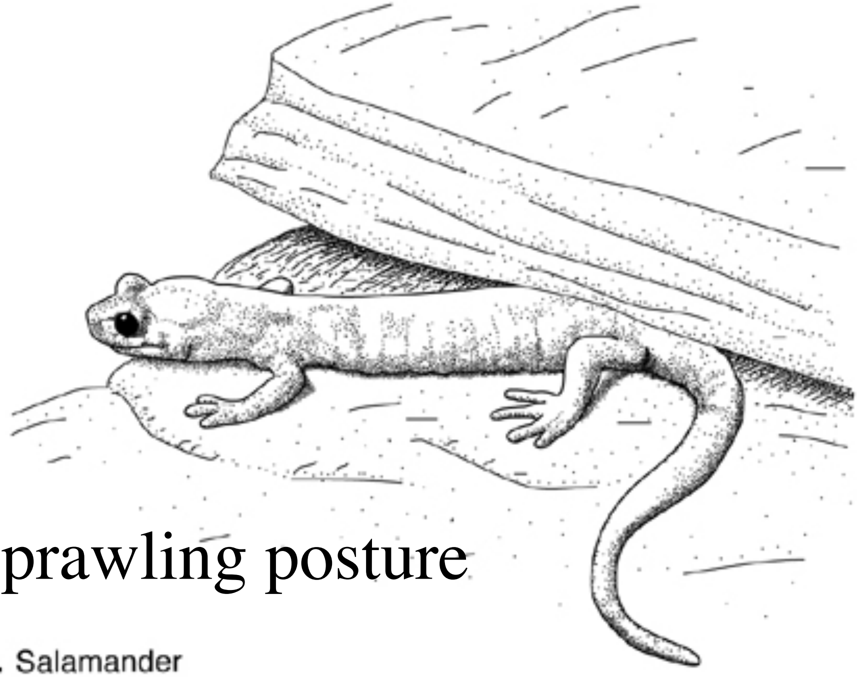
Zebra-tailed

Basiliscus

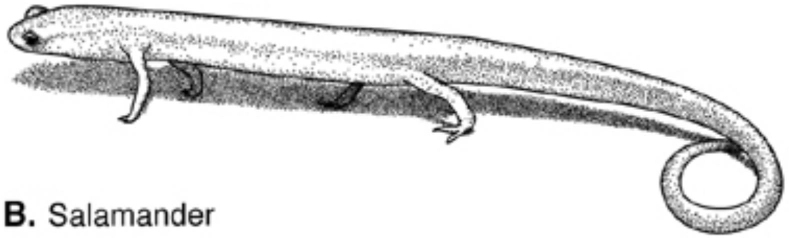
Cursorial mammals

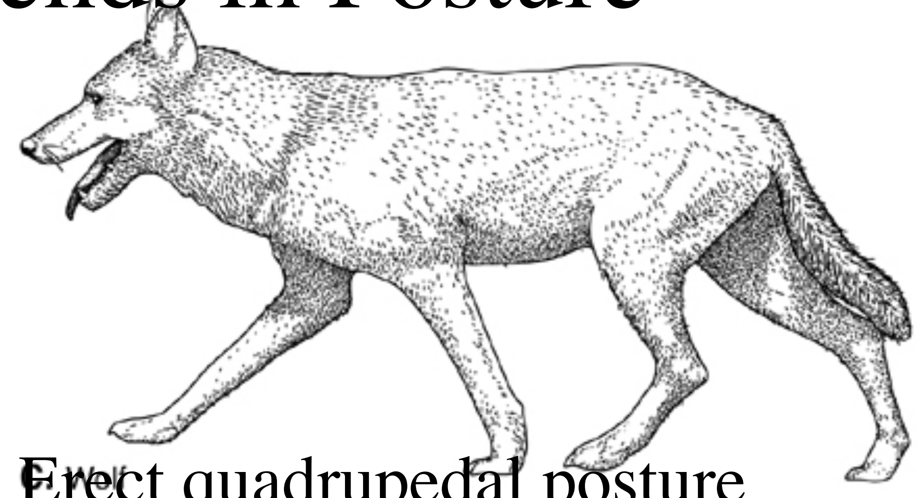
Cursorial lagomorphs

Support on Land: Getting the body off the ground -- Evolutionary Trends in Posture

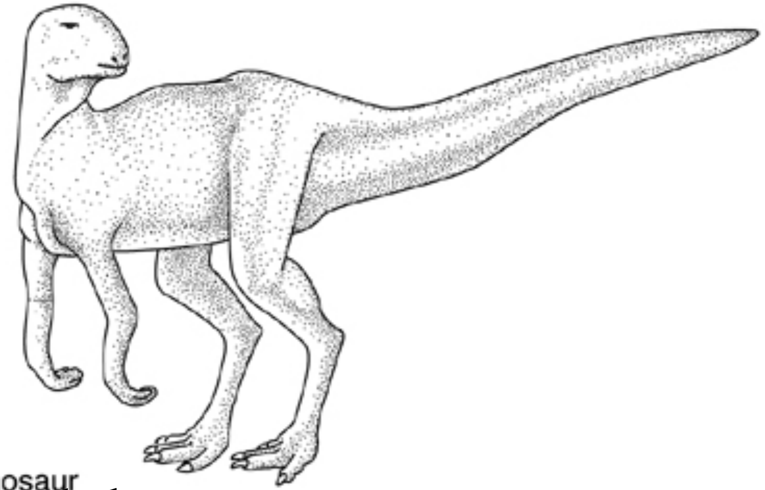


Sprawling posture





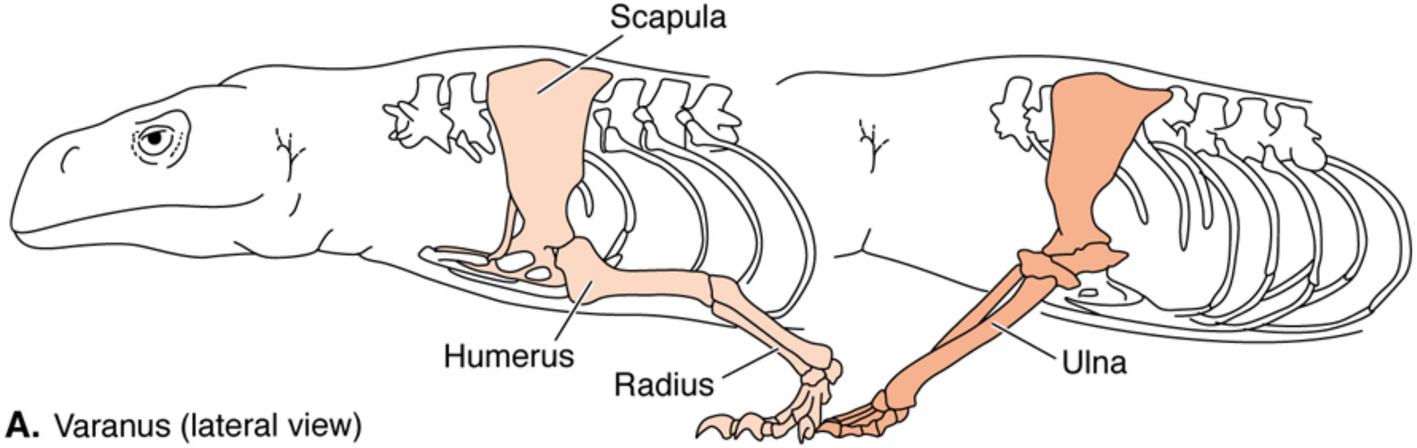
Erect quadrupedal posture



Bipedal posture

Fig. 11.7

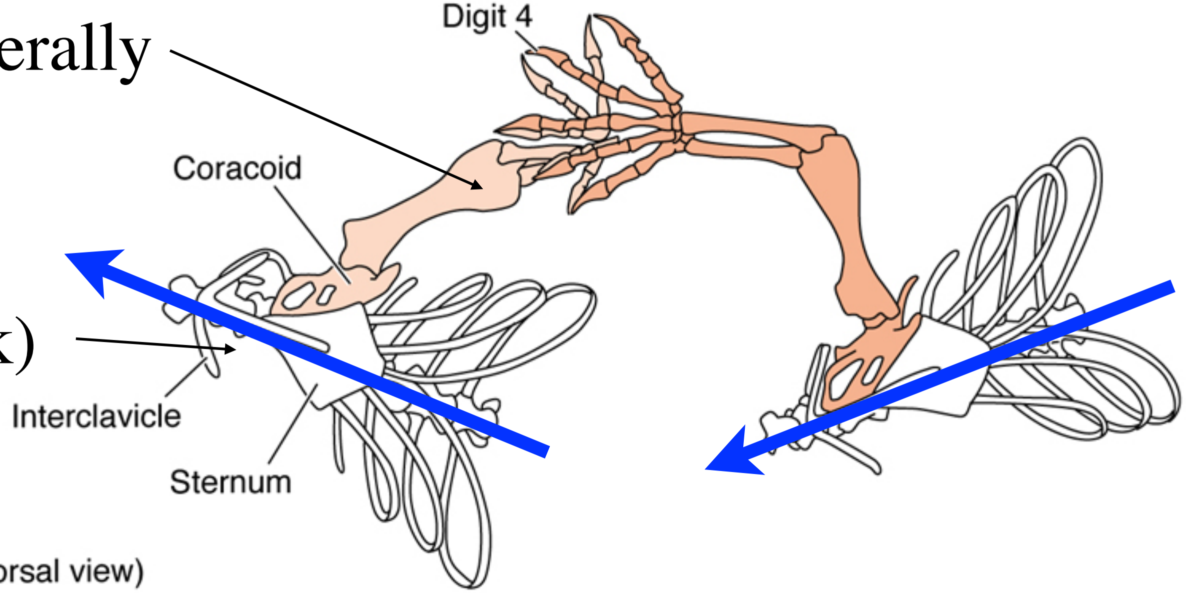
Early Tetrapods have **Sprawling Locomotion**



A. Varanus (lateral view)

Humerus held laterally

Lateral undulation (see trunk)

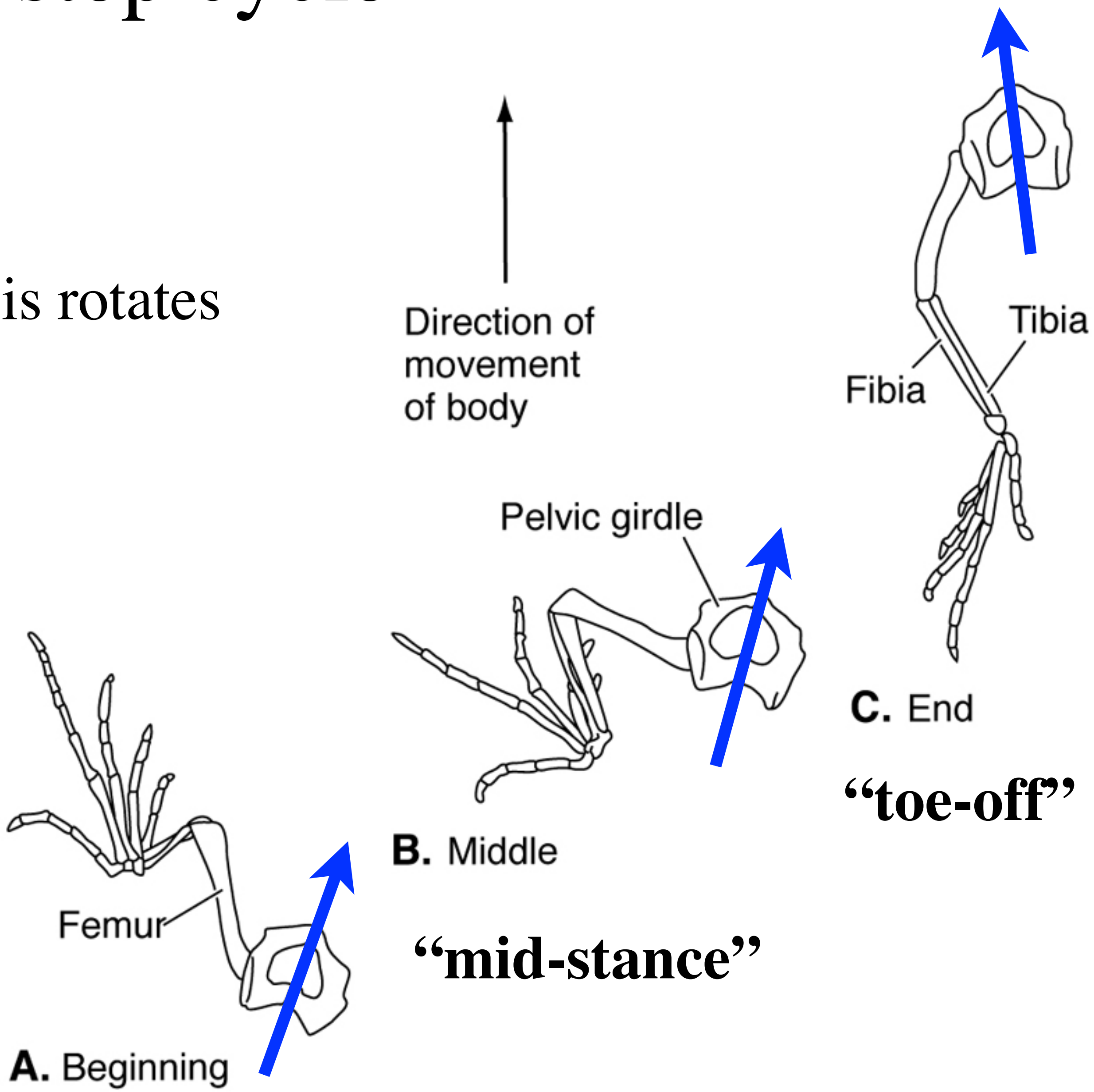


B. Varanus (dorsal view)

Fig. 11.14

Iguana hind limb step cycle

Note: Limbs lateral, pelvis rotates

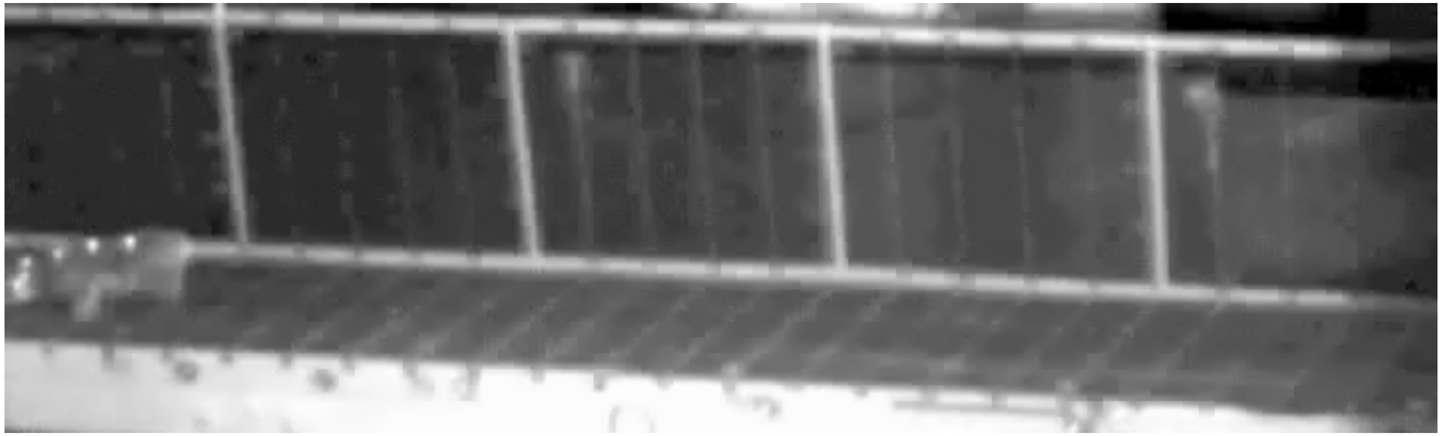


"toe-off"

"mid-stance"

"foot down"

Fig. 11.15



In sprawling tetrapods, the humerus or femur rotates

Bones are not well-designed for rotational stress.

