Lecture 3: Allometry in flying; Cellular Structure and Composition (Sept. 13)

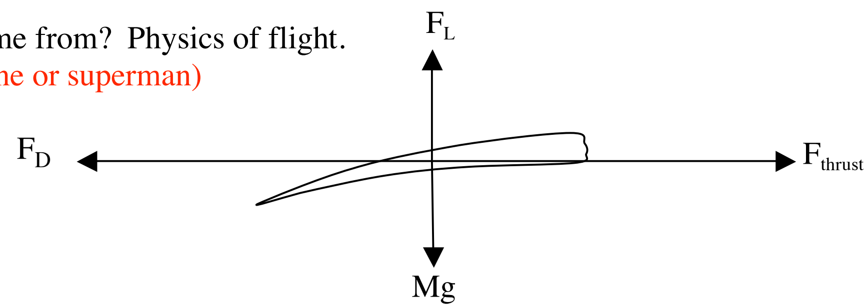
Reading Assignment for Lectures 3-4: PKT Chapter 2

- Do you all have (partial) Problem Set 1?
- Mr. Caulfield has dropped course and would like to sell his copy of the text. Contact me for his e-mail.
- Tutorial Tuesday will cover Problem 1 (global warming calculations).

Some non-trivial scaling laws can be derived from physical principles:

A. Example (minimal) constant speed of objects flying on a horizontal trajectory scales as $U_{\min} \approx M^{1/6}$. (747's fly faster than birds, which flay faster than midges)
(see graphic from Ahlborn, Fig. 6.20)

Where does this come from? Physics of flight.
(wing of bird or plane or superman)



For flight at constant velocity:

$F_L = Mg$ ("lift" balances gravity)

$F_D = F_{\text{thrust}}$ ("drag" of air friction balances "thrust" provided by engine or wing)

Lift and drag are generated by the action of the air against the wing surface (and Newton's third law). Angle of attack and Bernoulli. At the very lowest speeds these may be expected to vary linearly with speed U (the laminar regime); however, for all realistic speeds for flow in air (c.f., water and bacterial swimming!), the flow is turbulent and $F_L, F_D \sim U^2$. The remainder of these formulas for lift and drag is nothing but dimensional analysis. We expect these forces to depend on the density ρ_{air} of air, on the surface area of the wing, and on the shape of the flying object.

$$[F] = \frac{ML}{T^2} = \left[\frac{M}{L}\right]\left[\frac{L}{T}\right]^2 = \left[\frac{M}{L^3}\right][L]^2\left[\frac{L}{T}\right]^2 = [\rho][S][U]^2$$

It follows that we can write,

$$(a) \quad F_L = \frac{1}{2} C_L \rho_{air} A_L U^2$$

$$(b) \quad F_D = \frac{1}{2} C_D \rho_{air} A_D U^2,$$

(the factors ½ are conventional)
and the only questions are:

(i) What are the relevant areas $A_{L,D}$?
A_L = wing surface area; A_D = X-section area, so ("spherical cow")

$$A_{L,D} = B_{L,D}\pi R^2 \text{ with (approximately) } B_L = 9; B_D = 1.5$$

(ii) What are the (shape-dependent numerical constants) $C_{L,D}$? (order 1)

$$C_L = 0.6; C_D = 0.1$$

It follows from (a) that **3.2**

$$F_L = Mg = \frac{1}{2} C_L \rho_{air} \left(B_L \pi R^2 \right) U^2 \text{ with } R = \left(\frac{3}{4\pi} \right)^{1/3} \left(\frac{1}{\rho_{water}} \right)^{1/3} M^{1/3},$$

so $M \sim M^{2/3} U^2$, so $U_{min} \sim M^{1/6}$.

Note: If you go faster than this speed, bird/plane will accelerate upwards, unless you change the shape of the wing to get less lift. If you go slower, bird/plane will accelerate downwards (start to fall). There is a "best" shape which gives maximum lift at minimum speed. Assume that is what we are set at.

