BIOMECHANICS: SIMPLE CONSEQUENCES OF SCALING

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1. INTRODUCTION

This document is a set of notes for the course "Biomechanics: simple consequences of scaling" taught by the author at cSplash at the Courant Institute of Mathematical Sciences, New York University on April 4, 2009. The course description is as follows:

> How high can an animal jump? Why can a small animal survive a high drop? How come an ant can lift up to twenty times its own body weight, but we struggle with half of ours? These are the kinds of questions that we will try to answer in this class, using simple mechanical arguments to explain (and explore!) the consequences of size in nature. If you have an interest in applying maths and physics to biology, then this class is for you (just one installment in a million-part series in using mathematics to understand the natural world)!

In this course, we will basically work through a series of examples with the aim of gaining some intuitive understanding of how the physics of various activities fundamentally depend on size.

Much of the material in this course is taken from a set of lectures [1] by Dr. Kalvis M. Jansons at University College London. Here, we will only cover the portion of [1] that pertains to scaling; if you are interested in related and more advanced material, let me know and I can send you the rest!

1.1. **Basic physics.** In the following, we will primarily use mechanical arguments, so a basic understanding of the concepts of force, energy, and power is essential. For those who are not entirely comfortable with these, here is a very brief and intuitive refresher.

A *force* is something that can act on an object to cause it to move, bend, stretch, rotate, or otherwise experience some sort of displacement or deformation. Forces are everywhere; we are constantly under the effect of gravity, and, for a more local example, you need look no further than your own muscles, which generate forces to allow you to walk, run, jump, grip, and even breathe.

The amount of work that can be performed by a force is called *energy*. We typically concern ourselves with two types of energy: the potential energy $U = mgh$ due to gravity, and the kinetic energy $V = mv^2/2$ due to motion, where m is the mass of the object, g is the gravitational constant, h is the height of the object above ground, and v is the velocity of the object. It is also useful to think of energy as the work $W = Fd$ performed by a force F acting over a distance d; to see the equivalence with the above, think of applying a force of magnitude $F = mg$ counteracting gravity over a distance $d = h$ to get U, and of accelerating an object at rate a from rest by applying a force $F = ma$ over a distance $d = v^2/(2a)^1$ to get V.

The *power* now is the rate at which work is done, i.e., $P = W/t$, where t is the time over which W is performed. The most common reference to power in our daily lives is probably the wattage system for electrical power, which describes how much electrical energy is delivered per unit time. More generally, though, power can describe many important quantities, including the rate at which you use energy during strenuous exercise, the rate at which you gain energy by eating a (delicious) meal, or even the rate at which you lose heat through your skin.

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[1]If you know about integral calculus, this comes from noting that it takes time $t = v/a$ to accelerate to velocity v at rate a, so the distance is $d = \int_0^{v/a} v'(t) \, dt = \int_0^{v/a} at \, dt = v^2/(2a)$.

2. Simple scaling arguments

Suppose that we have a family of animals that are similar in all respects apart from their linear dimension l; by this, we mean that they are similar in the mathematical sense[2] and so differ only in scale. We will make the following generic assumptions, which are not exactly true but are reasonable nonetheless: lengths are proportional to l, areas to l^2, and volumes to l^3; to see why these might be true, just think of the animal as a box with sides of length l (a mathematician's favorite trick!).

In the following, we will make heavy use of proportionalities, often written between two quantities A and B as $A \propto B$. This means that $A = cB$ for some constant c; in fact, c need not be a "true" constant (e.g., $c = 3$), just one with respect to the quantity of interest. This may be a little confusing, but an example will clear that right up: suppose that we are traveling in a car moving at some speed v when we decide to hit the brakes. How does the distance d required for the car to come to a stop depend on v?

The relevant quantity to think about here is the kinetic energy of the car, in this case $V = mv^2/2$. Since we are interested only in v (and since clearly m does not depend on v), we can write this as $V \propto v^2$. Now what about the brakes? We can think of them as applying a braking force of magnitude F per unit distance. Thus, the total work that the brakes do in dissipating the kinetic energy of the car is $W = Fd \propto d$. At rest, we must have $V = W$ since all kinetic energy must be depleted, so $d \propto W = V \propto v^2$.