May explain thicker limb bones in sprawling tetrapods

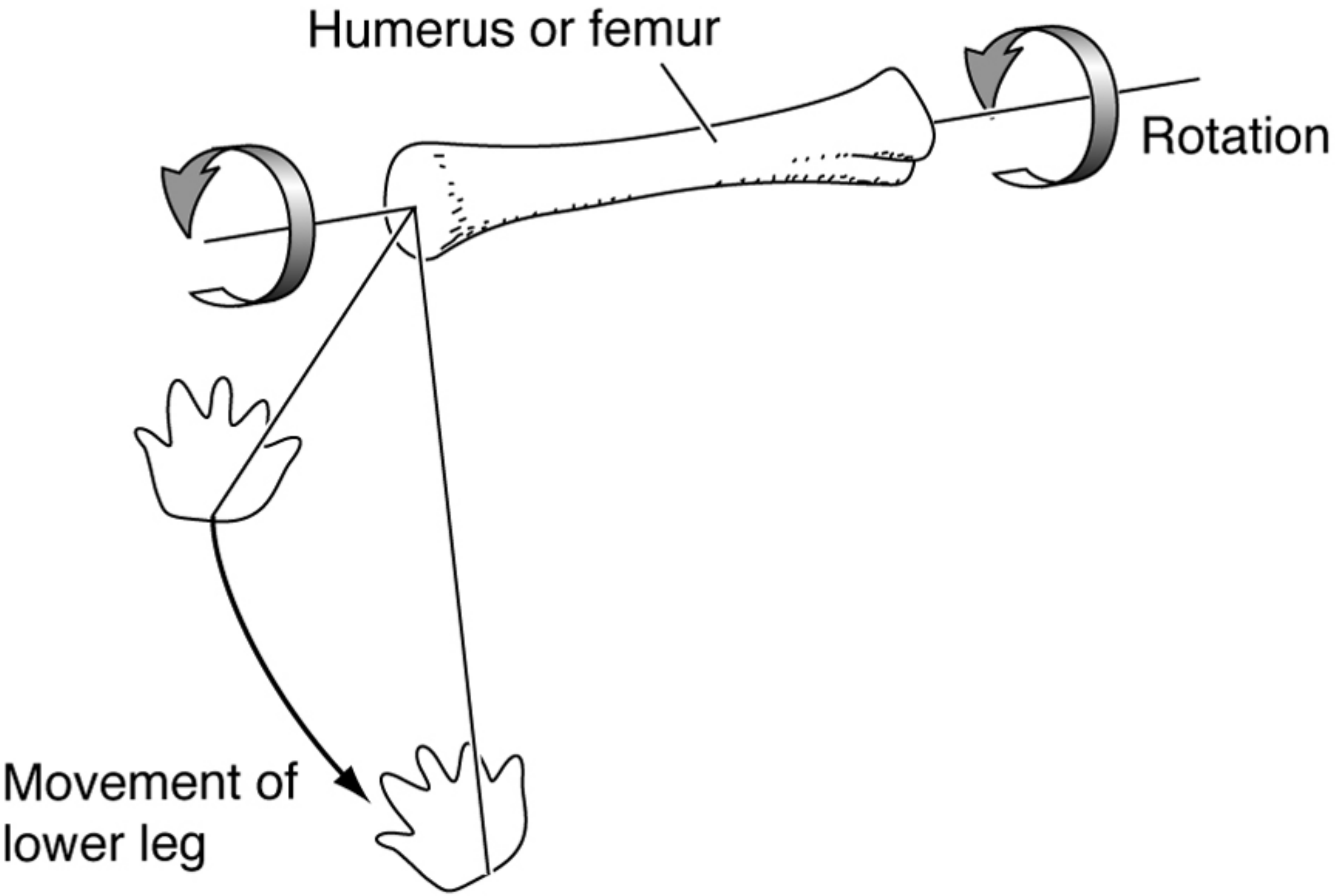
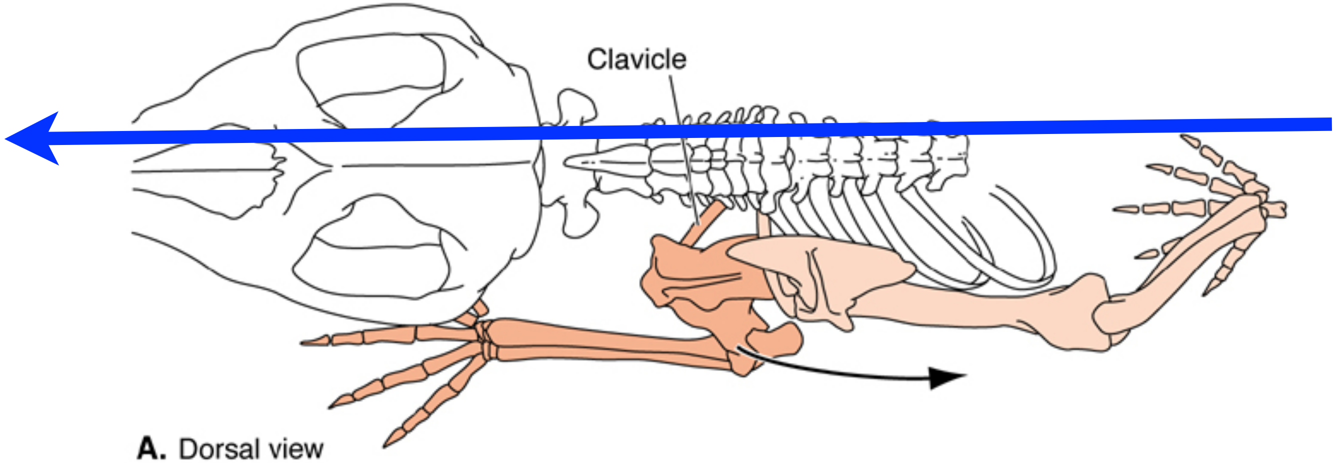


Fig. 11.16

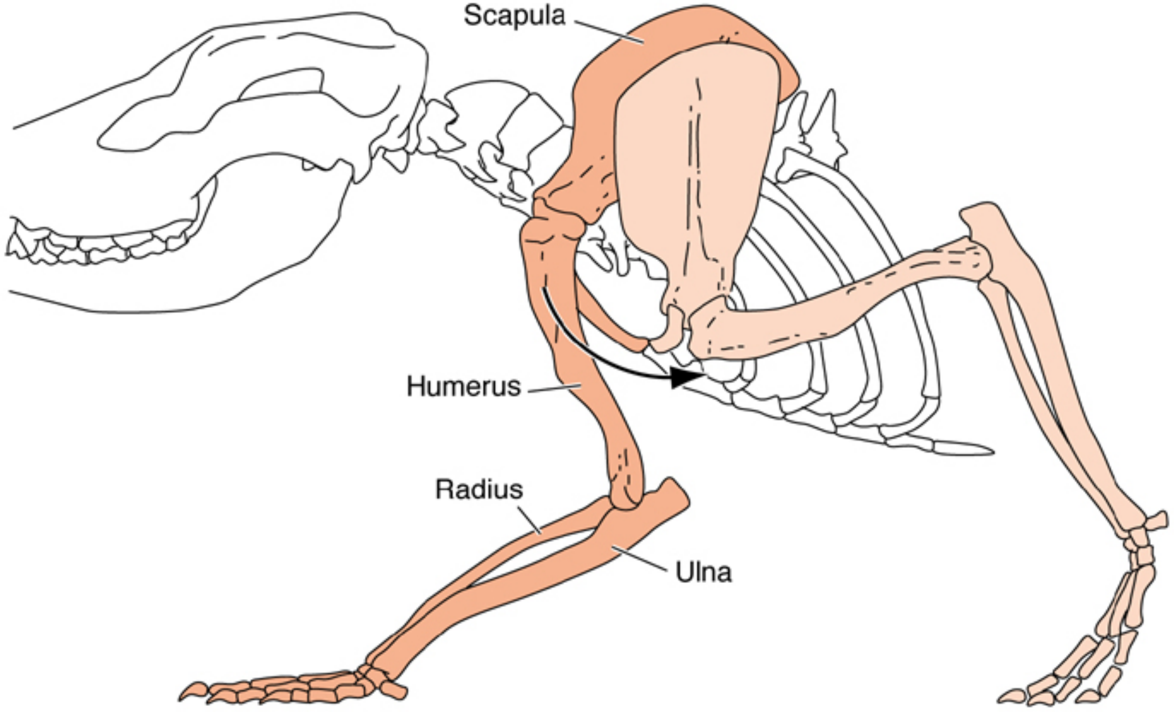
Mammal limb cycle (opposum)

Limb under body



A. Dorsal view

Notice movement of scapula



B. Lateral view

Hind Limb cycle in opposum

Limb moves in parasagittal plane.

Pelvis moves little.

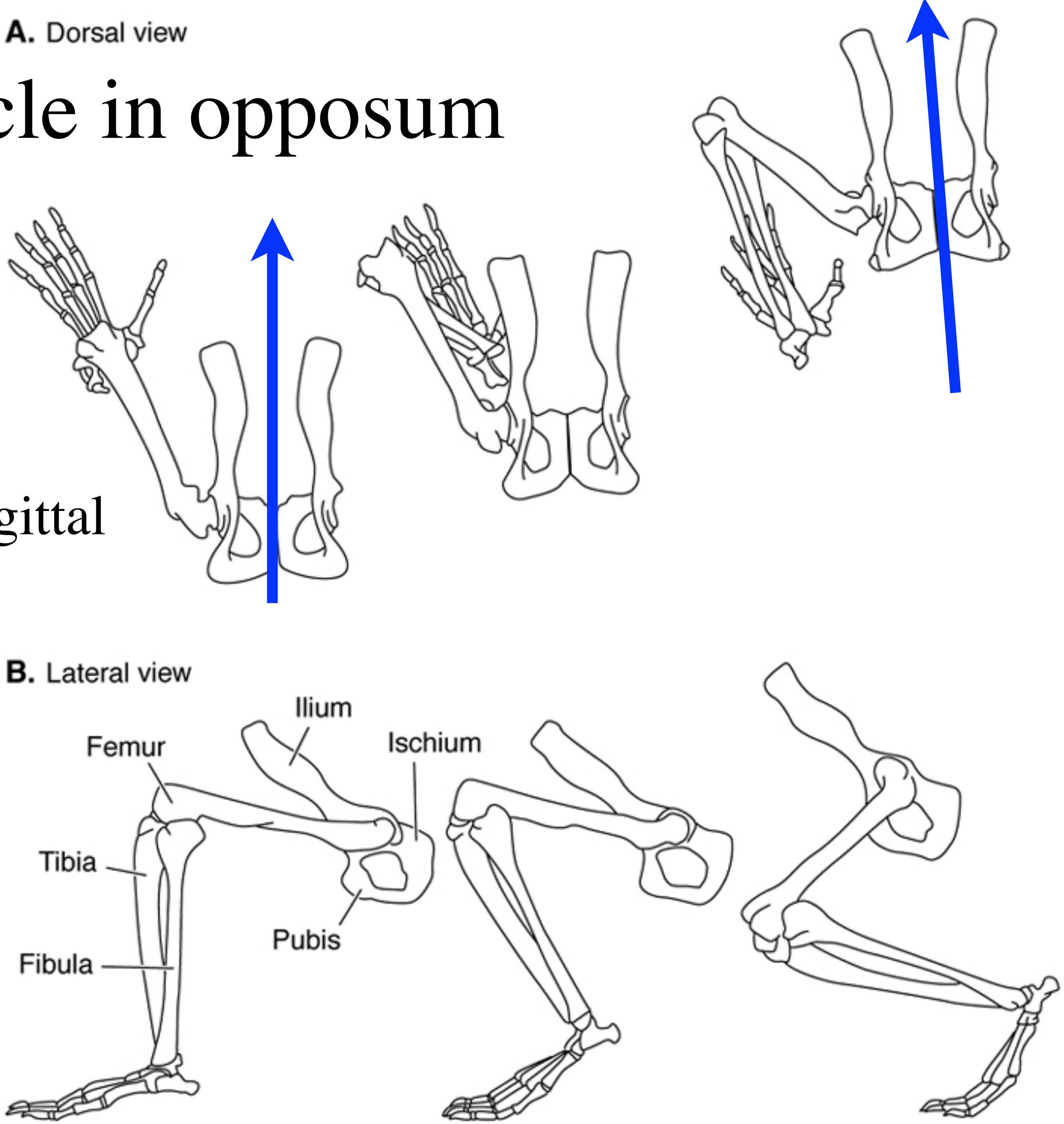
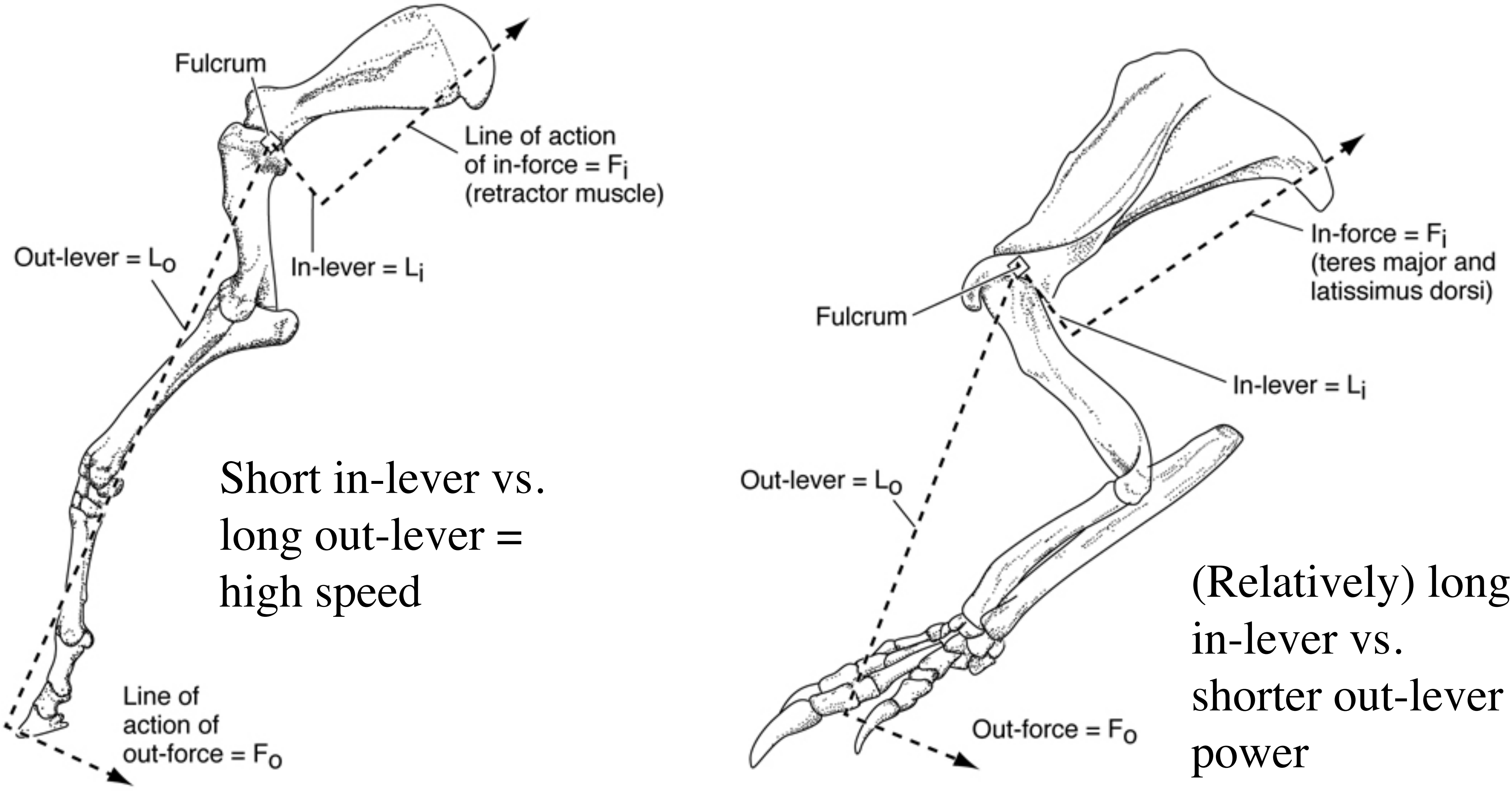


Fig. 11.18

Power vs. speed **lever arm tradeoff**



Short in-lever vs.
long out-lever =
high speed

(Relatively) longer
in-lever vs.
shorter out-lever =
power

A. Design for speed (Equus)

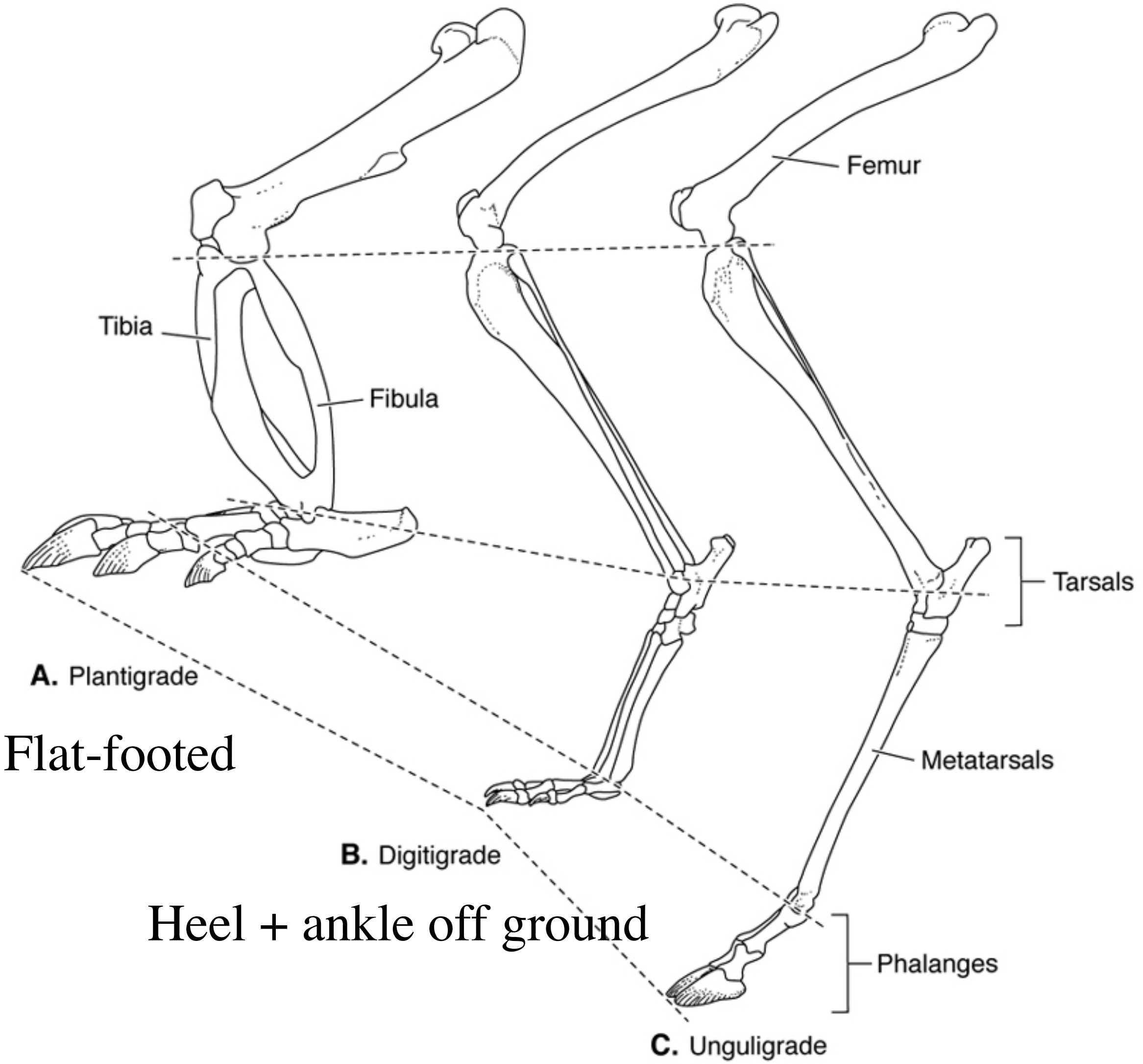
B. Design for power (Armadillo)

Fig. 11.21

Limb elements lengthened for speed

Increased limb length -> increased stride length -> incr. speed

Some mammals increase limb length by “walking on their toes”



Flat-footed

Heel + ankle off ground

Walking on tips of toes

Fig. 11.22

Longer limbs achieve faster velocities at foot.

