Anatomical Adaptations for Cursorial Locomotion
and
Impact of Diet

(Designed for Running Web Site)

http://vanat.cvm.umn.edu/run

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Contents:

Running:

Running (cursorial locomotion) involves over-land progression by a repetitive, cyclic, pattern of limb movements. A "**stride**" is one cycle of limb movement at a particular gait. Gait refers to a particular foot-fall pattern (walk, trot, gallop, etc.). Gait is selected for efficiency, terrain, and various circumstances related to survival. [For more information about quadruped gaits, see: http://vanat.cvm.umn.edu/gaits/].

Running success is ultimately about speed (catching prey & escaping predators). Speed is obtained by maximizing stride rate and stride length. **Stride length** is gained by increasing limb length, either anatomically or virtually (via physiological trunk flexion/extension). **Stride rate** is favored by reducing limb mass, especially distally. (NOTE: For linear acceleration, inertia = mass; for angular acceleration, inertia = mass x radial-distance^2.) <u>Stride length and stride rate are antagonistic</u>—enhancing one impairs the other; thus, compromise is necessary.

To improve stride rate, distally positioned limb mass can be reduced anatomically (permanently) and/or physiologically (temporary limb flexion). Anatomical strategies include: concentrating musculature proximally, reducing number of digits, and elongating the distal, least massive segments of the limb. Physiologically, distal limb mass is reduced by flexing the limb during protraction. The degree of physiological limb flexion is proportional to the speed of the gait, minimal at a walk and maximal at a gallop.

Below, we will first consider general anatomical adaptations associated with running, focusing initially on forelimbs and then on forelimb-hindlimb differences. Next, we will discuss constraints imposed by the carnivore vs herbivore lifestyle. (Locomotion and digestion are linked in evolution.) Finally, for the fun of it, we will compare digestive tracts of carnivores (dog) and herbivores (ruminants and the horse)

Limb adaptations for running:

Anatomically, cursorial adaptation has involved limb elongation and musculoskeletal modification away from a more primitive, flexible, grasping, multi-use limb design toward a more specialized, stable, locomotion-dedicated limb support. All limb design involves anatomical compromises between flexibility (rotation, dexterity, manipulation capacity) and stability (joint support, secure surface-contact). Anatomical specialization has evolved to include different functional roles for thoracic and pelvic limbs.

Generalized limb anatomy (evident in non-cursorial mammals, reptiles & birds)
• scapula positioned dorsally on a dorsoventrally flattened thorax
• shoulder joint fixed & capable of circumduction (ball & socket joint)
• two bones in the forearm, enabling rotation while providing stability
 — ulna firmly attached to elbow (loosely attached to wrist)
 — radius firmly attached to wrist (loosely attached to elbow)
• plantigrade contact with the ground
• multiple digits (typically five)
• unguis (nails, claws vs hoof)

Various anatomical adaptations for running (to enhance stride length/rate)
• mediolaterally flattened thorax with the scapula positioned laterally (which lengthens the limb)
• scapula and shoulder joint free to move (shoulder becomes a hinge joint stabilized by muscles)
• brachium remains highly muscular & relatively short (keeps limb mass proximal)
• one bone (radius) becomes dominant bone in the antebrachium (stability favored over rotation)
• reduction of digits in the manus & pes (stability favored over manipulative dexterity)
• conversion of musculature to ligament (reduced mass & more reliance on passive mechanics)
• elongation of the manus/pes (particularly the metacarpus/metatarsus and digits)
• ground contact made with digits (digitigrade) or hoof (unguligrade), vs plantigrade contact

Forelimb - Hindlimb Comparison

Forelimbs and hindlimbs have different roles in cursorial quadrupeds. Consequently they are anatomically different:

Forelimbs (thoracic limbs) carry more static body weight (about 60%). Thoracic limbs are designed to catch body weight (mass x velocity) as it is thrown forward by the pelvic limbs. Forelimbs are designed to improve gait efficiency by minimizing wasteful up/down energy expenditure. (Ligaments absorb the kinetic energy of downward movement and store it as potential energy in stretched ligaments; then, during ligament rebound the stored energy is converted to upward kinetic energy, elevating the thorax with minimal muscle involvement).

Anatomical features of the forelimb include:
- shorter and straighter than the pelvic limb
- connected to the trunk only by muscle and ligament (not bone to bone articulation)
- broader, more rounded hoof (horse)

Hindlimbs (pelvic limbs) are the "motors" of locomotion. They drive the trunk forward and propel the body up/over obstacles during jumps. Anatomical features of the hindlimb include:

- longer and more angular than the thoracic limb
- osseous articulation to the trunk (axial skeleton) through a sacroiliac joint
- musculature capable of simultaneously extending hip, stifle, & hock
- narrower, more pointed hoof (horse)

Carnivore vs Herbivore:

The carnivore lifestyle requires limb flexibility for grasping and manipulating prey and for fighting to defend self, offspring, and territory. Thus, carnivores require multipurpose limbs (used for both running and manipulating). Therefore, anatomical specialization (limb elongation, bone reduction, digit elimination, conversion of muscle to ligament, and ungulate ground contact) is moderated in the carnivore. Since the carnivore unguis (nail) is not used for locomotion, it is available to be used as a "tool/weapon".

Carnivores are fast because they have flexible spines. To catch long-leg prey, the carnivore must obtain long stride length physiologically, by trunk flexion and extension (which requires high energy expenditure). Trunk flexibility is feasible because carnivores have a relatively small intestinal volume, due to a meat diet (which is why they need multipurpose limbs in the first place).

Herbivores, with roughage diets and bulky abdominal viscera, have a more limited capacity for trunk flexion. However, herbivore limbs, since they are not needed for grasping, are freed to be devoted entirely to locomotion. Cursorial herbivores become ungulates, limbs make ground contact with a hoof (unguis). The equine limb exhibits extreme anatomical specialization for running.

Equine limbs have become so specialized, they resemble "machines" (reliance more on bone & ligament connections and less nerve & muscle control). The horse walks on the hoof of a single digit of an elongated manus/pes where muscle has been replaced by ligament.

In contrast to ruminant herbivores (voluminous stomach for fermentation), the digestive apparatus of the horse (small stomach and large cecum/colon for fermentation) predisposes it to continual grazing (in the wild). Accordingly, the horse has evolved ligament structures that facilitate such a lifestyle, including prolonged standing with minimal expenditure of muscular energy (stay apparatus), mechanical joint linkage (reciprocal apparatus), and mechanical energy conservation through potential/kinetic energy exchange (e.g., fetlock translation).

Alimentary modifications

The alimentary tract consists of esophagus, stomach, small intestine, and large intestine, including cecum and anal canal. As mentioned, the different alimentary tracts and diets of domestic mammals have implications for behavior and thus locomotion. Features of three types of digestive tracts are presented below:

Canine digestive tract
- simple glandular stomach
- small cecum and simple colon
- small abdominal volume, especially when fasted
- high protein diet

Ruminant digestive tract (cattle, sheep, goat, deer, etc.)
- huge stomach with four compartments (fermentation chambers and a glandular compartment)
- large cecum and coiled ascending colon
- large abdominal volume even if fasted
- rumen flora and fermentation products supplement a roughage diet

Equine digestive tract
- simple stomach (half glandular)
- huge cecum and ascending colon
- large abdominal volume even if fasted
- roughage diet requires a protein source (obtained via grain or in the wild, coprophagy)

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