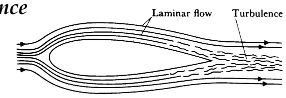
Movement and Metabolic Rate

- **If animals were inactive, using metabolism only to maintain body temperature, and heat was lost only radiation, then metabolic rate would scale only with the surface area:**
  - **Heat loss/unit skin area is constant, i.e., ∝ $M^{0.67}$**
  - **Places a lower limit on size-dependency of metabolic rate**
- **At the other extreme, organisms use the most power (highest rate of work) when moving as rapidly as possible:**
  - **This power goes to fuel the muscles to do *work* (= force × distance)**
  - **Need to know the force that muscles can exert, how far and how often they can contract**
- **When an animal is running at maximum speed, the force per unit cross section developed in its leg muscles depends on:**
  - **the proportion of the stride when the limb is in contact with the ground (the *duty factor*, β)**
  - **the cross-sectional area of the muscles**
  - **the animal's body mass, M**
  - **the nature of the running surface**

Locomotion

- ***Drag* (*D*) is produced by the viscosity of the medium through which the animal is traveling**
  - **For any given shape, D ∝ surface area, therefore**
  - **Large animals exhibit less drag per unit mass**
- **Flow patterns also important: density, viscosity, and velocity also affect *turbulence***



  - ***Laminar flow*: pressure gradients between surface of body and surrounding fluid layers are small. Change in the velocity of fluid is gradual as it moves away from body.**
  - ***Turbulent flow*: steep gradients in change of fluid velocity form eddy currents**
    - **Lowers efficiency of conversion of energy into movement.**
    - **Animal body shapes evolve to reduce turbulent flow.**

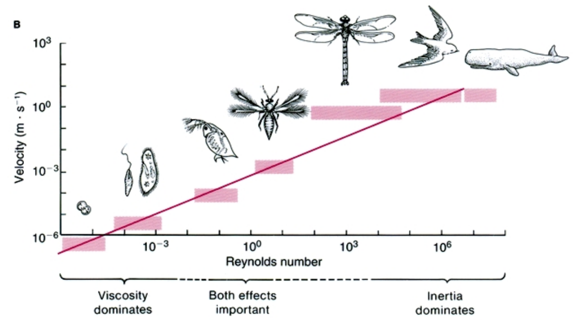
Reynolds Number (R_E)

$$R_E = \frac{l\,V\,\rho}{\mu}$$

l = length of organism (cm)
V = velocity in fluid medium (cm s^{-1})
ρ = density of of fluid medium (g cm^{-3})
μ = dynamic viscosity of fluid medium (g cm^{-2} s^{-1})

Ranges from <<10^{-4} to >10^{8}. *Some actual values:*

Reynolds Number (R_E)



Reynolds Number (R_E)

Low (<1) Reynolds Number (Stokes flow):

- **Inertia negligible, viscosity important**
  - **When external forces removed, motion stops instantly**
- **Flow is:**
  - ***Reversible* (viscous forces dominate)**
  - ***Symmetrical* (no preferred orientation)**
- **Body has large region of influence relative to length**
- **Drag (*D*): $D \propto V\,l$ (speed × length)**

Reynolds Number (R_E)

High (>10^5) Reynolds Number:

- **Inertial forces important**
  - **When external forces removed, organism keeps moving**
  - **Eddies and turbulence occur in the wake**
- **Flow is:**
  - ***Irreversible* (viscous forces negligible away from boundary layers and wakes, important in them)**
  - ***Asymmetrical* (preferred orientation)**
- **Body has small region of influence relative to length**
- **Drag: $D \propto V^2\,l^2$**
  - **Form drag from shape and orientation**
  - **Skin friction from boundary layer viscosity**

At intermediate R_E (≈10), both viscous and inertial flow regimes important

Cost of Transport (*C*)

$$C = \frac{P_i}{M \times v}$$

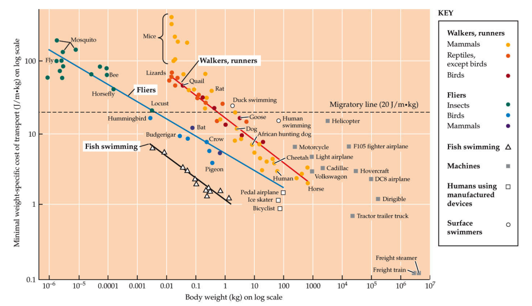
P_i = power expended by organism (W)

M = mass of organism (kg)

v = velocity of organism (m s^{-1})

- The higher the value of C, the more energy it takes to transport a given mass over a given distance.
- About half of the energy is to counteract falling. Organisms fall more slowly in water.