Reduce costs of swinging limbs by reducing mass of foot.

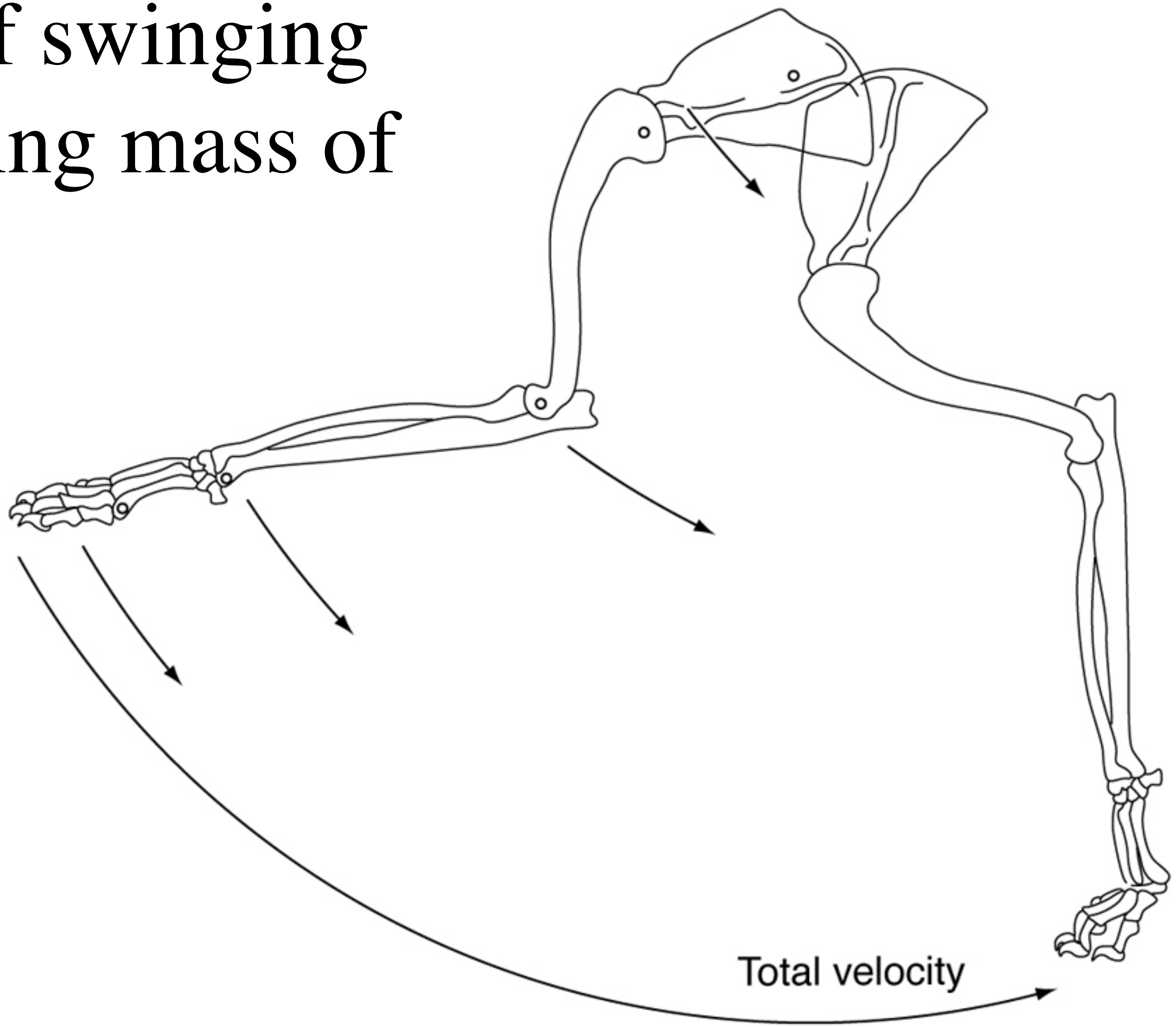


Fig. 11.24

Toe reduction reduces mass of distal element

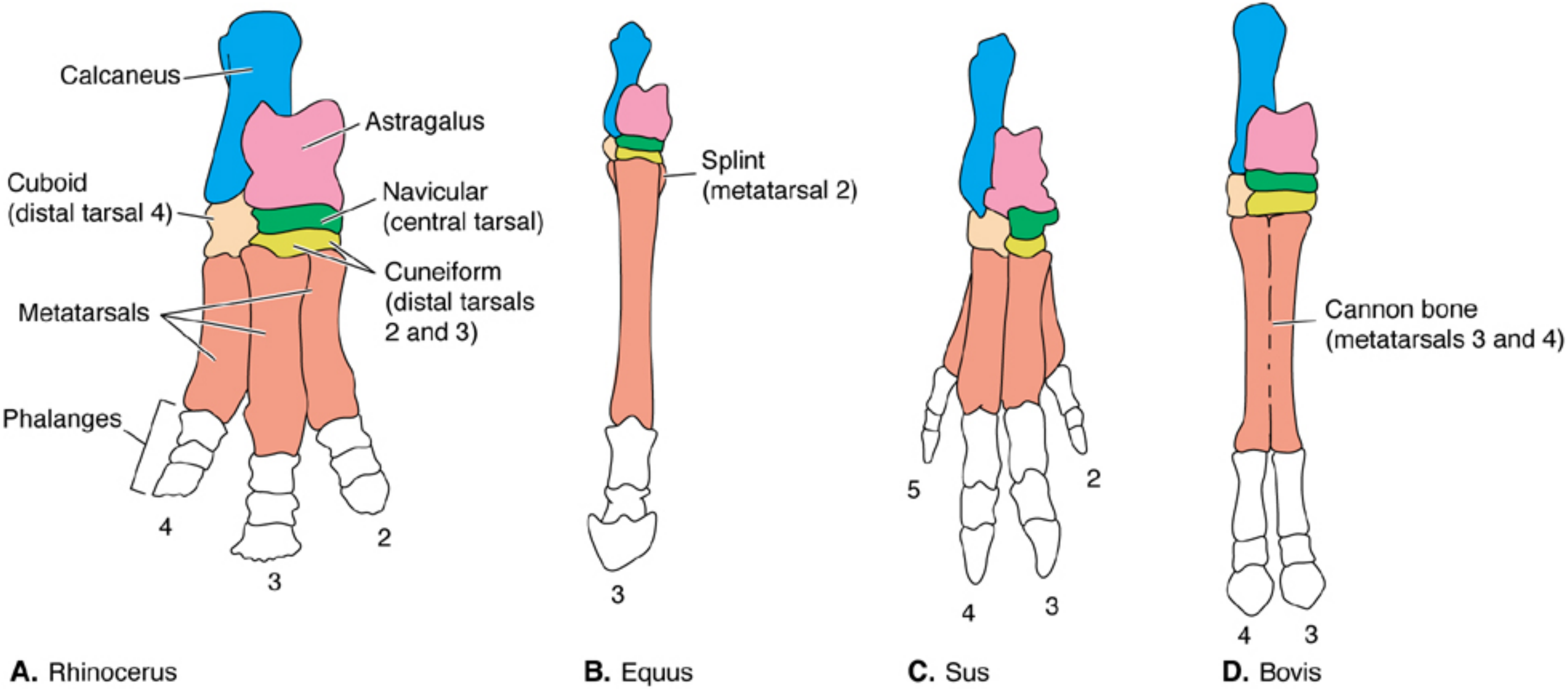
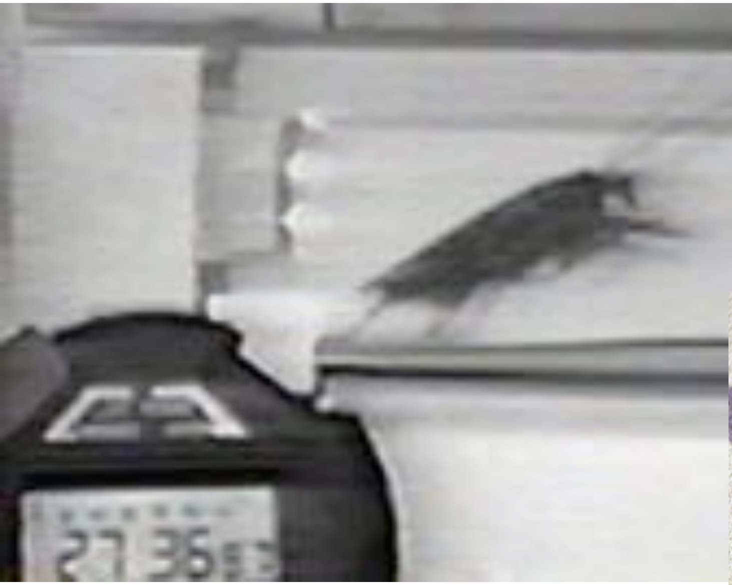


Fig. 11.23

Are there any Models that can explain Walking and Running?

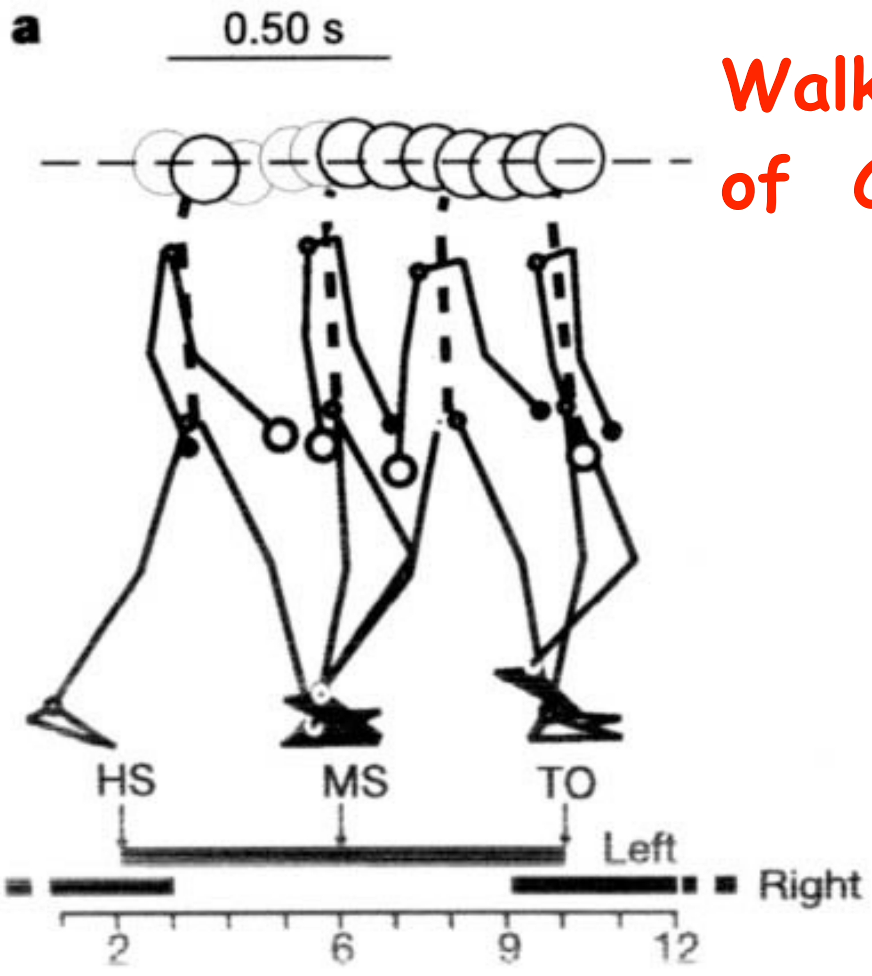
Are the mechanics of walking and running (at steady speed) designed to conserve energy?

In terms of biomechanics and energetics



We all walk and run the same way.

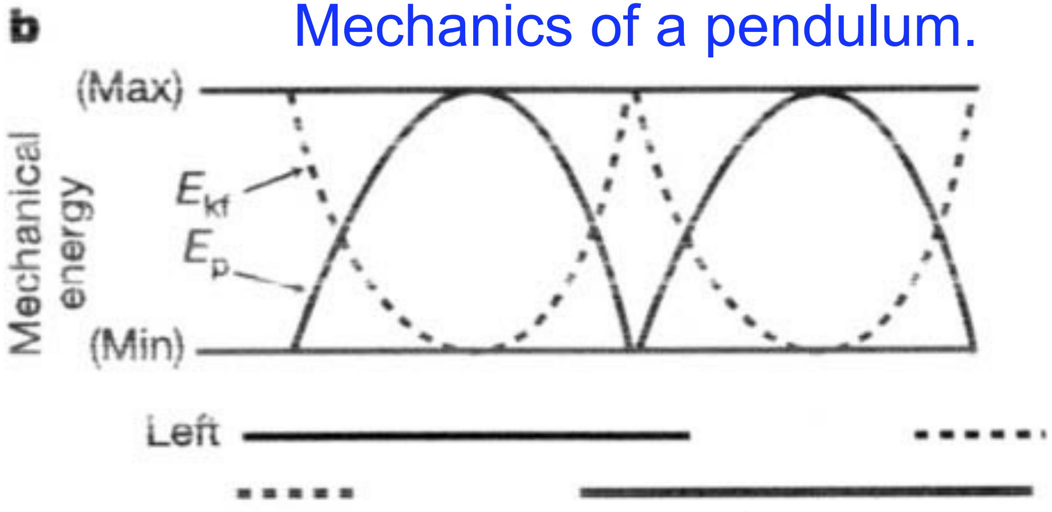
Walking Animals take advantage of Conservation of Energy



Walking is a transfer of kinetic and potential energy. With each step we fall forward and then catch ourselves.

At steady speed, not all of the force required for walking is powered by muscles -- some of it is "recycled"

Mechanics of a pendulum.

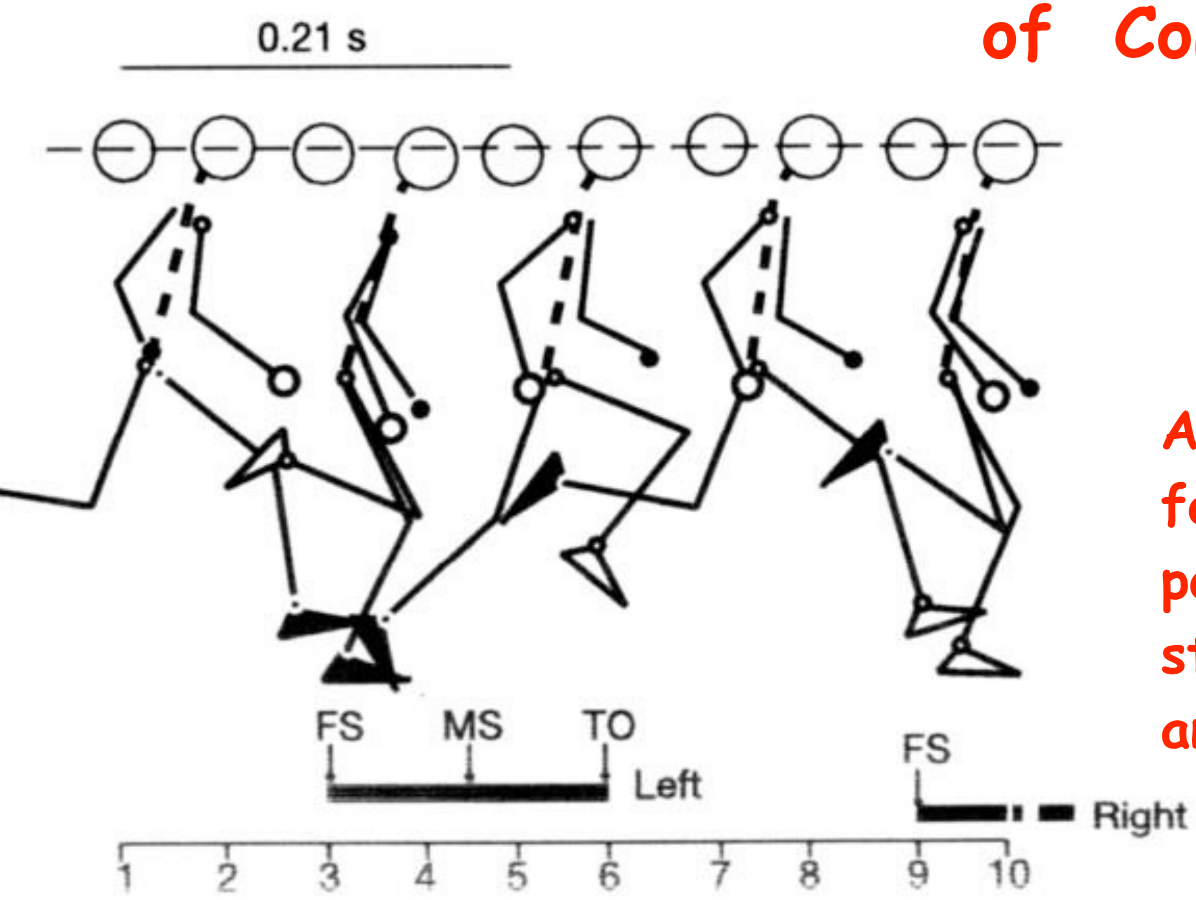


$E_{kf} = 1/2mV^2$

$Ep = mgh$

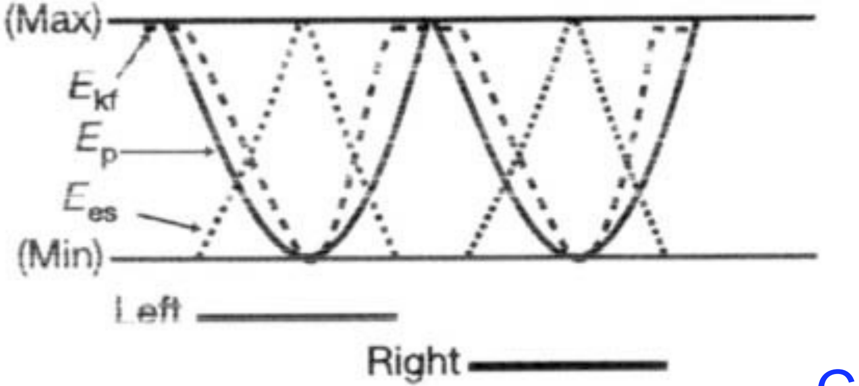
Changes in KE and PE are in out of phase

Running Animals take advantage of Conservation of Energy



Running is a bounce, a mass and a spring.

