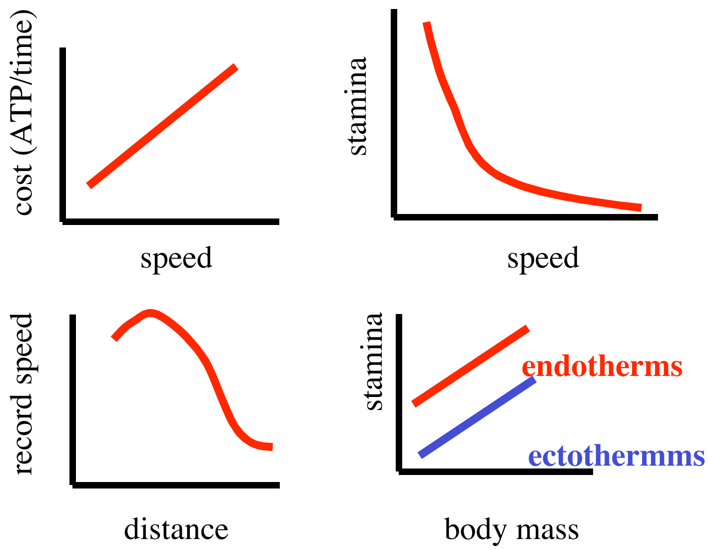
28 October 2005 **Physiology of Locomotion** R. B. Huey

I. Some Basic Issues to Explain

A. Here are some basic patterns: (i) the "<u>cost</u>" of locomotion (that is, ATP consumed *per time*) increases with speed, (ii) stamina decreases with speed, (iii) the world record speed declines as the distance of a race increases.



B. Also, ectotherms and endotherms have similar "<u>burst</u>" (or "sprint") capacities, but ectotherms <u>have much less stamina</u>. Thus most ectotherms are poor marathon runners.

II. Why is locomotion energetically expensive?

A. Energy must be used to <u>overcome inertia</u> and thus move a body. Note that muscles contract at high rates **(1 Hz (Hertz) = 1 cycle/second)**

mouse	7.5Hz	blow fly	120
elephant	1.4	mosquito	600
budgerigar	14	lizard	16
rattlesnake tail	100		

B. Energy must be used to <u>overcome frictional drag</u> from the environment
1. For human at moderate speed, 7.5% total cost for friction
2. For sprinter, 13% (recall drag increases as velocity squared)
3. For birds, which fly at high speed, 25% cost goes to overcome drag
4. Drag can be much higher in water than in air, especially for a small animal, which can find water to be very "viscous."

C. Terrestrial animals must use energy to <u>overcome gravity</u> (aquatic animals are essentially neutrally buoyant).

D. ➔ Other physiological "side-effects" -- increased metabolism caused by activity will influence food needs, thermoregulation, water balance, circulation, etc. Why?

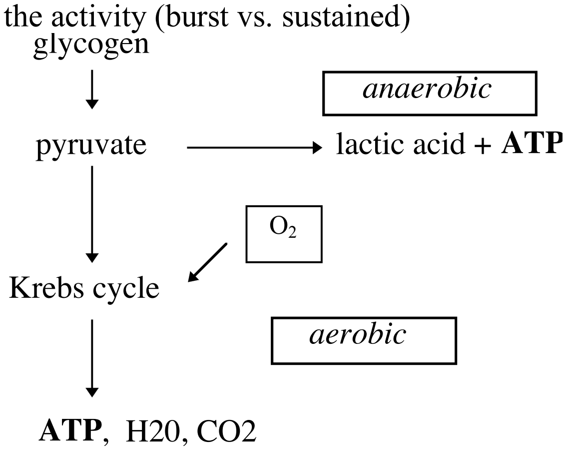
III. Where do animals obtain energy for locomotion?

A. Muscle contraction takes considerable energy. Human muscles consume only 15% of animal's total metabolic rate at rest, but 90% during maximal activity.

B. ATP is the fuel for all muscular contraction. At the muscle level, ATP utilization rates can increase 1000 fold during locomotion! A dynamic shift in usage.

C. So, where does the ATP come from?

1. From existing muscle stores (= a battery)? No, very small amounts of ATP are stored in muscle -- only enough for a few twitches during initial activity.
2. Is it then synthesized de novo? Yes, via two pathways: a) **Anaerobic metabolism** (pathways not using oxygen, see also below) or b) **Aerobic metabolism** (pathways using oxygen) or both.
3. Which of these pathways is used depends on level of activity, and the time course of the activity (burst vs. sustained)



4. If O_2 supplies sufficient, the reaction via Krebs cycle (***aerobic***) is favored. But **if O_2 supplies are not sufficient**, pyruvate is instead converted to lactic acid (***anaerobic***). So which pathway is used depends on O_2 supply.

E. ATP used *at the very beginning of activity* is supplied from "phosphagens"

1. **Creatine phosphate** (PCr) is the phosphagen in vertebrates and also in some invertebrates

$$PCr + ADP \overset{}{\underset{CK}{<\!\!-\!\!->}} ATP + Cr$$

2. Creatine kinase (*CK*) is the enzyme that catalyzes this exchange

[3. Arginine phosphate (not PCr) is the phosphagen for most invertebrates]

4. No oxygen involved, so these are "anaerobic" pathways
5. PCr provides ATP during initial stages of activity -- about 100 twitches.

[6. Note, however, that the resynthesis of PCr stores (following activity) of PCr requires ATP, which comes from oxidative metabolism. So ultimately oxygen is required.]