Putting in all the factors:

$$U_{min} = \left[\frac{2g}{\pi^{1/3}} \cdot \frac{1}{C_L B_L} \cdot \frac{\rho_{water}^{2/3}}{\rho_{air}} \cdot \left(\frac{4}{3} \right)^{2/3} \right]^{1/2} M^{1/6} = 16 \cdot M^{1/6},$$

where I have used:
$g = 9.8$ m/s^2
$\rho_{water} = 1000$ kg/m^3
$\rho_{air} = 1.2$ kg/m^3
$C_L = 0.6$
$B_L = 9$

Compare with data from Alborn, Fig 6.20:

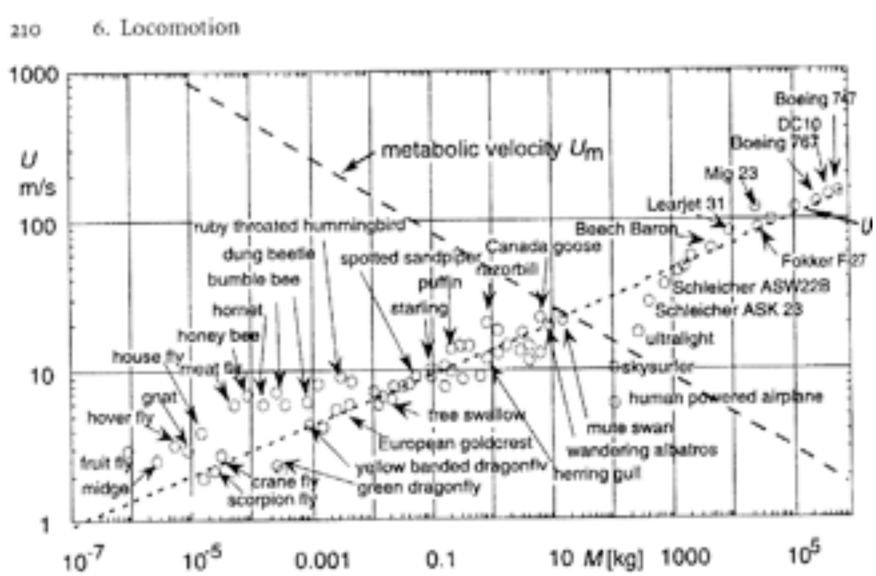


Fig. 6.20. The great flight diagram. Data adopted from Tennekes [1997]

Notes:
Twelve decades of data. Midge to 747.
Outliers?

B. What is the maximum mass of a bird that can fly? **3.3**

Note: The largest flying bird is the mute swan at 15 kg. There are birds larger than this; but, they can't fly.

Ostriches can weigh up to 100-150 kg, but they don't fly!

The (extinct) flightless dodo is estimated to have weighed 15—23 kg.

In order to fly at some arbitrary speed U, a bird must provide a thrust force F_{thrust} sufficient to overcome the drag force F_D at U.

This requires a metabolic power, $P = F_D U = \frac{1}{2} C_D \rho_{air} A_D U^3$.

Thus, the maximum speed U_{max} that a bird can fly is limited by the maximum metabolic power available $P_{max} = \eta b \Gamma_0$, where

b is the number of times the basal metabolic rate which is possible and

$\eta \quad (<1)$ is the overall efficiency of the mechanics.

Note that $P_{max} \sim M^{3/4} \sim M^{2/3} U_{max}^3$, so $U_{max} \sim M^{1/36}$.

Compare $U_{min} \sim M^{1/6}$. This is OK at small mass, where $U_{min} < U_{max}$. But, eventually, at sufficiently high mass U_{min} reaches U_{max}, and the maximum metabolically possible speed is insufficient to provide the life to keep you aloft. Hence, the limit M_{max} on mass.

Put in the amplitude factors:

$$U_{max} = \left[\frac{2\eta b a}{\pi^{1/3}} \cdot \frac{1}{C_D B_D} \cdot \frac{\rho_{water}^{2/3}}{\rho_{air}} \cdot \left(\frac{4}{3}\right)^{2/3} \right]^{1/3} M^{1/36} = 24 M^{1/36},$$

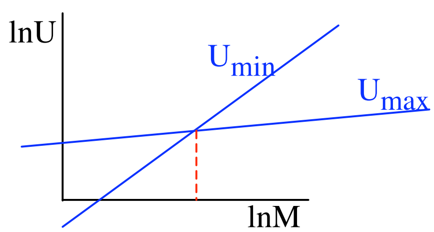
where I have used:

$\eta = 0.6$

$b = 6$

$C_D = 0.1$

$B_D = 1.5$



The crossing point is given by $16 M^{1/6} = 24 M^{1/36}$ which yields M_{max}=19 kg as the dividing line between flying and not.