At steady speed, not all of the force required for running is powered by muscles -- some of it is stored in elastic elements (tendons) and recovered.



E_{es} = elastic strain energy

Changes in KE and PE are in phase

Masters of Elastic Storage and Recovery: Kangaroos

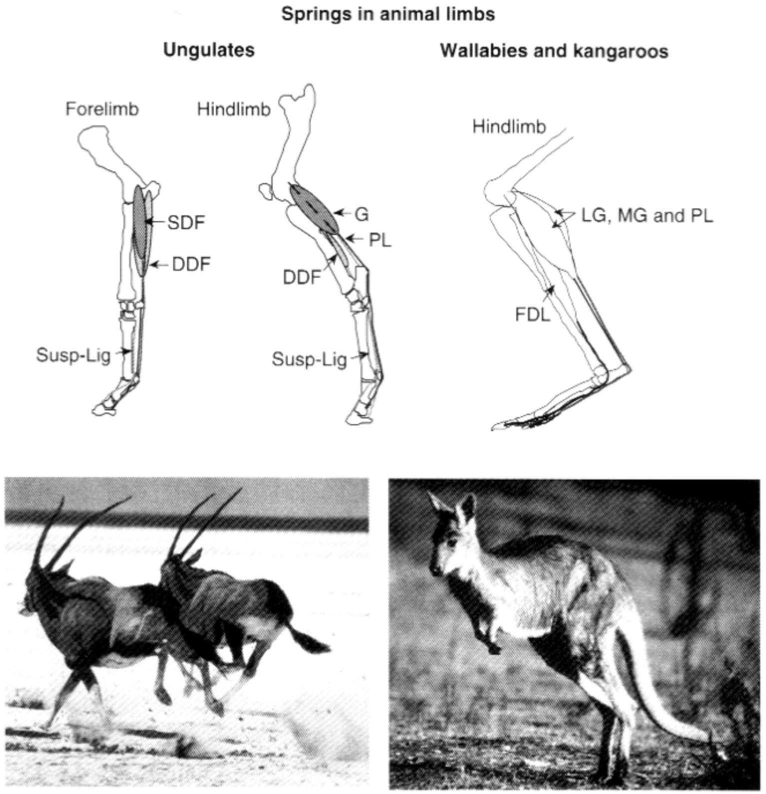
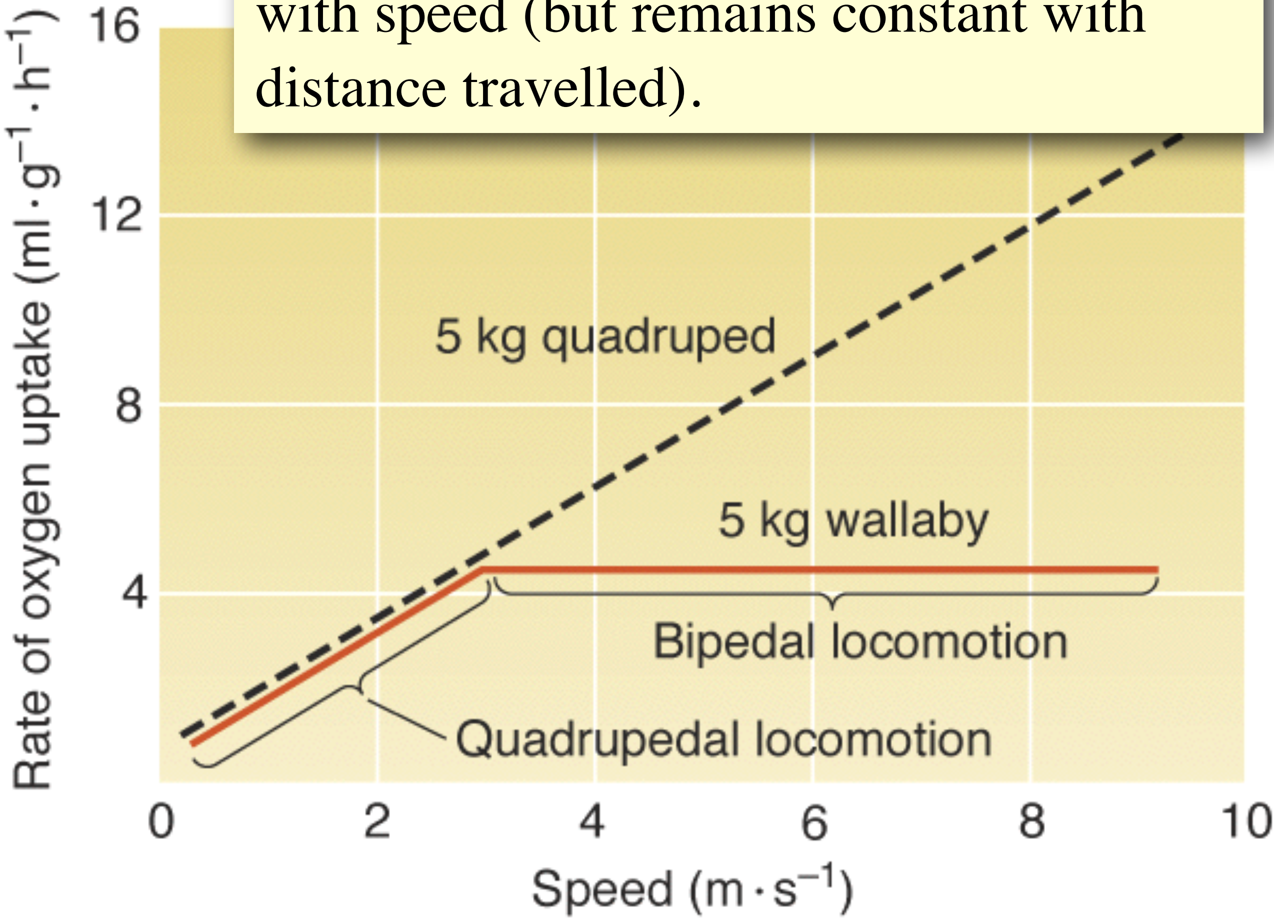


Fig. 3.14 The principal muscle–tendon units in (a) the hind legs of kangaroos and wallabies and (b) the limbs of horses and other ungulates that are specialized for economical force generation by short-fibered muscles which attach to long tendons for elastic energy savings.

Generally, Cost of Transport increases with speed (but remains constant with distance travelled).



BUT in Kangaroos and wallabies, COT stays same or DECREASES with speed. HOPPING -> Greater KE->PE storage and recovery?

Gaits

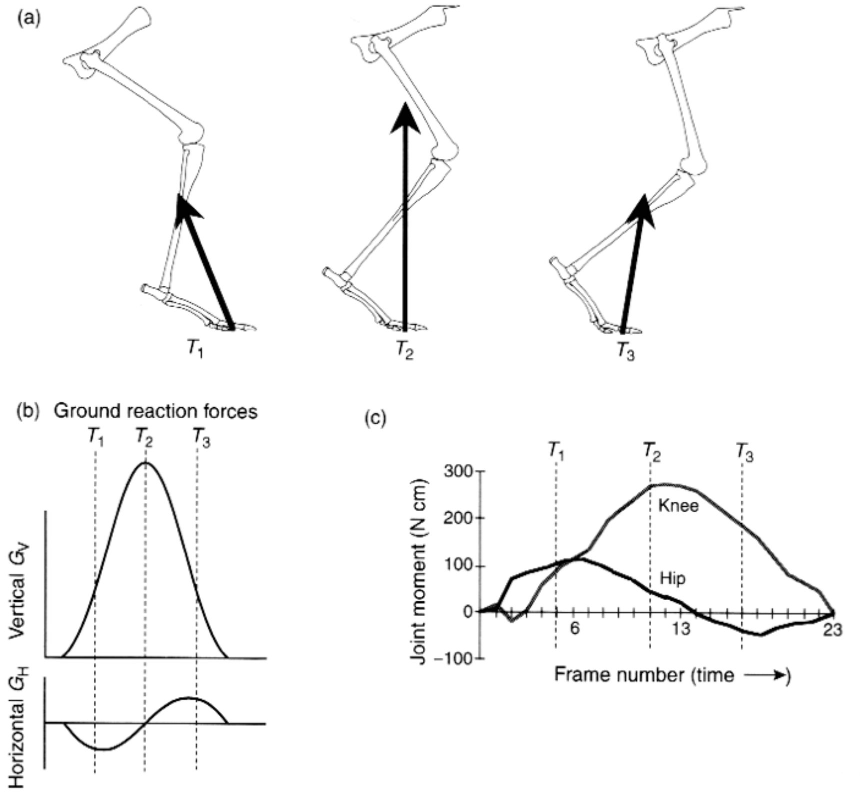
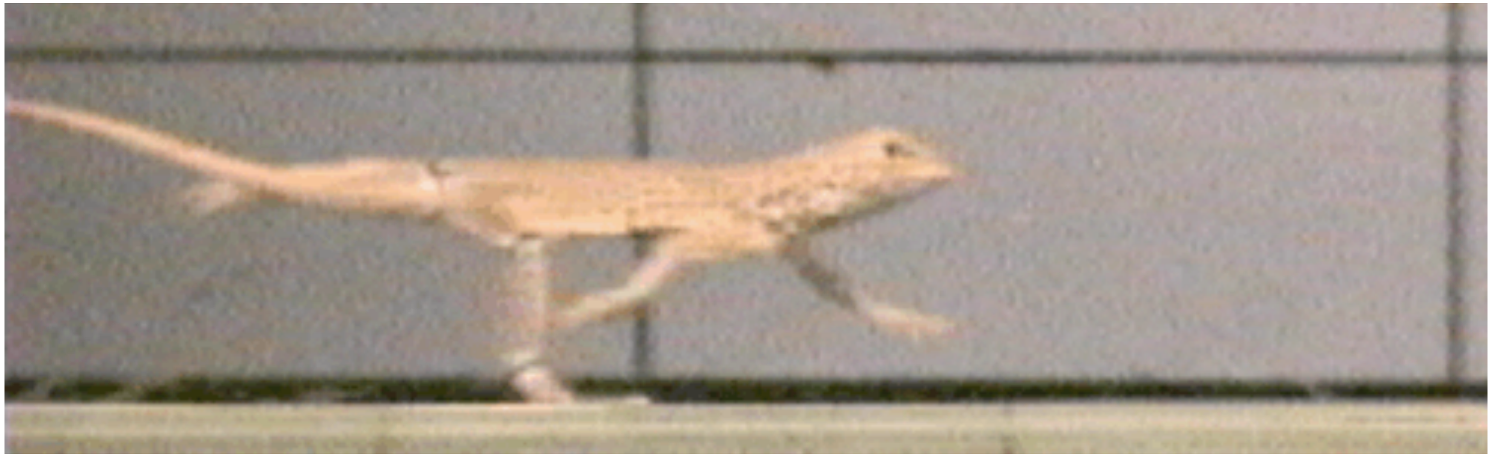


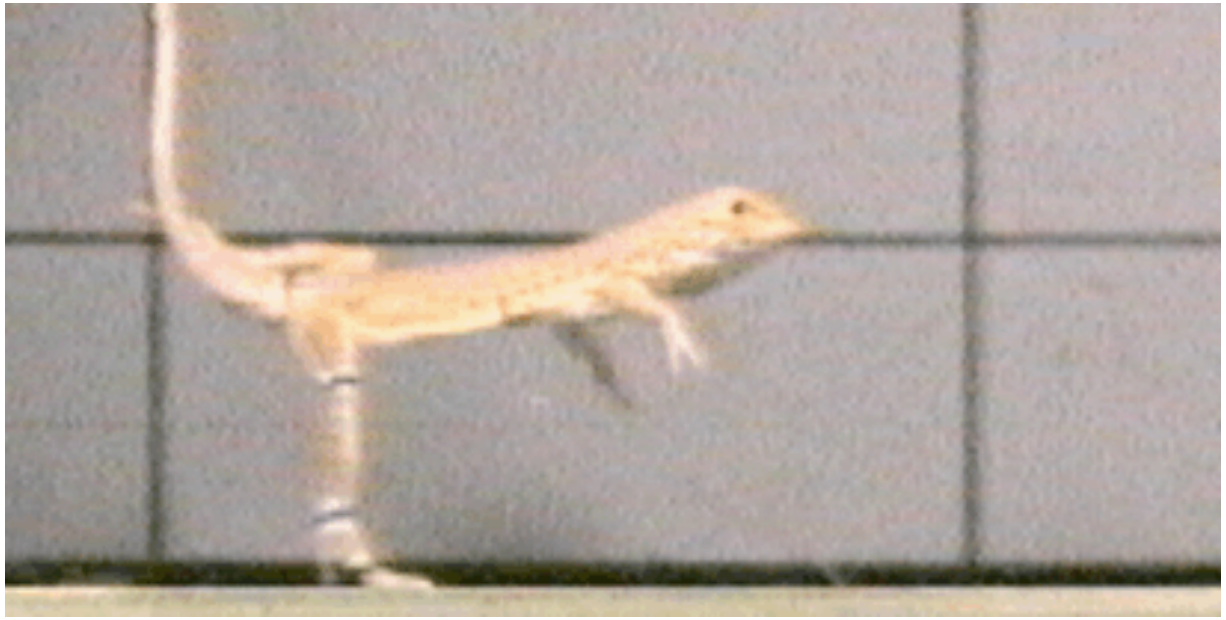
Fig. 3.5 (a) Changes in limb configuration with respect to the net ground reaction force G for three frames (times T_1, T_2 and T_3) corresponding to the vertical and horizontal ground forces shown in (b). (c) Changes in ground reaction force moments acting at the hip and knee versus time. G exerts a flexor moment at the knee throughout most of limb support (requiring knee muscle extensor force to counter this). G also exerts a flexor moment at the hip (requiring hip extensor force) during the first 60 per cent of limb support but, as G passes behind the hip joint, it exerts an extensor moment during the latter 40 per cent of limb support (which must be balanced by hip flexor activity).

Basal tetrapods can trot (not gallop)

Quadrupedal trot
Uma scoparia



Bipedal trot
Uma scoparia



http://www.biology.uc.edu/faculty/jayne/videos.htm

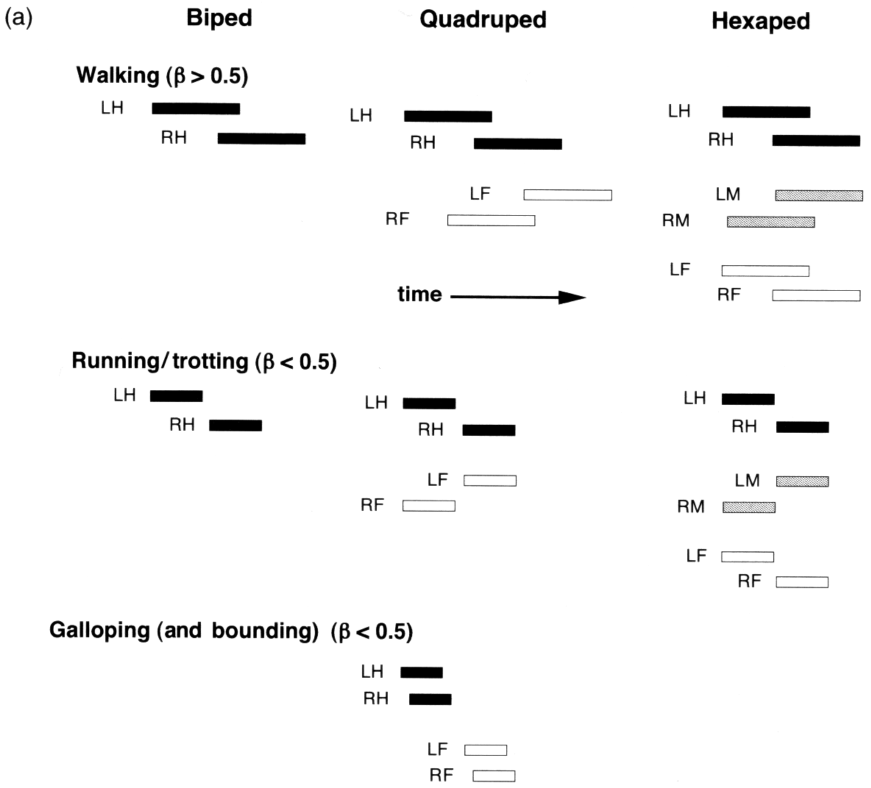
Crocodiles and Mammals can gallop

Gaits of land animals

Walk > 50% duty factor
No aerial phase
In quadruped, triangles of support.