This is a basic result in mechanics and is often used as support (and rightfully so!) against high-speed driving; just think of it this way, if you double your speed, then you need to go four times as far to stop!

Let's look at some more biologically inspired examples now.

2.1. **Muscle force generation.** How much force can a muscle generate? Let's think of a muscle as a cylinder, with muscle fibers running down the length of the axis. Suppose that each fiber generates a fixed amount of force; the problem then reduces to figuring out the total number of fibers. But this is just proportional to the cross-sectional area of the muscle, which we assume is proportional to l^2. Therefore, the amount of force that a muscle can generate is $F \propto l^2$.

What about the amount of work that a muscle can do? We know that $F \propto l^2$; what is the distance d over which F can act? For a muscle, d is the length of the limb (e.g., your arm), so $d \propto l$. Hence the amount of work that can be done is $W = Fd \propto l^3$.

2.2. **Speed of limb movement.** What is the maximum speed of limb movement? The muscles of a limb can generate a force $F \propto l^2$, which acts through a distance $d \propto l$, and so can supply a maximum amount of energy $E = Fd \propto l^3$. If all of this is converted into kinetic energy, then we obtain $E = mv^2/2$. But m is just the product of some density, which we assume to be constant, and the volume, so $m \propto l^3$. Therefore, $E \propto l^3 v^2$, so by comparison we must have $v \propto l^0$, i.e., v is constant.

Note that the assumption that $m \propto l^3$ is, while reasonable, not exactly correct as the legs of larger animals tend to be proportionally thicker, and thus more massive, than those of smaller animals. We can pursue this a little further below.

2.3. **Leg size.** What is the size of an animal's legs? Suppose that an animal's mass is supported purely by its legs. Then we need to impose a balance between the force $F_g = mg \propto l^3$ of gravity and the force $F_a \propto A$ applied in opposition by the legs, where A is the leg cross-sectional area. Setting $F_g = F_a$ gives $A \propto l^3$.

What if we were interested in the diameter d of the legs? This is simply nothing more than $d \propto A^{1/2} \propto l^{3/2}$. Notice that d grows faster than l, consistent with most natural observations.

2.4. **Height of a jump.** Let us turn now to our first "surprising" example. We have all seen small animals like rabbits and grasshoppers jump many times their own height, far more in proportion than we are capable of. So suppose that there were a human-sized grasshopper; would it really be able to jump fifty feet into the air? More generally, we want to answer the following question: how does the height h of a jump scale with l?

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[2]Remember similar triangles? Now just think of similar animals!

The main idea here is to consider the potential energy $U = mgh \propto l^3 h$ and to compare that to the work that an animal is capable of producing, which, from above, we know is $W = Fd \propto l^3$. Equate U with W now to obtain $h \propto l^0$—the height of a jump is independent of size!

This is a bit surprising, and you may (should) wonder if it is really correct. But in fact this result holds quite well: humans can jump about three or four feet high, which is approximately what rabbits and cats—and, yes, even grasshoppers, can achieve. So next time that someone tries to scare you off with giant jumping insects, throw this *remarkably* simple argument back in their face!

Something to consider if you're bored: does this result change if we consider a long jump instead of a high jump, i.e., how far horizontally can an animal jump?

2.5. **Weightlifting.** How much can a weightlifter lift in proportion to his weight? The maximum weight w that a weightlifter can lift is proportional to the maximum force that he can exert, which is proportional to l^2, so $w \propto l^2$. Thus, as a proportion of his body weight $W = mg \propto l^3$, this is $w/W \propto l^{-1}$.

This is our first example of a negative exponent, which implies that a quantity decreases as l is increased. In this case, we are talking about the relative mass that an animal can lift or carry, for example, the amount of food that can be brought along—so there is definitely an advantage to being small here! This also explains why ants, being so tiny, can lift up to twenty times their own body weight, but we (at least I) have such a hard time with even just half of our own.