See graph (Ahlborn has this wrong).

OK, so I fudged the numbers a bit to make this work!

Part 2: PKT Chapter 2

Structure and Composition of the Cell

Comment on the Text:

Written by an applied physicist (Phillips), a physicist (Kondev), and a biologist (Theriot). Compared to other texts (often written by physicists), it has a distinctly "biological" flavor. That's why I chose it. However, you are taking this course to learn about physics as applied to biology or, more broadly, to learn something about applying quantitative methods to biological systems. To do this, you need to start by knowing something qualitative/descriptive about biological organisms, including both structure and function. But, that is not the primary content of this course. In general, I am NOT going to test you on this material.

Notes:
1. Biologists probably know what you need about this already. Physicists/engineers may need to learn as they go along. (BISC 101 used to be a prerequisite!) For them, this is an important part of the course, even though it is not tested. (Interdisciplinary subjects)
2. For physicists working on cellular biophysics Alberts et al., *Molecular Biology of the Cell* is referred to as "The Bible." Very well written and useful reference.

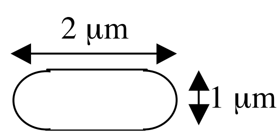
What I want everyone to take away from this course is the ability to think about biological systems in a quantitative, physical way. This is what I will give you problems on and it is what I will test you on.
Thus, when you read the text, read everything but DO NOT feel that you must memorize all the biological information, nomenclature, etc. On the other hand, when you see a calculation or a formula, be sure to stop and understand it.

Chapter 2 is entitled "What and Where: Construction Plans for Cells and Organisms."
Its purpose is to give you a quick run-through of biological structures from the atomic scale, through the cellular scale, which is the focus of the book (and of this course), right on up to the organismal level (with a nod to the ecosystem level). Thus, biologists will see much that they already know, although for others it will be an opportunity to learn. But, what I want you to focus on is the numbers and the logic which connects them (mostly counting and geometry here).

Numbers:
When you are dealing with Physics 101, 120, etc., you are mainly dealing with macroscopic, everyday object like baseballs, hockey pucks, cars, etc. You know a lot about these things from your everyday life: What are they made of, how big are they, what do they weigh, how many are there, how fast do they go? Physics then relates these number to one another. (A 2 kg mass subject to a 6 N force undergoes a 3 m/s^2 acceleration.) When you want to apply physical ideas/methods to any new area, you need to develop a similar feeling for the basic numbers.
Chapter 2 focuses on:
- What is there?
- How many of them?
- How big, massive, etc.?

I will expect you to know (i.e., to memorize) certain basic numbers. I will let you know these as we go along. See "Useful Data" on website. Don't feel that you need to memorize all numbers. We will try to develop a basic list, from which (most others can be derived or, at least, estimated).

Vast biological diversity. But, we will focus on generic issues.



Example: E. Coli (bacterium): "bacterial yardstick"
Typical bacterial cell E. (Escherichia) coli:

$$V_{E\,coli} = \pi R^2 L + \frac{4\pi}{3}R^3 = \pi(0.5)^2 \cdot 1 + \frac{4\pi}{3}(0.5)^3 = 1.309\,(\mu m)^3 \approx \boxed{1\,(\mu m)^3} = 1\times 10^{-18}\ m^3$$

$$A_{E\,coli} = 2\pi RL + 4\pi R^2 = 2\pi(0.5)1 + 4\pi(0.5)^2 = 6.2832\,(\mu m)^2 \approx \boxed{6\,(\mu m)^2} = 6\times 10^{-12}\ m^3,$$

where I have used $R = 0.5\ \mu m$, $L = 1\ \mu m$.
Note: one "micron" = one micro-meter = 10^{-6} m, is a typical bacterial dimension.

Nomenclature:	peta,	tera,	giga,	mega,	kilo,	1,	milli,	micro,	nano,	pico,	femto.
	10^{15}	10^{12}	10^{9}	10^{6}	10^{3}	1	10^{-3}	10^{-6}	10^{-9}	10^{-12}	10^{-15}

And, finally, the mass: $m_{E\,coli} = \rho_{water} V_{E\,coli} = 10^3 \cdot 10^{-18} = 1\times 10^{-15}\ kg = \boxed{1\ pg.}$

Size, volume, and area connected by geometry. You really only need size (spherical cow) to estimate. We will soon be providing other connections between numbers via physics.