Run < 50% duty factor
Have aerial phase
In quadruped: run, trot, gallop. Each gait has a different pattern of support.

Gait diagrams



Quadrupedal Limb support patterns

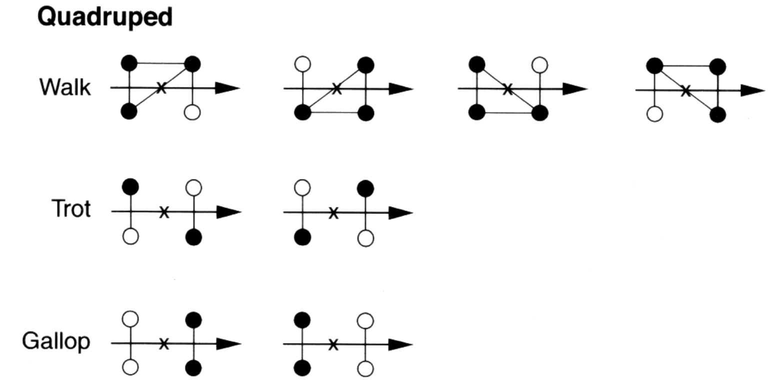
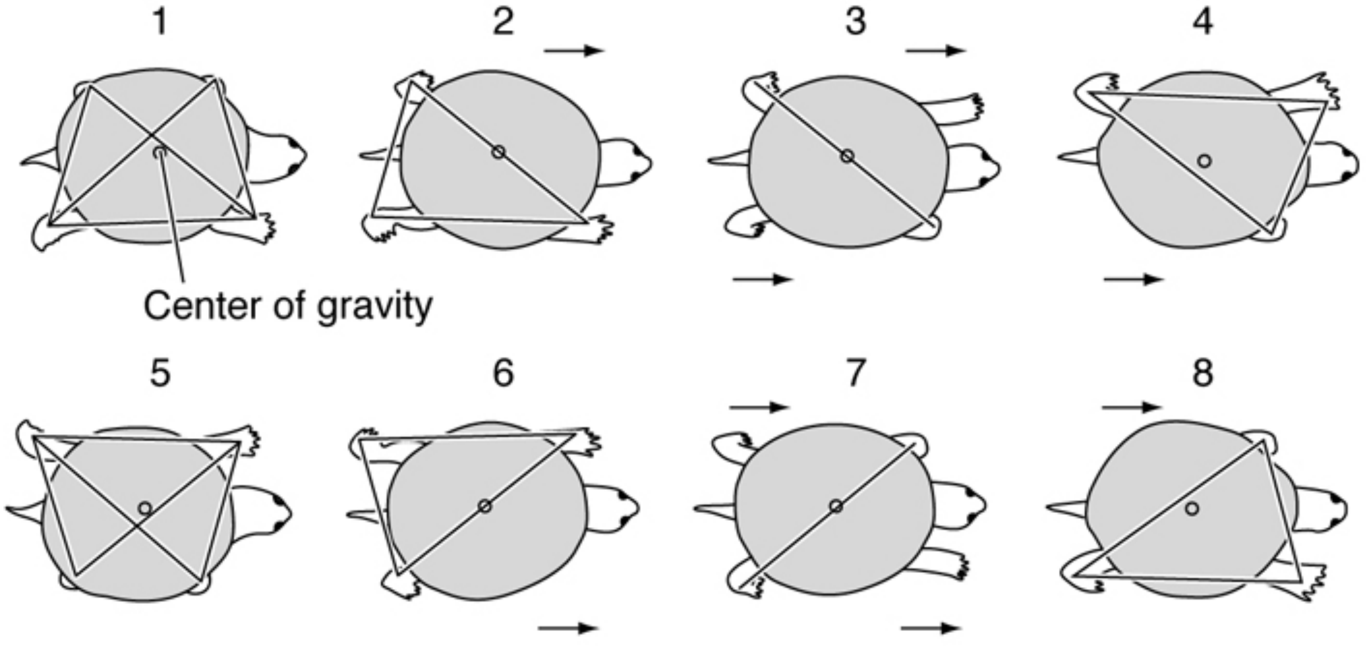
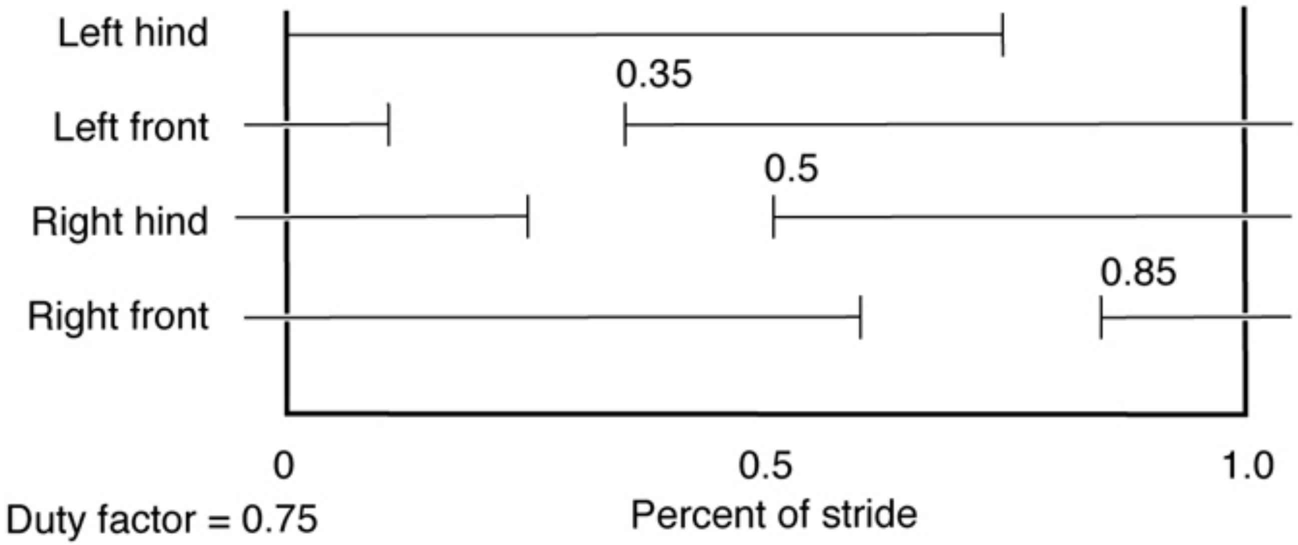


Fig. 3.7 (a) Gait diagrams for a biped, a quadruped and a hexaped using different gaits:LF, left forelimb; RF, right forelimb; LH, left hindlimb; RH, right hindlimb; LM, left middle limb; RM, right middle limb). The timing and duration of foot support periods is shown by the rectangles (β is the duty factor). (b) Representation of the pattern of limb support for a quadruped moving to the right (arrow) for each gait. Solid circles depict the limb's support phase and open circles the limb's swing phase (the cross represents the location of the animal's CM).

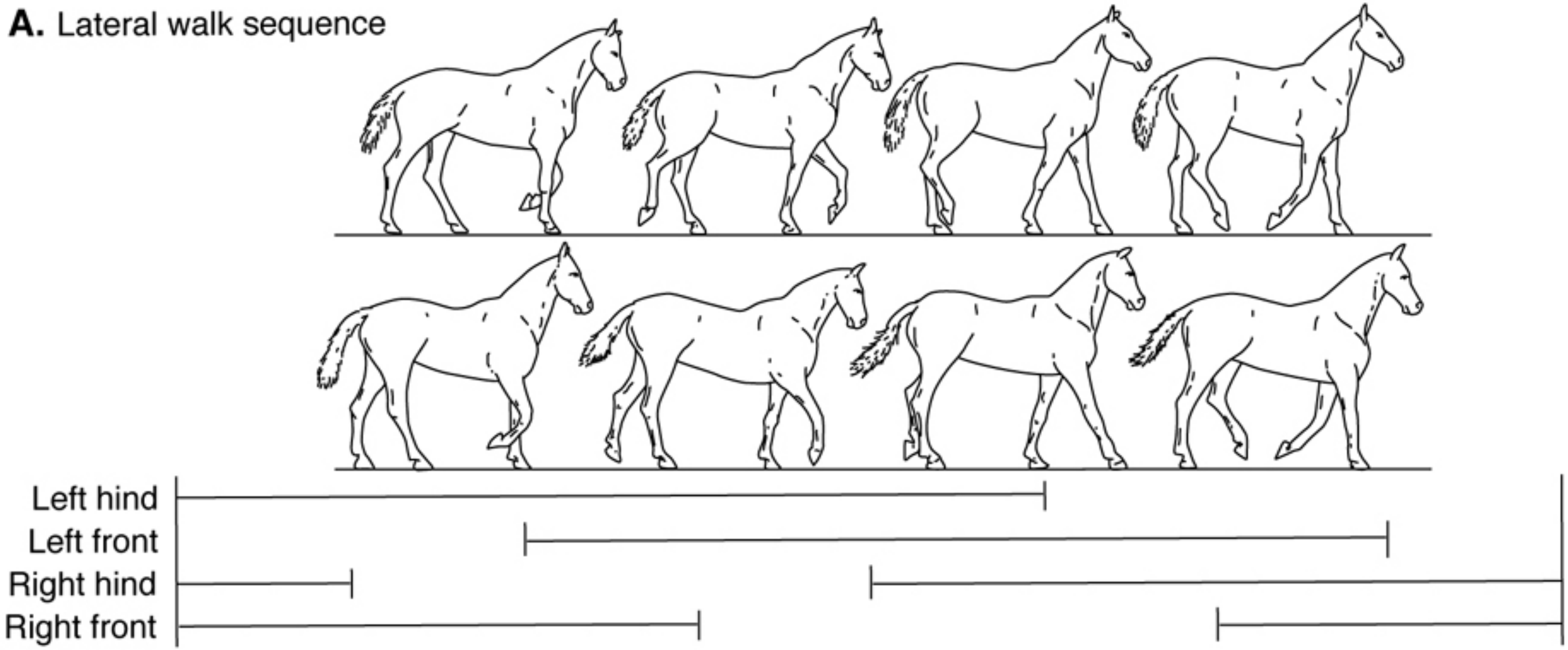
Fig. 11.19



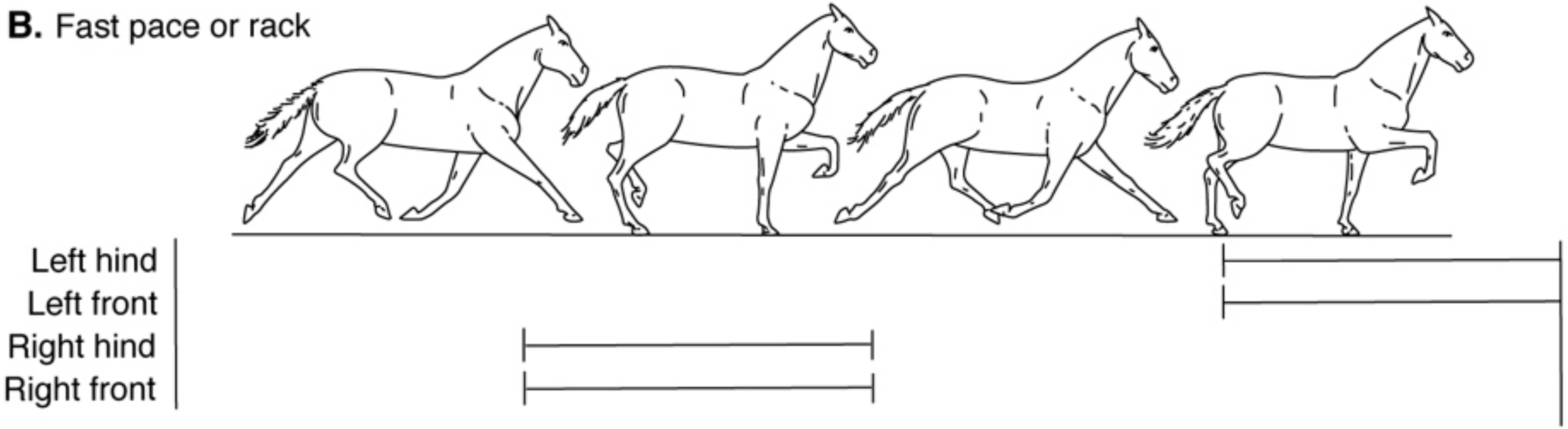
A. Limb movements and foot placements during one stride of a turtle