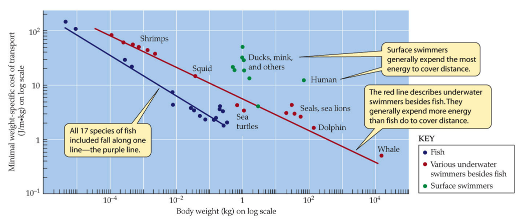
Figure 8.7 The minimal weight-specific cost of transport in relation to body weight for running, flying, and swimming animals and for machines



Swiped from Tucker, V.A. 1975. The energetic cost of moving about. *Amer. Sci.* 63:413-419.

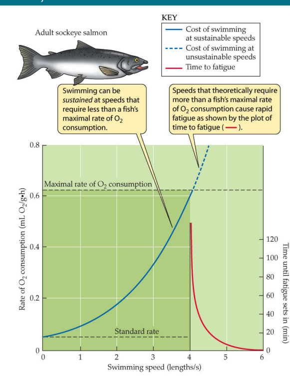
Animal Physiology 2e, Figure 8.7

Figure 8.8 The minimal weight-specific cost of transport during swimming



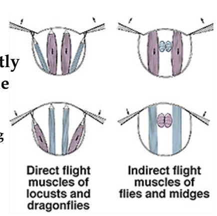
Animal Physiology 2e, Figure 8.8

Figure 8.3 The rate of O_2 consumption as a function of swimming speed in yearling sockeye salmon (*Oncorhynchus nerka*) studied in a water tunnel

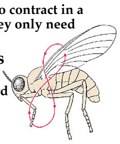


Animal Physiology 2e, Figure 8.3

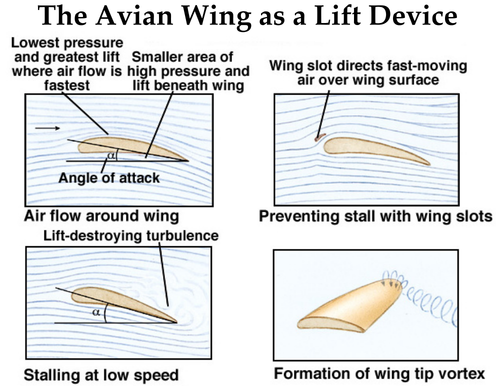
Insect Flight



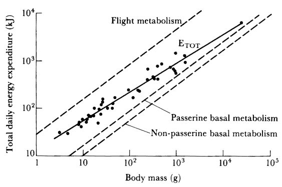
- Direct flight muscles attach to a wing directly
- Indirect flight muscles alter the shape of the thorax to cause wing movement
  - The wing is hinged on a pleural process that forms a fulcrum; all insects cause the upstroke by contracting indirect muscles that pull the tergum down toward the sternum
  - Dragonflies and cockroaches contract direct muscles to pull the wing downward
  - Bees, wasps and flies arch the tergum to cause the downstroke indirectly
  - Beetles and grasshoppers use a combination of direct and indirect muscles
- Flight muscle contraction has two kinds of control:
  - Synchronous muscle control uses a single volley of nerve impulses to stimulate a wing
  - Asynchronous muscles stretch the antagonistic muscle and cause it to contract in a recoil fashion (potential energy can be stored in resilient tissues); they only need occasional nervous stimulation
- Wing beats vary from 4/s in butterflies to>1000/s in flies
  - Direct flight muscles also alter the angle of wings to twist the leading edge to provide lift. Figure-8 movement drives insect forward
  - Fast flight requires long, narrow wings and a strong tilt, (e.g., dragonflies)

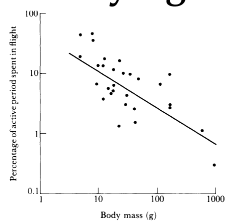


The Avian Wing as a Lift Device



Energetic Cost of Flying



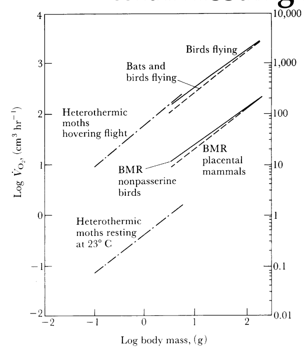


Relationship between "basal" metabolism, flight metabolism, and total energy expediture (E_{tot}) as a function of body mass.