G. Energy source during **low-level** activity? Aerobic metabolism (*"Pay as you go"*)

1. Aerobic metabolism supplies energy **at rest and during low-level activity**
2. Fuels -- oxidation of carbon fuels (fats, carbohydrates, amino acids)
3. Very **efficient** -- 12 to 15 more ATP per mole glucose than anaerobic glycolysis. Also relatively "**clean**" -- produces water and CO_2.
3. The "Bad" -- **requires** O_2. Only small intracellular stores of O_2 are available, and environmental sources (air, water) of new O_2 are **distant** from mitochondria in muscles. There is be a **time lag** to get new O_2 to the contracting muscle fibers **--** maximal O_2 consumption isn't reached for 1 to 2 min after exercise begins.
5. Moreover, aerobic metabolism has **limited "scope"** for expansion above rest (below), such that it can generate only a limited amount of ATP.

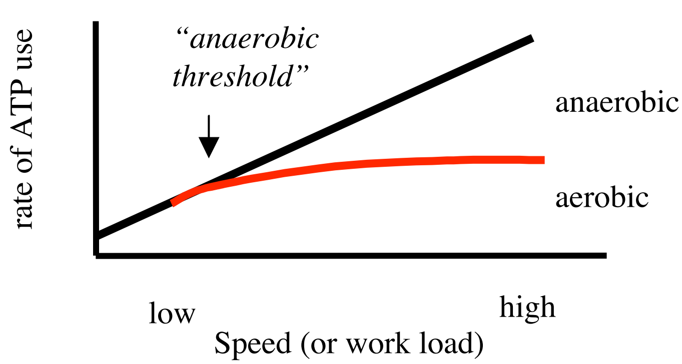
6. Vertebrates increase aerobic metabolism **(ATP production)** by **only 5 to 20X above rest**, though some insects can achieve > 100X! (**"Metabolic scope"** = maximum O_2 - standard O_2; **"factorial scope"** = maximum O_2/standard O_2).

	1 kg reptile	1 kg moth	1 kg bird
Stand O_2	.1ccO_2/g·h	.1	.8
Max O_2	.4	14.6	9.5
Metabolic Scope	.3	14.4	8.7
Factorial Scope	5.7	121	12

7. Why is limited scope a problem? A factorial scope of "10" means that the maximum amount of ATP produced aerobically is only 10X that produced at rest. If more ATP are needed (e.g., to sprint), then an animal **must** obtain the extra ATP via anaerobic pathways.

H. Anaerobic glycolysis (*"Twitch now, pay later"*)

1. As ATP needs begin to exceed aerobic capacity, anaerobic metabolism begins to help supply ATP. The work load at which anaerobic metabolism kicks in is called the "anaerobic threshold."



2. Fuel for anaerobic metabolism -- glycogen, stored as granules in skeletal muscle cells
3. The "Good" -- because fuel is in the muscles and does not require O_2, anaerobic glycolysis delivers ATP very quickly. But intense activity can't be sustained.
4. The "Bad" -- is **inefficient** – relatively few ATP fewer ATP per mole of fuel.
5. Also "**dirty**" -- increase in lactate, a drop in pH, a temporary loss of calcium from bone, and fatigue. In fact, high lactate suppresses further glycolysis.
6. ⇒ Insects do **not** use anaerobic glycolysis (but apparently spiders do).

IV. "Oxygen debt"

A. After strenuous activity, animal continues breathing rapidly (thus, maintains high level O_2 consumption) for some time. Why is this necessary, if activity has stopped? The "extra" O_2 helps return the body to its original (pre-exercise) chemical state and is called (appropriately) the oxygen debt.

B. Primary functions of the oxygen debt

1. To resynthesize glycogen from the accumulated lactic acid (done mainly in liver) that resulted from anaerobic activity (called "lactacid debt"). Requires O_2.
2. To replenish creatine phosphate. Requires O_2, creatine, ATP ("alactacid debt").

C. Duration of oxygen debt is shorter in endotherms than in ectotherms, and is shorter in small than in large animals. Why?

V. Putting it all together

A. Why is stamina inversely related to work load? Aerobic metabolism, which is physiologically "clean" and efficient, can sustain modest work loads for very long periods. But at higher work loads, ATP demands exceed the capacity of aerobic pathways ("anaerobic threshold") and anaerobic metabolism kicks in. Although anaerobic pathways can produce lots of ATP quickly, they are non-sustainable (above). These reasons explain why stamina is much greater at low work loads, and why the world record speeds are high only in short races.

B. Endotherms versus ectotherms.

1. All vertebrates use **both** aerobic and anaerobic metabolism, and both rely on aerobic metabolism at rest.
2. Ectotherms sprint as fast as endotherms – anaerobic capacities similar.
3. However, a 1 kg iguana can support (aerobically) speeds of only 0.5 km/h, a 1 kg rat can run aerobically at 4 km/h. Why do endotherms have greater stamina than do ectotherms? This takes us back to "aerobic scope."
4. Recall that aerobic output of ATP can increase by roughly 10X (= factorial scope) in both vertebrate ectotherms and endotherms. But compare instead their "metabolic scopes," which are proportional to the amount of ATP that can be produced for above-rest needs. Aerobic scopes of

endotherms are much greater than those of ectotherms (see table above), so can produce more "extra" ATP, which can be used for activity.

C. What work loads to "endurance workers" (e.g., lumberjacks, migrating animals) sustain? Usually 4X rest, thus well below the maximum aerobic rates (which are about 10X resting levels), but just below anaerobic threshold!