3. AIR RESISTANCE AND FLIGHT

We turn now to examples involving air resistance and flight. First, though, we will need some preliminary results from fluid mechanics, which we will take as given:

- The lift, a force directed perpendicular to the direction of motion, is proportional to $A_w v^2$, where $A_w \propto l^2$ is the wing area.
- The drag, a force directed opposite the direction of motion, is roughly proportional to $l^2 v^2$.

3.1. **Size of a flying animal.** Why do large birds find it harder to fly? Some large birds, like the ostrich or the emu, cannot fly at all. Similarly, why is human-powered flight so difficult?

To give some insight into answering these questions, we begin by writing the lift $L \propto l^2 v^2$. For flight to occur, this must be enough to overcome gravity, so the minimum flying speed v is given by $L = mg \propto l^3$, hence $v \propto l^{1/2}$. Thus, the minimum power required for flight is $P = Dv \propto l^2 v^3 \propto l^{7/2}$, where $D \propto l^2 v^2$ is the drag.

What is the maximum power that an animal can supply? Well, how does an animal get its nutrients? Typically, this comes in the form of food and air, both of which depend on surface area in some way. Thus, we may assume that the power supplied is $P_a \propto l^2$. Observe now that the power P required grows faster than the power P_a available, so there is an upper limit on the size of a flying animal!

Note that it wasn't entirely crucial that $P_a \propto l^2$ in this argument; in fact, we could just as well have taken $P_a \propto l^3$. The real dependence is something like $P_a \propto l^{9/4}$, as we'll see later.

3.2. **Best gliding angle and speed.** Does the best glide angle depend on size? Does the glide speed, at the best glide angle, depend on size? Let θ be the best glide angle (of descent), and let u be the best glide speed, i.e., $u = v \cos \theta$. A bird flying under these conditions experiences a lift force $L \propto l^2 v^2$ acting perpendicularly to the direction of motion, a drag force $D \propto l^2 v^2$ acting oppositely the direction of motion, and a force mg due to gravity acting vertically downward.

Draw a force diagram and impose a force balance at equilibrium to obtain $L = mg \cos \theta$ and $D = mg \sin \theta$, so $\tan \theta = D/L \propto l^0$, i.e., θ is independent of l. Now for the best glide speed, consider for instance the proportionalities $L \propto l^2 v^2$ and $L \propto mg \propto l^3$. Comparing the two, we get $v \propto l^{1/2}$, so $u \propto l^{1/2}$ as well.

3.3. **Survivability of a high drop.** Let's go for something a bit more interesting now: would any animal die if dropped from 10,000 feet? According to JBS Haldane, a famous British geneticist:

TABLE 1. Experimental scaling data for mammals, where m is mass in kg.

Property	Units	Scaling
Oxygen consumption rate	L/min	$0.0116\ m^{0.76}$
Lung volume	L	$0.063\ m^{1.02}$
Respiration frequency	min^{-1}	$53.5\ m^{-0.26}$
Blood volume	L	$0.055\ m^{0.99}$
Heart mass	kg	$0.0058\ m^{0.99}$
Heart rate	min^{-1}	$241\ m^{-0.25}$
Skeletal mass	kg	$0.1\ m^{1.13}$
Brain mass (non-human)	kg	$0.01\ m^{0.70}$
Brain mass (human)	kg	$(0.08\text{ to }0.09)\ m^{0.66}$

> You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away, provided that the ground is fairly soft. A rat is killed, a man is broken, a horse splashes [2].

Haldane seemed a rather cerebral fellow (just look at the picture on his Wikipedia page; it's fantastic), so let's just assume that he arrived at this conclusion through pure force of mind—as we are about to do—rather than, say, by actually dropping animals down a mineshaft.

First, let's assume that an animal dropped from this height attains terminal velocity v. What does this mean? Basically, terminal velocity occurs when the force of gravity $mg \propto l^3$ is exactly counterbalanced by the drag force $D \propto l^2 v^2$ so that no further acceleration is possible. Thus, setting the two equal, we derive $v \propto l^{1/2}$, so the kinetic energy on impact is $K = mv^2/2 \propto l^4$.

Now what kind of resistive force can the animal apply? The force that its bones can withstand is $F \propto l^2$, which acts through a distance $d \propto l$, so the animal can do work $W = Fd \propto l^3$ in resisting the impact. But this grows slower than the kinetic energy K, i.e., $W/K \propto l^{-1}$, so there is a critical size below which the animal lives and above which it dies!