Compare this with size of a water molecule:

$$D_{water} \approx 3\times 10^{-10}\ m = 3\times 10^{-4}\ \mu m = 0.3\ nm$$ (how to calculate this?)

H_2O has molecular weight 18 Da (16+2x1), so 1 cc (i.e., 10^{-6} m^3) contains 1/18 times $N_{Avogadro}$ water molecules. Thus, the volume per molecule is

$$V_{water} = \frac{10^{-6}}{\frac{1}{18}6.02\times 10^{23}} = 2.99\times 10^{-29}\ m^3 \approx \boxed{0.03\,(nm)^3},$$

so the characteristic dimension defined by $(D_{water})^3 = V_{water}$ is

$$D_{water} = \left(2.99\times 10^{-29}\right)^{1/3} = 3.1\times 10^{-10}\ m \approx \boxed{0.3\ nm.}$$

And, finally,

$$m_{water} = \rho_{water} V_{water} = 10^3 \cdot \left(3\times 10^{-29}\right) = 3\times 10^{-26}\ kg,$$ which must, of course, agree with $m_{water} = 18\ Da = 18\left(1.66\times 10^{-27}\right) \approx 3\times 10^{-26}\ kg$.

Other Useful Numbers: **3.6**

See PKT Table 1.1 (p.26)

Table 1.1 Rules of thumb for biological estimates

	Quantity of interest	Symbol	Rule of thumb
E. coli	Cell volume	$V_{E.\ coli}$	$\approx 1\ \mu m^3$
	Cell mass	$m_{E.\ coli}$	≈ 1 pg
	Cell cycle time	$t_{E.\ coli}$	≈ 3000 s
	Cell surface area	$A_{E.\ coli}$	$\approx 6\ \mu m^2$
	Genome length	$N_{bp}^{E.\ coli}$	$\approx 5 \times 10^6$ bp
	Swimming speed	$v_{E.\ coli}$	$\approx 20\ \mu m/s$
Yeast	Volume of cell	V_{yeast}	$\approx 60\ \mu m^3$
	Mass of cell	m_{yeast}	≈ 60 pg
	Diameter of cell	d_{yeast}	$\approx 5\ \mu m$
	Cell cycle time	t_{yeast}	≈ 200 min
	Genome length	N_{bp}^{yeast}	$\approx 10^7$ bp
Organelles	Diameter of nucleus	$d_{nucleus}$	$\approx 5\ \mu m$
	Length of mitochondrion	l_{mito}	$\approx 2\ \mu m$
	Diameter of transport vesicles	$d_{vesicle}$	≈ 50 nm
Water	Volume of molecule	V_{H_2O}	$\approx 10^{-2}\ nm^3$
	Density of water	ρ	$1\ g/cm^3$
	Viscosity of water	η	≈ 1 centipoise (10^{-2} g/(cm s))
	Hydrophobic embedding energy	$\approx E_{hydr}$	25 cal/(mol Å^2)
DNA	Length per base pair	l_{bp}	$\approx 1/3$ nm
	Volume per base pair	V_{bp}	$\approx 1\ nm^3$
	Charge density	λ_{DNA}	2 e/0.34 nm
	Persistence length	ξ_P	50 nm
Amino acids and proteins	Radius of "average" protein	$r_{protein}$	≈ 2 nm
	Volume of "average" protein	$V_{protein}$	$\approx 25\ nm^3$
	Mass of "average" amino acid	M_{aa}	≈ 100 Da
	Mass of "average" protein	$M_{protein}$	$\approx 30{,}000$ Da
	Protein concentration in cytoplasm	$c_{protein}$	≈ 300 mg/mL
	Characteristic force of protein motor	F_{motor}	≈ 5 pN
	Characteristic speed of protein motor	v_{motor}	≈ 200 nm/s
	Diffusion constant of "average" protein	$D_{protein}$	$\approx 100\ \mu m^2/s$
Lipid bilayers	Thickness of lipid bilayer	d	≈ 5 nm
	Area per molecule	A_{lipid}	$\approx \frac{1}{2}\ nm^2$
	Mass of lipid molecule	m_{lipid}	≈ 800 Da

Table 1.1 Physical Biology of the Cell (© Garland Science 2009)

More on various numbers in PKT Ch. 2.