B. Gait diagram of the stride shown in A



A. Lateral walk sequence



B. Fast pace or rack

Fig. 11.20

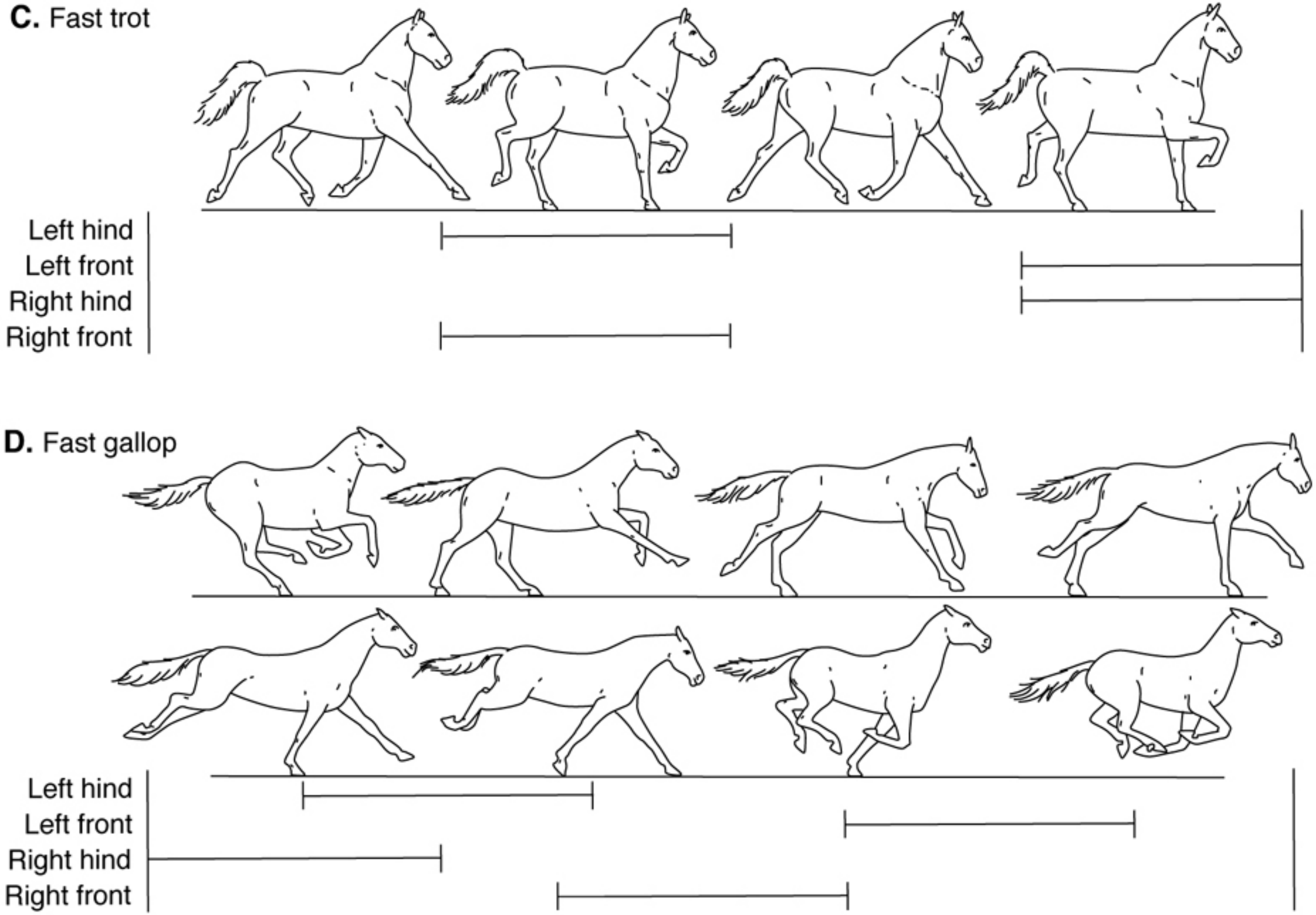

C. Fast trot
Left hind
Left front
Right hind
Right front
D. Fast gallop
Left hind
Left front
Right hind
Right front

Fig. 11.20

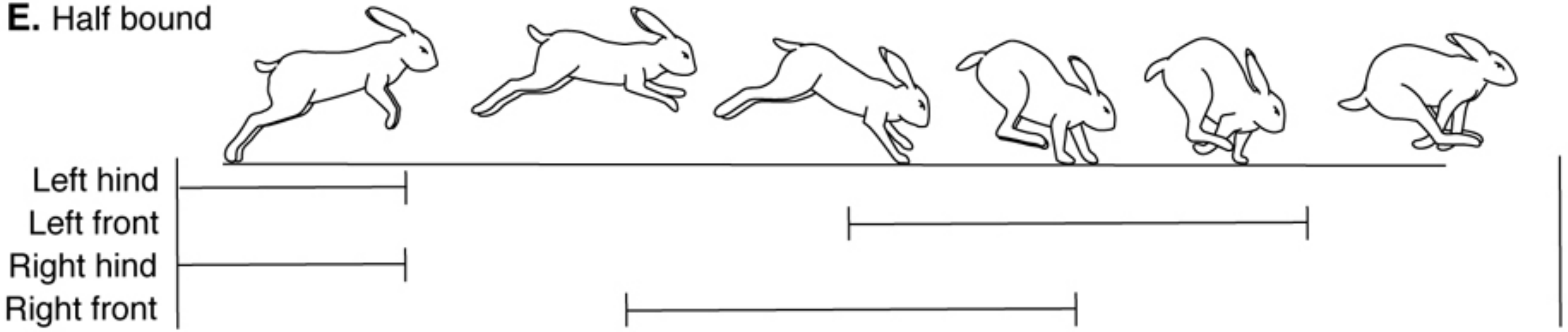


Fig. 11.20

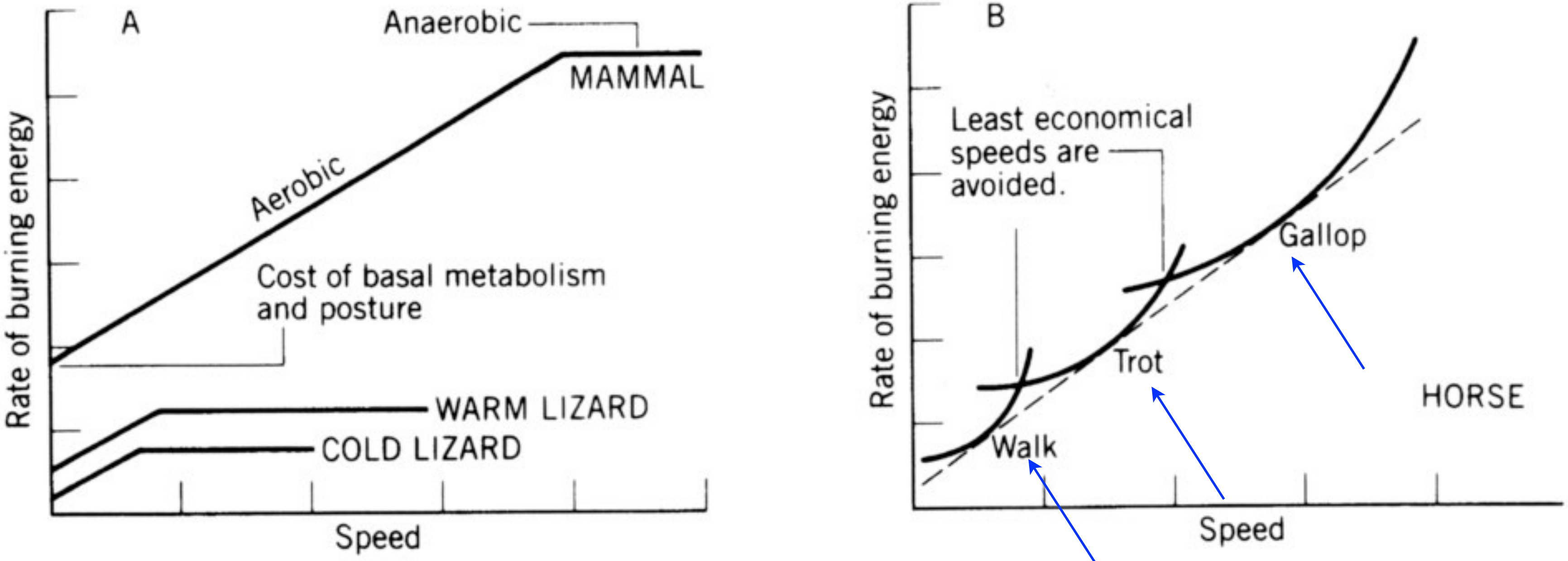
Animals prefer different gaits for different speeds

- Walk = slowest gait = no aerial phase (one foot always on ground). Usually Duty factor < 0.5
- Running gaits:
  - Trot
  - Gallop
  - Bound/Half Bound

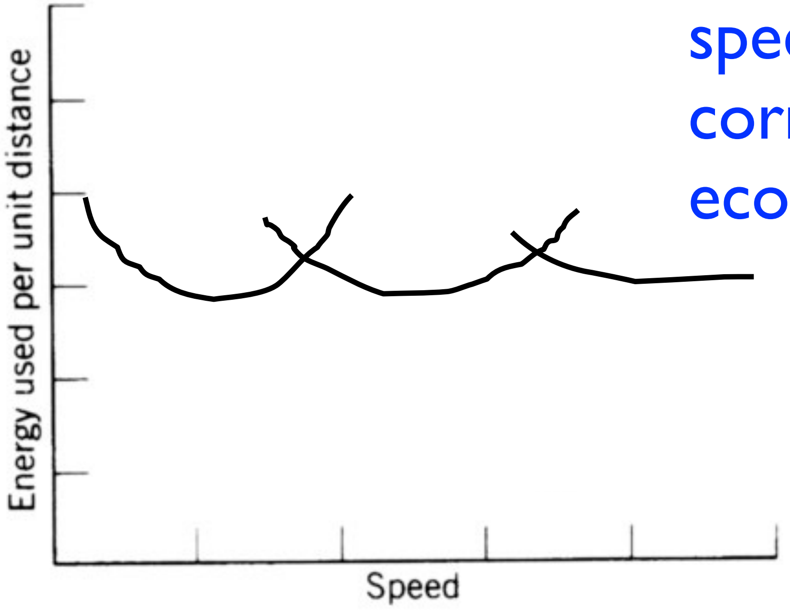
WHY?

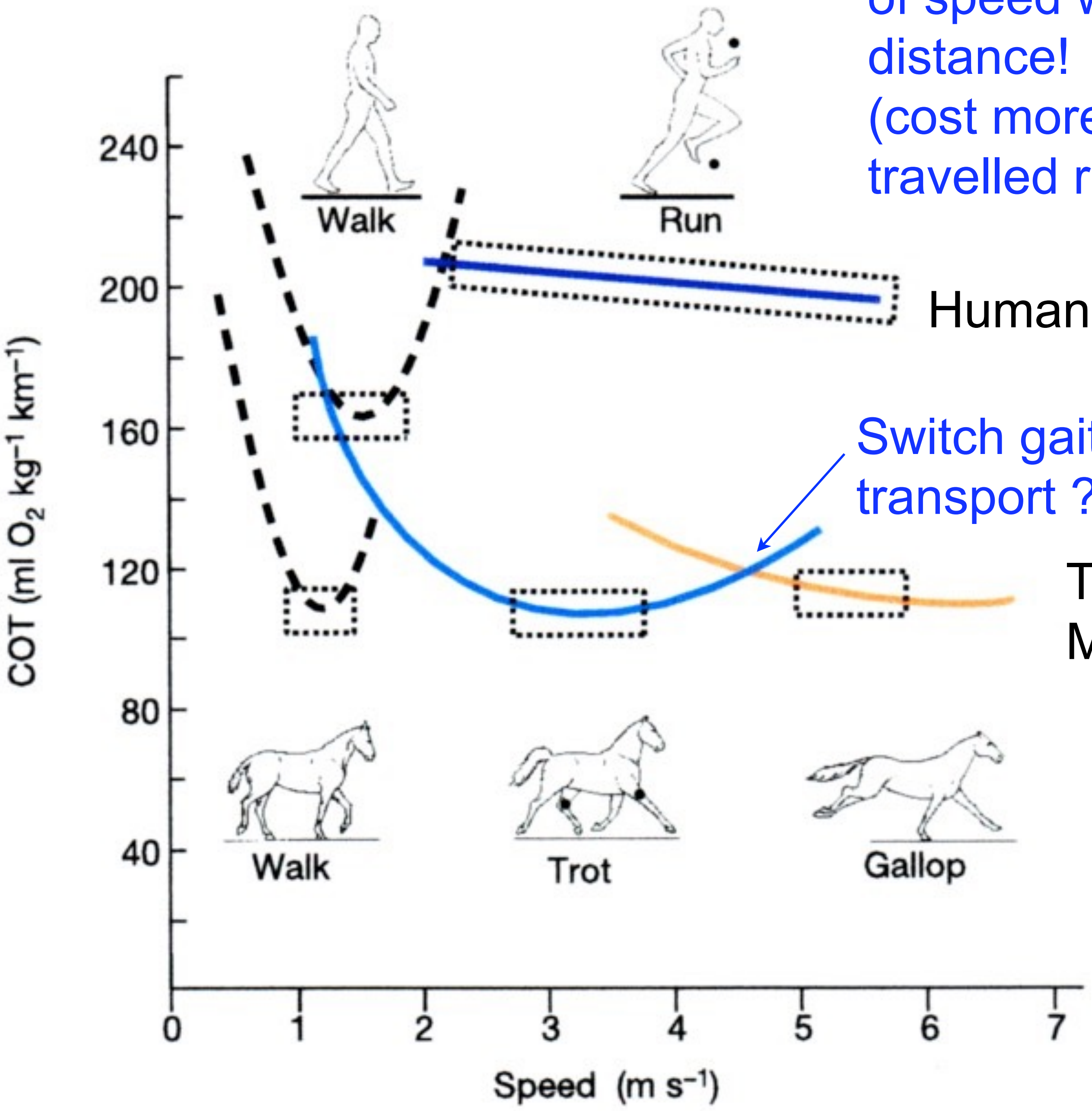
Maximize Speed?

Locomotor energetics



Animals have preferred speeds for each gait which corresponds to energy economy



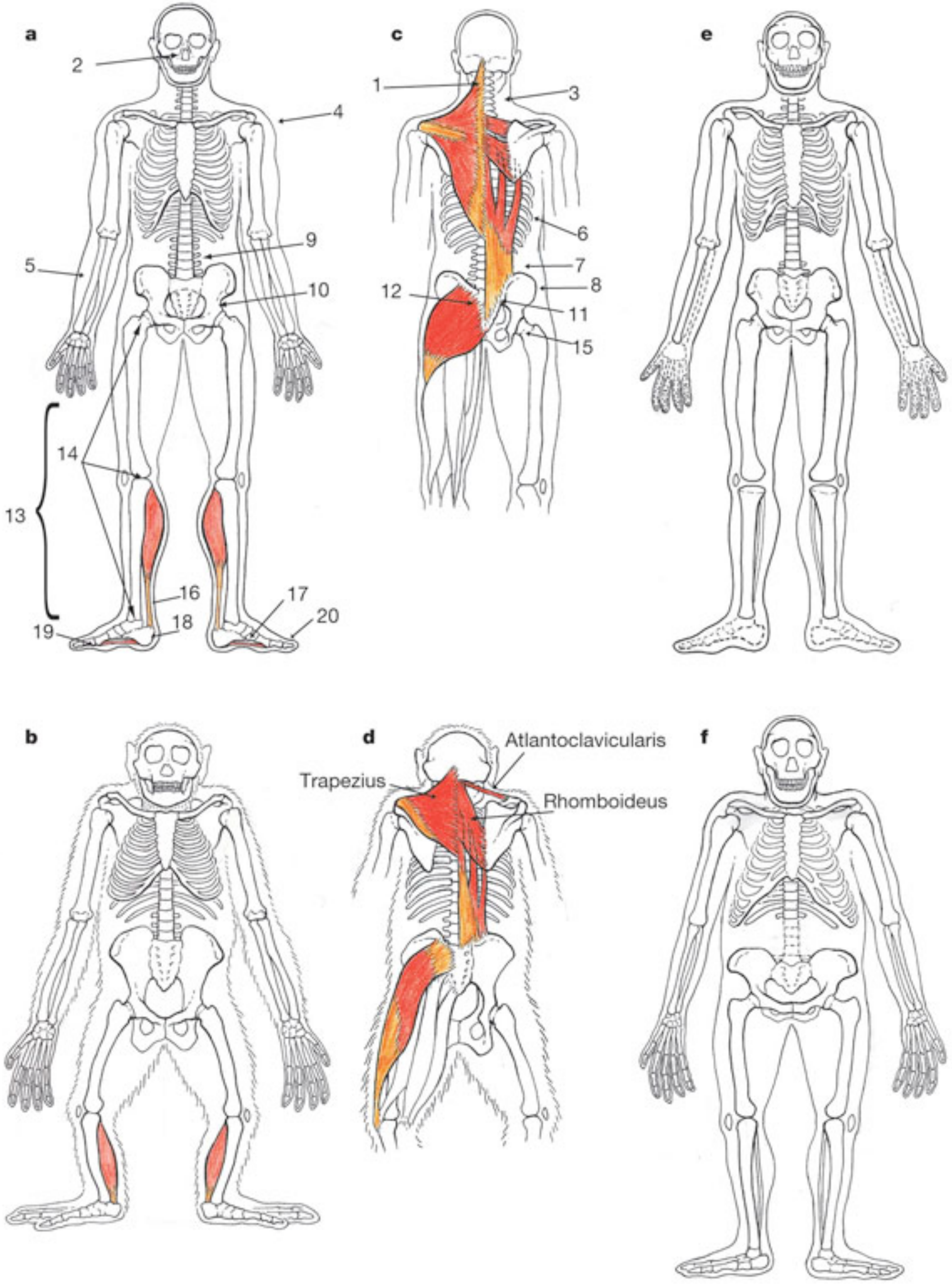


Cost of running nearly independent of speed when we normalize for distance! -- change gaits? (cost more related to distance travelled rather than speed)

Human: Adapted for distance?

Switch gaits to Minimize Cost of transport ?

Typical Quadrupedal Mammal Pattern



From the following article:
Endurance running and the evolution of *Homo*
Dennis M. Bramble and Daniel E. Lieberman
Nature **432**, *345-352(18 November 2004)*
doi:10.1038/nature03052

Can Elephants Run?

Walk

Biomechanics: Are fast-moving elephants really running?
John R. Hutchinson, Dan Famini, Richard Lair and Rodger Kram
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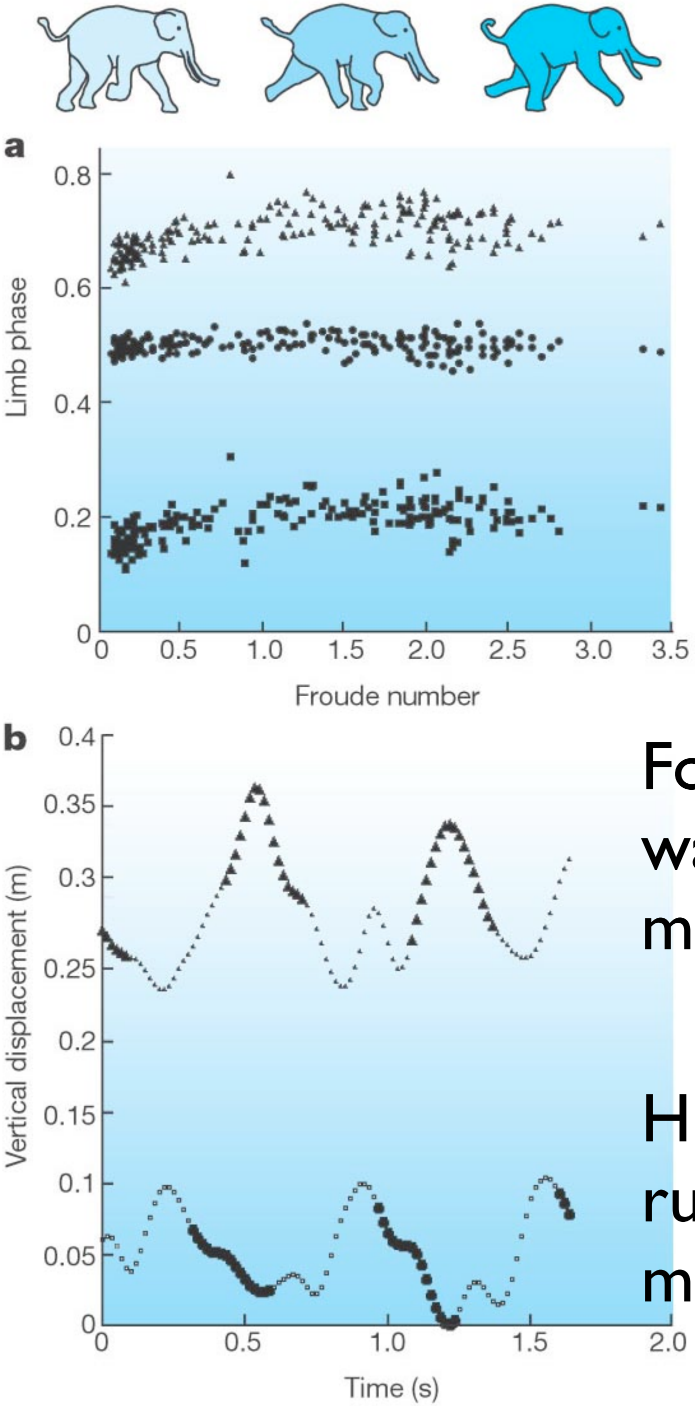
Can Elephants Run?

Run?



Forelimbs walking mechanics?