Relationship between body mass and the percentage of the active period spent in flight.

Redrawn from: Walsberg, G.E. 1983. Avian ecological energetics. In D.S., Farner, J.R. King, and K.C. Parkes (eds.) Avian biology, vol. 7. Academic Press, New York.

Energetic Costs of Flight Compared with Resting Metabolism



Relationships between body mass and O_2 consumption by insects, birds, and mammals at rest and in flight.

Redrawn from Bartholomew, G.A. 1982. Body temperature and energy metabolism. In M.S. Gordon (ed.) Animal physiology: principles and adaptations, 4th ed. Macmillan, New York.

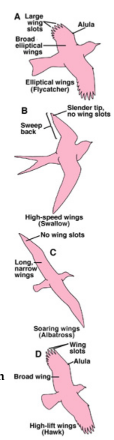
Basic Forms of Bird Wings

Elliptical Wings
- Birds that must maneuver in forested habitats have elliptical wings
- Elliptical wings are slotted between primary feathers to prevent stalling at low speeds, etc.

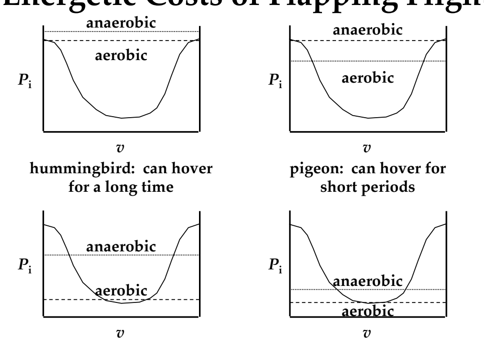
High-Speed Wings
- Birds that feed on the wing or make long migrations have high-speed wings
- These wings sweep back and taper to a slender tip; this reduces "tip vortex" turbulence
- They are flat in section and lack wing-tip slotting

Soaring Wings
- Albatrosses, gannets (frigate birds), and other oceanic soaring birds have long, narrow wings
- The high-aspect ratio of long, narrow wings lack wing slots and allow high speed, high lift and dynamic soaring
- Have the highest aerodynamic efficiency of any design, but are less maneuverable
- Exploit the highly reliable sea winds, and air currents of different velocities

High-Lift Wings
- Vultures, hawks, eagles, owls and other birds of prey that carry heavy loads have wings with slotting, alulas and pronounced camber. This produces high lift at slow speeds
- Many are land soarers; their broad, slotted wings allow sensitive response for static soaring



Energetic Costs of Flapping Flight



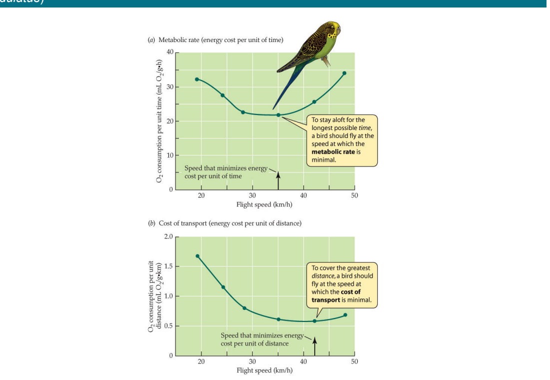
hummingbird: can hover for a long time

pigeon: can hover for short periods

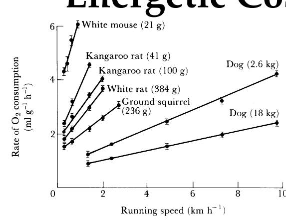
vulture: can fly actively only at optimal cruising speed

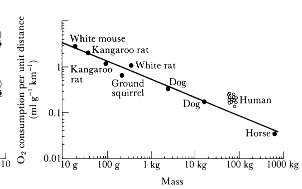
condor: can't hover, must reduce lactic acid buildup by soaring