Size Scales in the biological world:

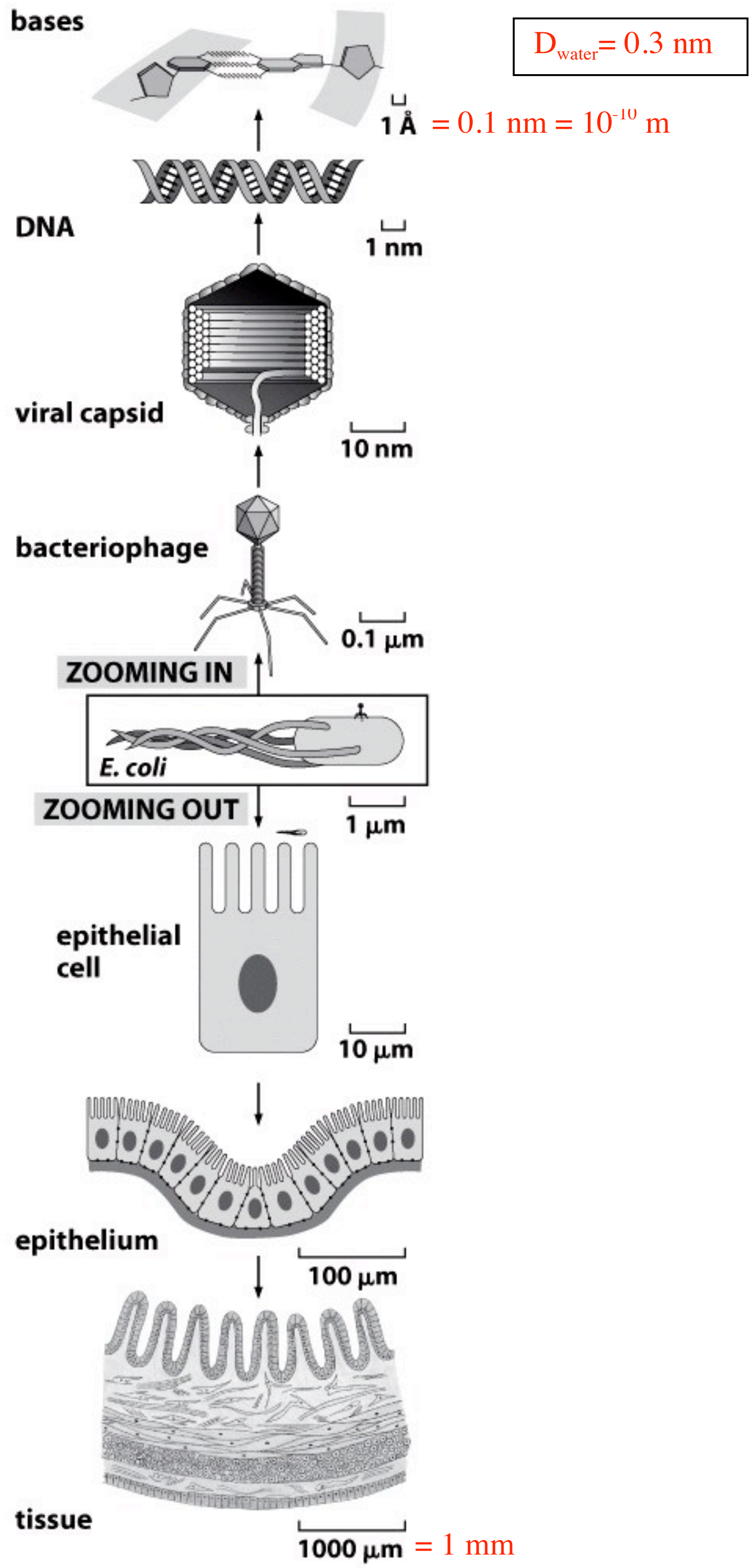


Figure 2.7 Physical Biology of the Cell (© Garland Science 2009)

Plus, organs and organisms at larger scales (See PKT Sec. 2.3)