Hindlimbs running mechanics?

cf_cheetah1.ram

Cheetahs lengthen stride even further by hyper-extension of spine

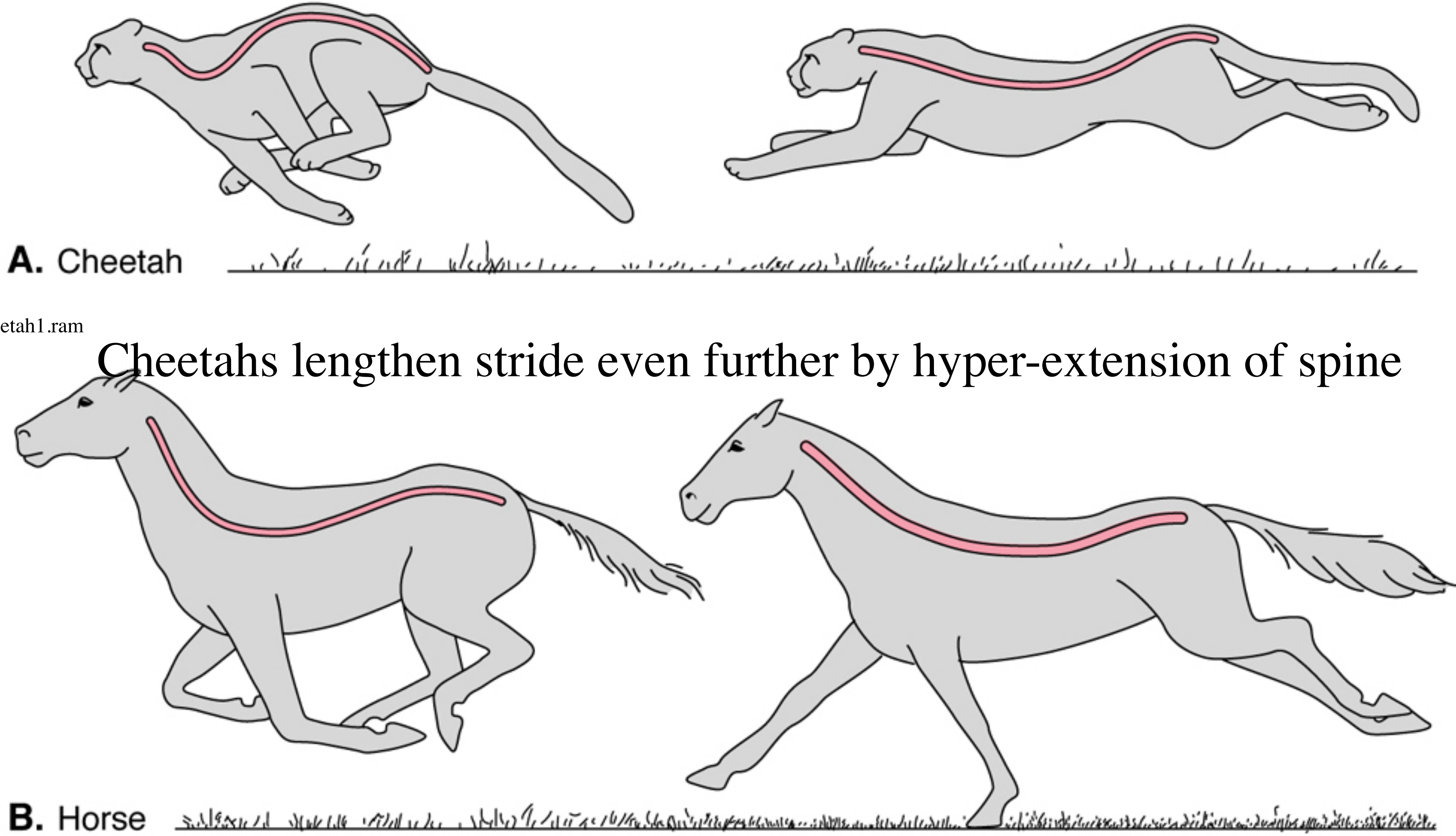
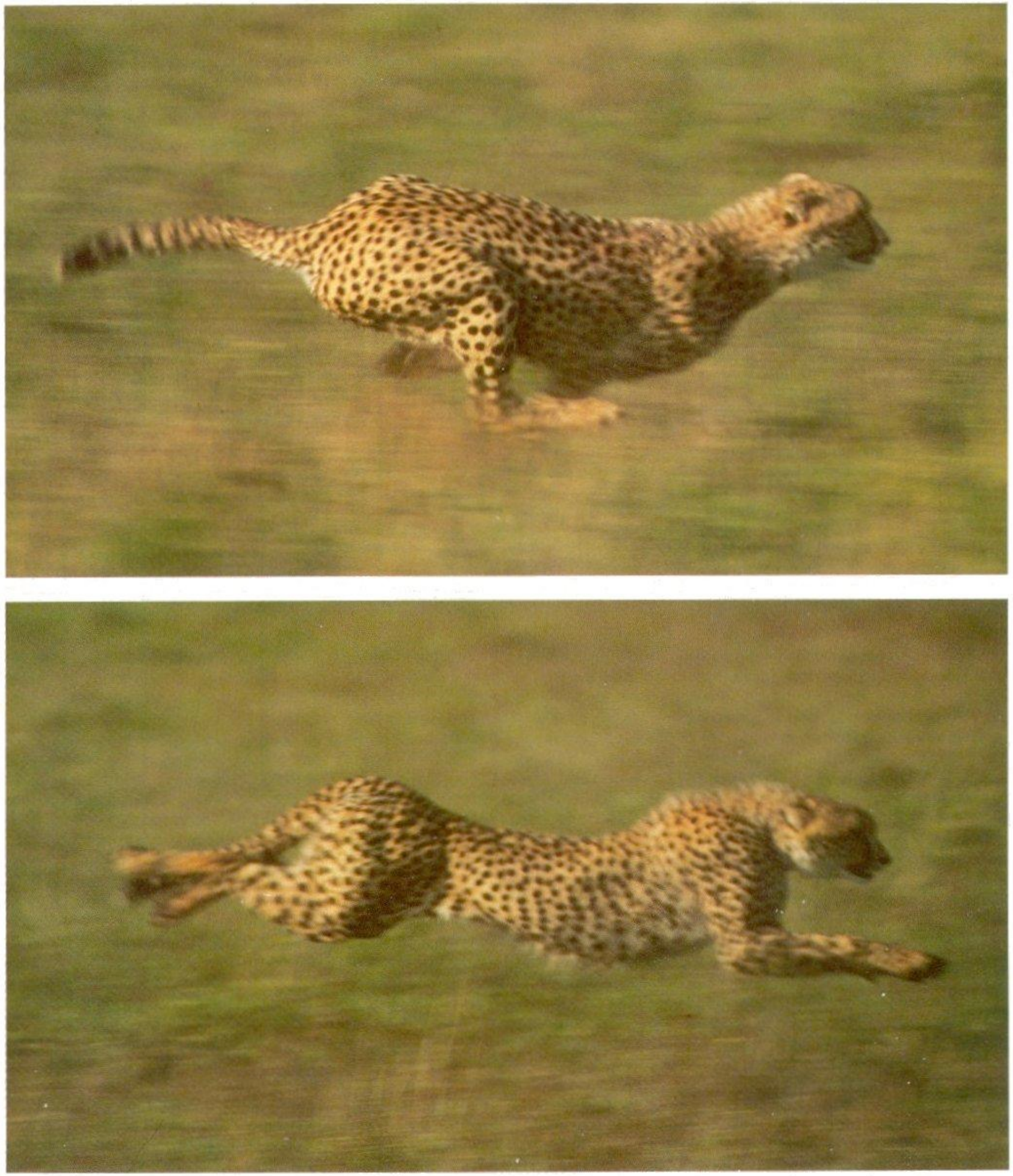


Fig. 11.26

http://www.youtube.com/watch?v=KIeXEiJuJUY



CHEETAH, the world's fastest sprinter, is shown in two of the positions it assumes while running at top speed. Often clocked at 70 miles per hour, the cheetah is airborne half of the time during a chase and can speed to 50 m.p.h. from a standing position in seconds.

http://www.animalpicturesarchive.com/animal/a6/MKramer-cheetah_running.jpg&imgrefurl=http://www.animalpicturesarchive.com/view.php%3Ftid%3D1%26did%3D122760&h=1260&w=1041&sz=168&tbnid=HIAb62AP7E8J:&tbnh=149&tbnw=123&start=22&prev=/images%3Fq%3Dcheetah%2Brunning%26start%3D20%26hl%3Den%26lr%3D%26sa%3DN

Other locomotor Modes

Avoid Drag -- Just Walk on the Water

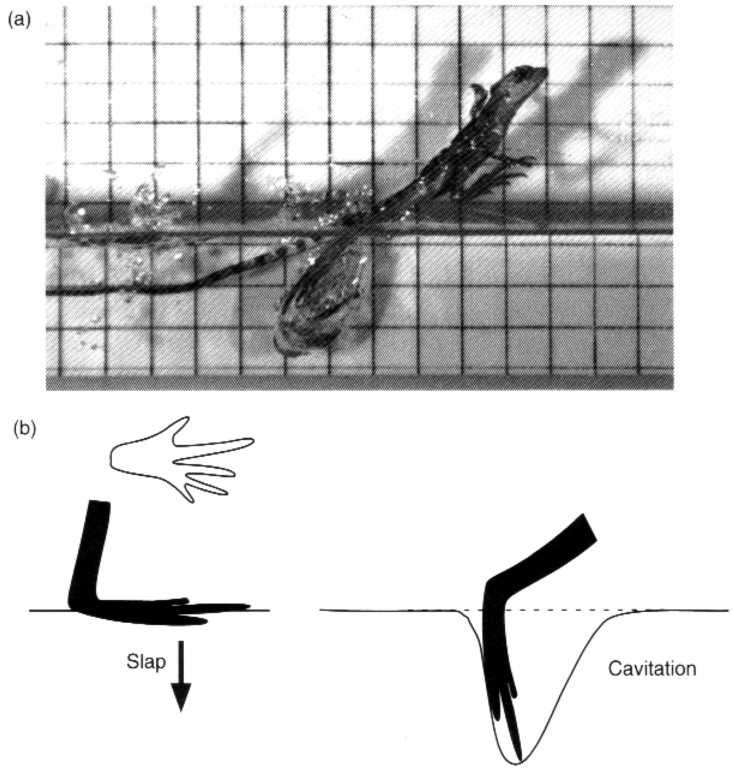
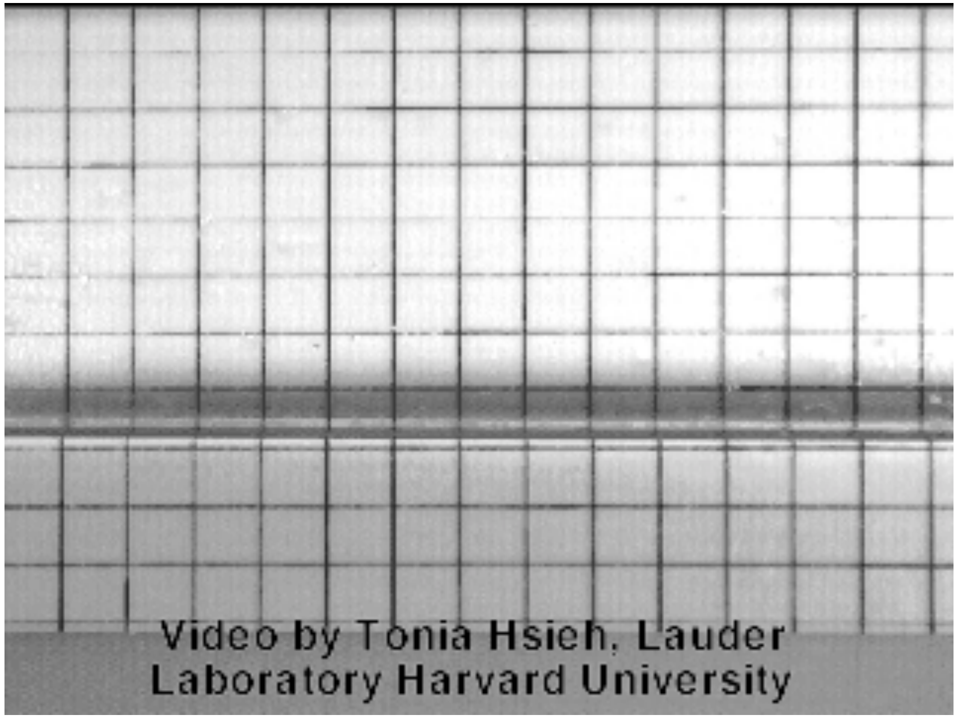
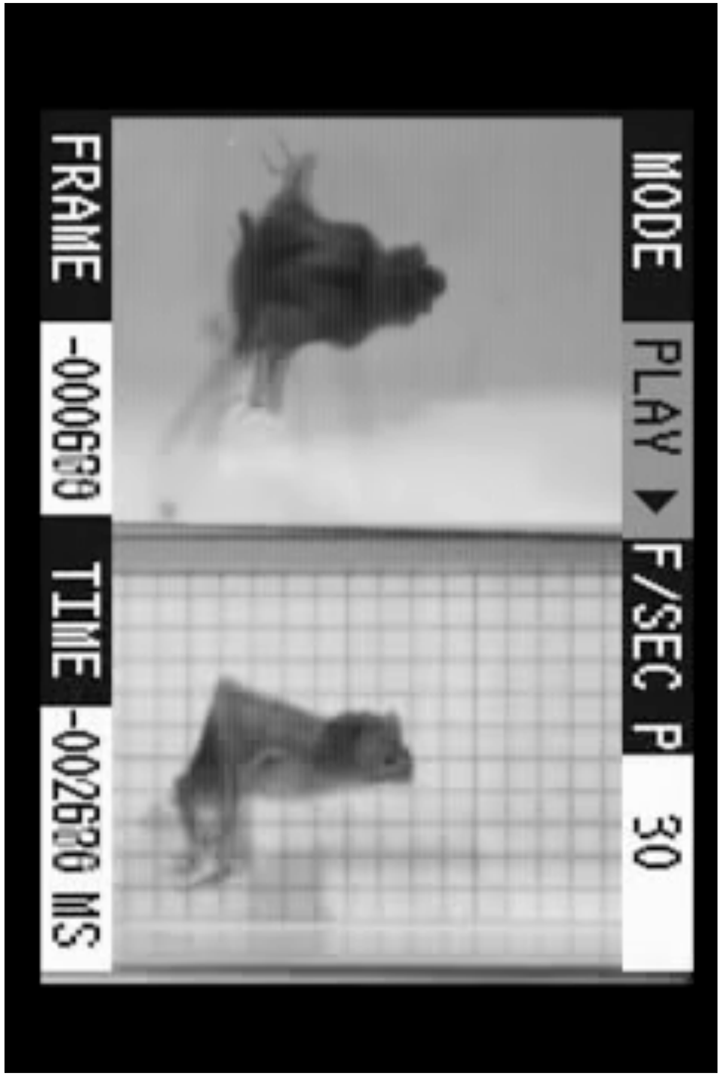


Fig. 4.13 (a) At a much larger size, a basilisk lizard runs over the water surface (b) by initially slapping the water surface to generate an impact reaction force and subsequently generating a cavitation reaction force produced by entraining air which displaces fluid from the foot cavity. This also allows the lizard to withdraw its foot with minimal drag from the air cavity produced.