Figure 8.6 Two ways to view the energetics of flapping flight by budgerigars (*Melopsittacus undulatus*)



Energetic Cost of Running



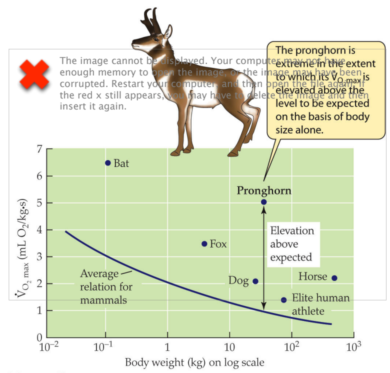


Energetic costs of running (per unit mass transported per unit distance) vs. running speed in mammals of different sizes. (see Fig. 8.4 in your text)

Energetic costs of transporting 1 g over a distance of 1 km in running mammals of different sizes.

Redrawn from: Taylor, C.R., K. Schmidt-Nielsen, and J.L. Raab. 1970. Scaling of energetic costs of running to body size in mammals. *Amer. J. Physiol*. 219:1104-1107.

Figure 8.9 The pronghorn (*Antilocapra americana*) represents an extreme case of evolutionary specialization for high V_{O_2max}

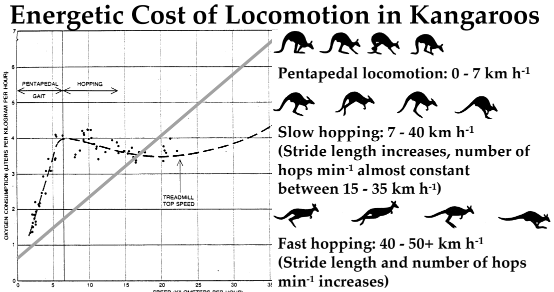


Animal Physiology 2e, Figure 8.9

Other Adaptations for Locomotion

- **Some animals utilize energy in tendons or exoskeletal structures**
  - **Grasshoppers, click beetles, and fleas strain and bend elastic, cartilaginous part of the exoskeleton (*apodeme*), increasing the potential energy stored in body parts**
  - **Tension on the structure is held in check by a "hook-and-eye" device on the exoskeleton. When this is released, the insect is catapulted into the air**
  - **May produce very high acceleration forces (over 300 *g* in fleas)**
- **May store potential energy on landing (recoil), use large fraction of energy for the next leap (kangaroos)**

Energetic Cost of Locomotion in Kangaroos



Energetic costs of locomotion for kangaroos on a treadmill at speeds up to 23 km h^{-1}. Energetic cost of 'pentapedal' locomotion increased rapidly, but once the animals began to hop the cost leveled off and even decreased. The gray line shows the comparative cost of locomotion for a quadruped of the same body mass. Beginning at about 17 km h^{-1}, hopping appears to be more economical of energy than quadrupedal locomotion. Projecting the curve beyond the maximum treadmill speed suggests that this may be true up to the maximum limit for sustained hopping (over 50 km h^{-1}).

Metabolic Costs of General Activity

- **In addition to routine locomotion, general activities will increase the energy costs of free existence**
- **Grazing, chewing, foraging, defense of self and territory, mating, and other activities all represent increases over RMR**

For a 100 kg ruminant:

Activity	*Multiple of RMR*
Standing	**1.1**
Running	**8.0**
Walking on level terrain	**1.6**
Walking on 10% gradient	**2.4**
Foraging	**1.6**
Playing	**3.0**
Ruminating	**1.3**

Moen, A.N. 1973. Wildlife ecology. Freeman, San Francisco.

TABLE 8.1 Representative metabolic rates of young adult people of average build during sustained forms of exercise

Type of activity	Metabolic rate[a] (kJ/minute)
Lying down	6.3
Sitting	7.1
Standing	8.8
Walking at 2 miles per hour (mph)	12
Walking at 4 mph	21
Bicycling at 13 mph	32
Jogging at 7 mph	59
Crawl swimming at 2 mph	59
Running at 10 mph	84

Source: After Åstrand and Rodahl 1986.

[a]All forms of locomotion are assumed to be on level ground. In aerobic catabolism 1 kJ = 49.5 mL O_2.

Animal Physiology 2e, Table 8.1