Video by Tonia Hsieh, Lauder Laboratory Harvard University

Vampire Bat “Hopping”



Frog Jumping -- Modifications of Pelvis

Long pelvis, highly kinetic sacroiliac joint (connection of pelvis to vertebral column)

Pennate muscles connecting Ilium to Urostyle -- storage of force before jumping

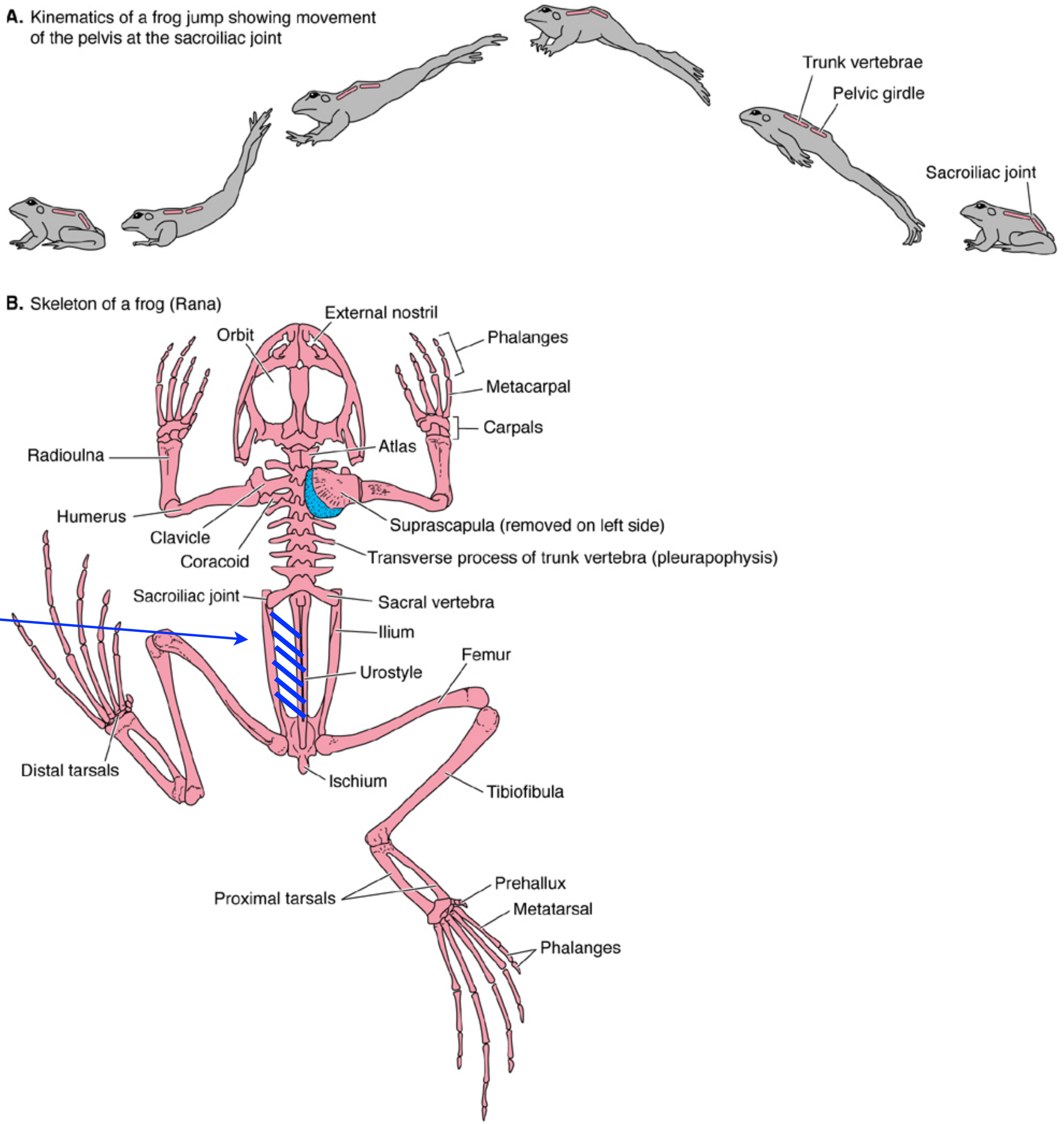


Fig. 11.27

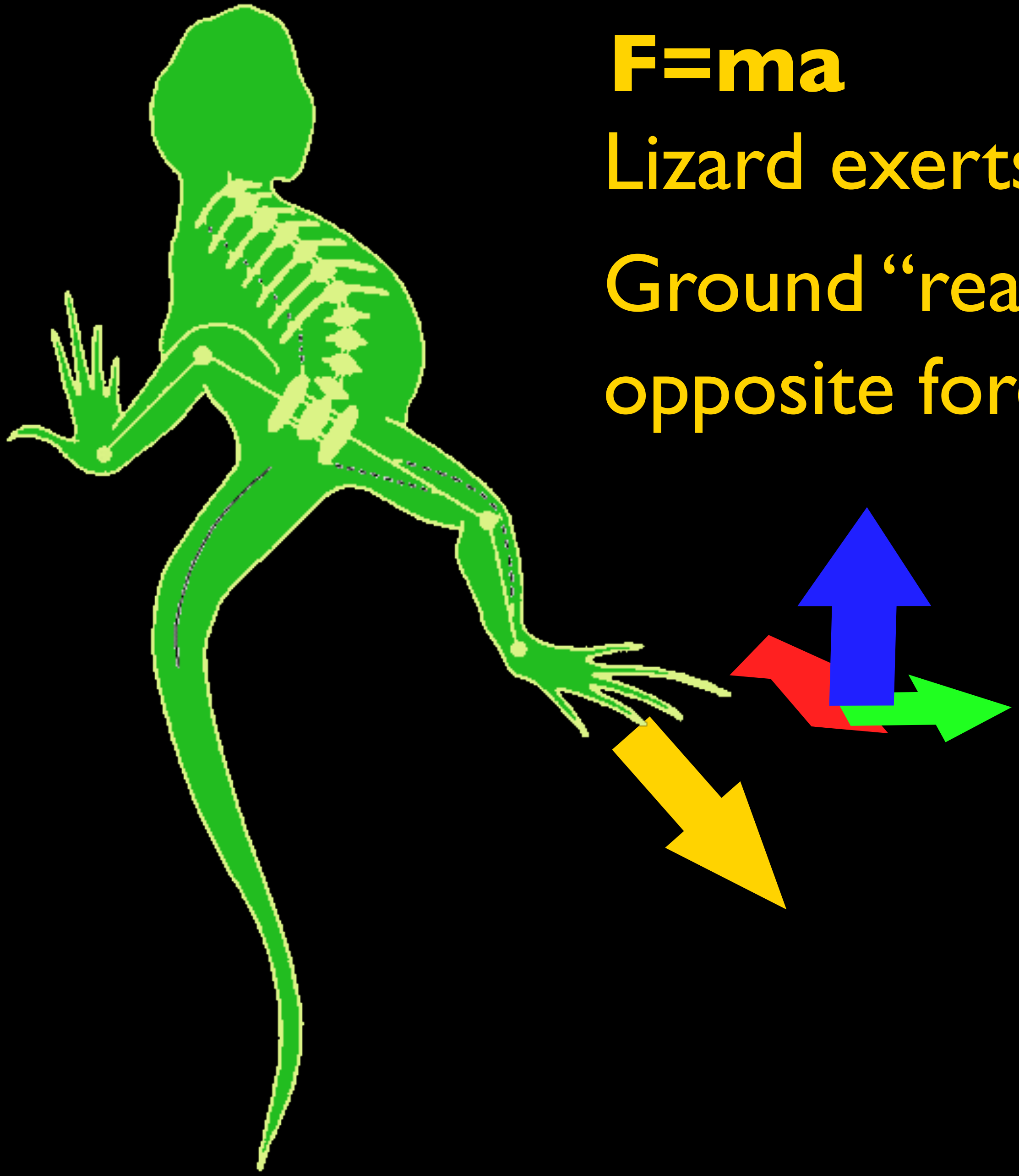
Studying Acceleration

- The take-off is probably the most expensive part of a movement.
- Animals run intermittently in nature
- It’s probably under strong selection if animals flee or run down prey
- Yet we know very little about acceleration and also how animals locomote under varying conditions

F=ma

Lizard exerts force on the ground

Ground "reacts" with equal but opposite force



x: direction of motion (propulsive)

y: lateral (stabilizing)

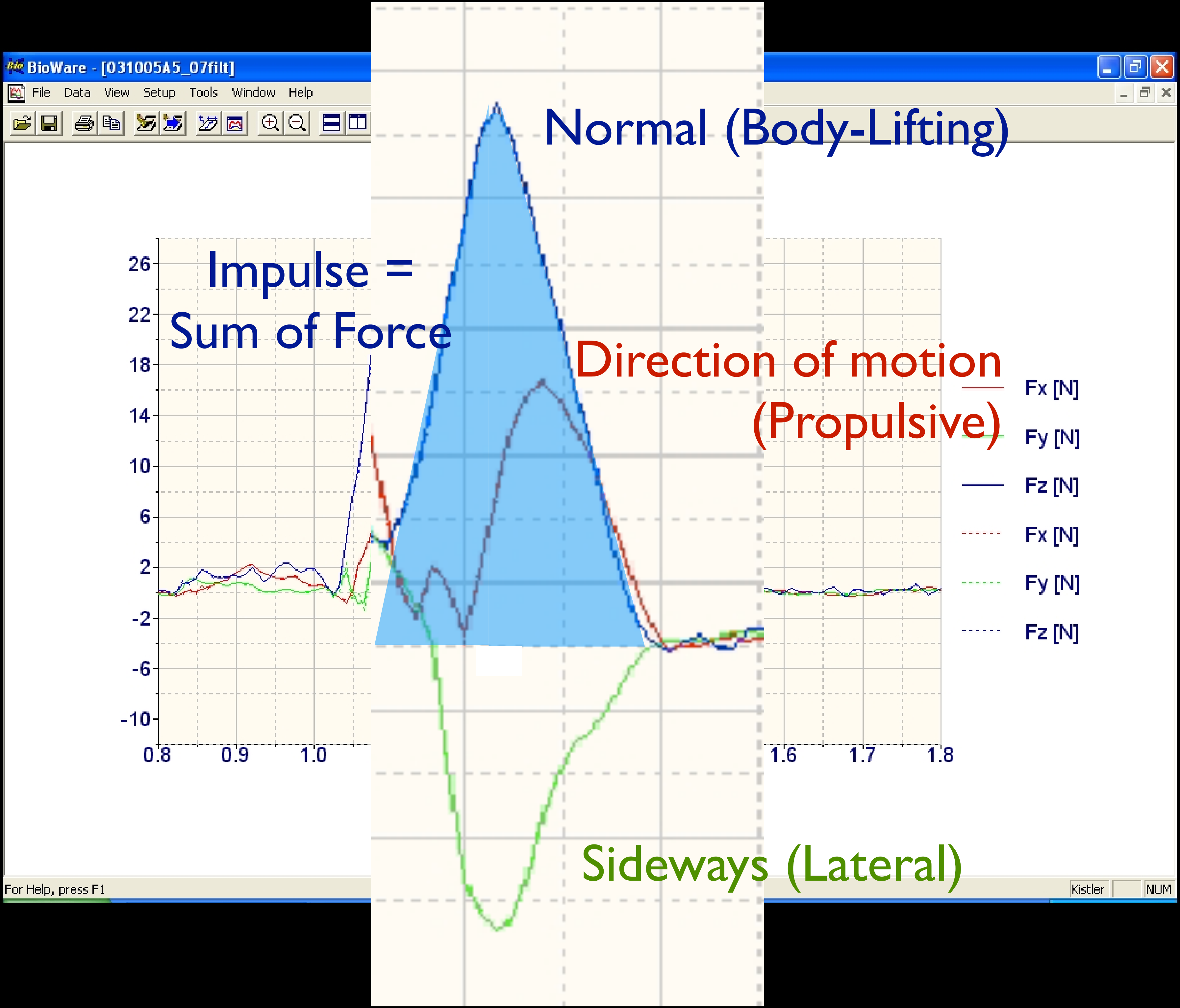
z: body lifting (stabilizing)

Force Plate Experiments

Measure forces in 3D as iguanas accelerate over the force plate

Analyzed best acceleration from each iguana in each reproductive state

>350 trials, 28 used



Impulse = Sum of Force

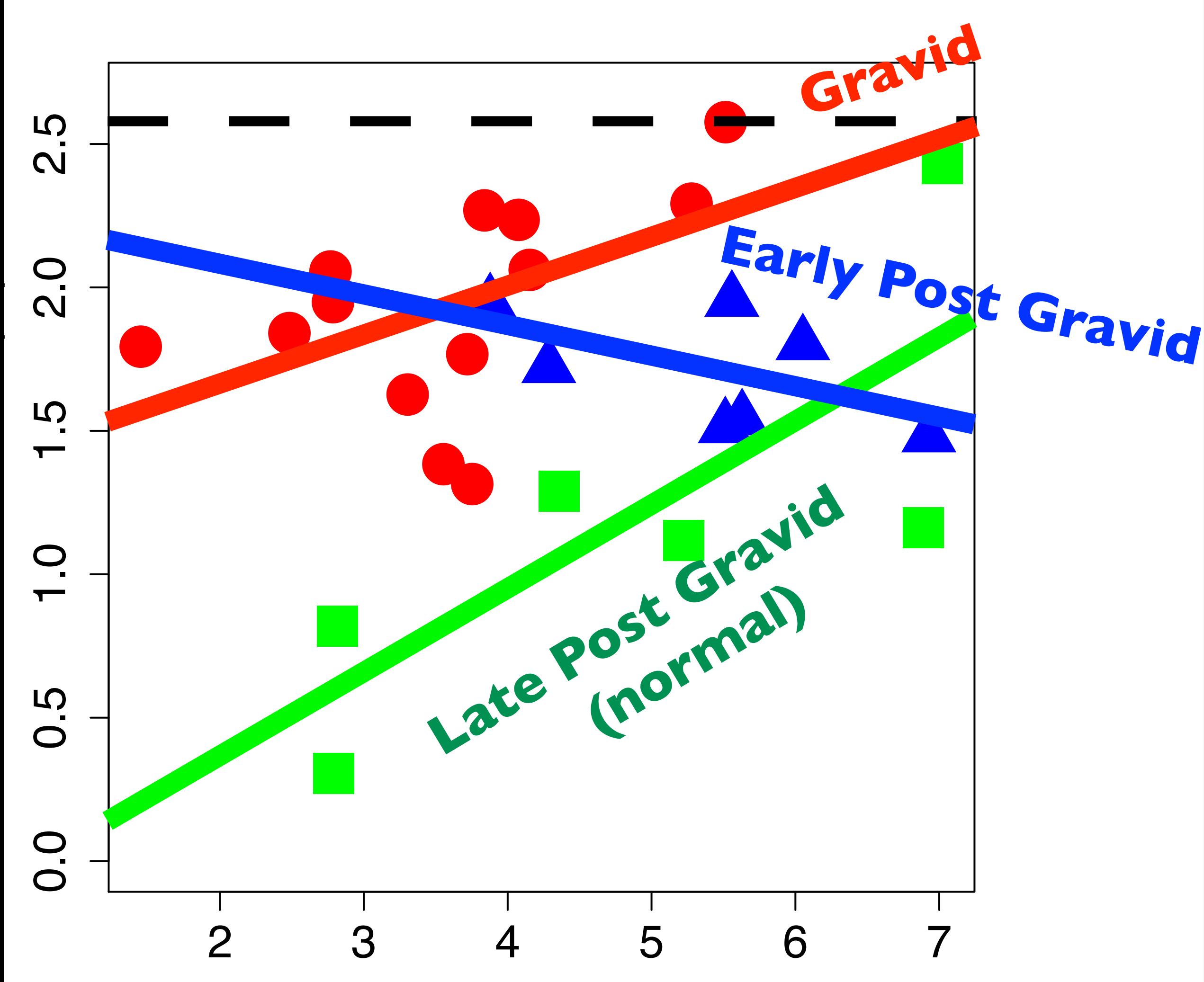
Normal (Body-Lifting)

Direction of motion (Propulsive)

Sideways (Lateral)

Who is Producing More Force?

Total Impulse
(3D Force in N)



Acceleration (m/sec^2)

slopes **

reproductive class **

Biomechanical analysis of Hip and Knee Joints

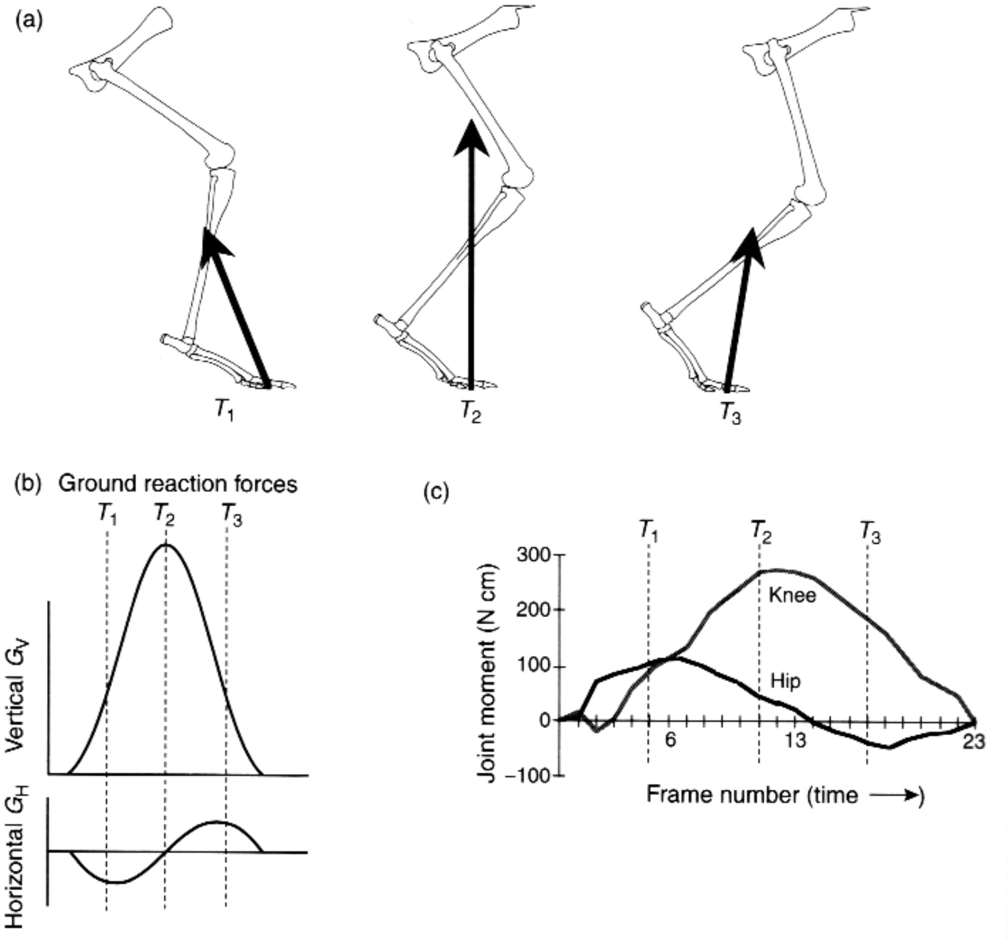


Fig. 3.5 (a) Changes in limb configuration with respect to the net ground reaction force *G* for three frames (times T_1, T_2 and T_3) corresponding to the vertical and horizontal ground forces shown in (b). (c) Changes in ground reaction force moments acting at the hip and knee versus time. *G* exerts a flexor moment at the knee throughout most of limb support (requiring knee muscle extensor force to counter this). *G* also exerts a flexor moment at the hip (requiring hip extensor force) during the first 60 per cent of limb support but, as *G* passes behind the hip joint, it exerts an extensor moment during the latter 40 per cent of limb support (which must be balanced by hip flexor activity).