4. BETTER SCALING LAWS

The main problem concerning the validity of such simple scaling arguments is the fact that animals are not geometrically similar over a large range of scales. For example, if I showed you a picture of the legs of a four-legged mammal, you would probably be able to give me a fairly good guess of its size; this is because large animals tend to have proportionally thicker (and straighter) legs than small animals, for reasons that we have already seen.

In this section, we consider some experimental data (Table 1), which we use to refine our simple arguments. The data in the table is for mammals and uses mass as the scaling variable. The reason for this is that mammals are not all similar in shape, so it is not easy to define a sensible characteristic linear dimension.

4.1. **Respiration frequency.** Can we derive the scaling for the breathing rate of a mammal from its metabolic costs? From Table 1, the power requirement is $m^{3/4}$; this must be balanced by the product of the breathing rate r and the oxygen intake per breath, which is dependent on the size of the lung and is therefore proportional to m. Equating these, we see that $mr \propto m^{3/4}$, so $r \propto m^{-1/4}$, which is just what we find in the data.

4.2. **Heart rate and aging.** What about the heart rate now? The rate of power usage is $P \propto m^{3/4}$ and must be equal to that supplied by the heart. But this is just proportional to the heart rate r times the heart volume V, which we may assume is proportional to the heart mass and so $V \propto m$. Thus, $r \propto P/V \propto m^{-1/4}$, as in the data.

Note that this result may be used to give a very rough upper bound on the lifespan of an animal. It is generally logical to suppose that an organ wears out at a rate proportional to its use. Under this assumption,

the lifetime of the heart is $T \propto r^{-1} \propto m^{1/4}$, and so larger animals tend to live longer—and from your own experience, of course, you know this to be true!

4.3. **Skeletal mass.** Is there a simple argument for why the skeletal mass does not scale as m? We explain this by considering the force of gravity $F_g = mg \propto l^3$ that must be supported by the animal's bones. The skeletal applied force is $F_a \propto A$, where A is the cross-sectional area of a bone. Therefore, setting $F_g = F_a$, we obtain $A \propto m$, hence the bone volume is $V \propto Al \propto m^{4/3}$, if we assume that $l \propto m^{1/3}$. The bone mass now is just a constant density times the bone volume, so this is proportional to $m^{4/3}$ as well.

To be sure, this isn't the exact scaling that we find in Table 1. However, we have reasoned in a very simple manner about why the exponent on m ought to be greater than one—this in itself is quite an achievement!

4.4. **Biomass in a pond.** Suppose that two ponds have the same surface area and the same distribution of fish sizes, but have very different average depths. How does the total mass of fish in each pond compare?

We may analyze this by considering the oxygen levels in each pond. The rate of oxygen input into each is proportional to the surface area A. At equilibrium, this is equal to the rate of oxygen consumption, which is proportional to $m^{3/4}$. Therefore, the expected total mass of fish in each pond is the same and scales as $m \propto A^{4/3}$. In particular, since the fish size distribution is the same, we also expect the same number of fish in each pond.

What if the fish in the first pond were, on average, α times the mass of those in the second? Then, since we expect still the same total mass, we should expect α^{-1} times the number of fish in the first than in the second.

5. ADDITIONAL SCALING EXAMPLES

If you've found this sort of thing interesting and fun so far, then here are some more! Be careful—some of these are a bit more involved than what we've thus seen, but the basic ideas are the same. Try and work through as much as you can!

5.1. **Dive duration.** How long can a mammal stay under water? A diving mammal stores oxygen in its blood, so the total power supply is proportional to the blood volume $V \propto m$. On the other hand, the rate at which oxygen is used is $r \propto m^{3/4}$, so the length of time that a mammal can hold its breath is $T \propto V/r \propto m^{1/4}$.

5.2. **Dive distance.** How deep can a mammal dive? First of all, I have to tell you that movement through water is much like movement through air: both are fluids and so there are drag forces[3].

With this in mind, an animal diving at a speed v experiences a drag force $D \propto l^2 v^2 \propto m^{2/3} v^2$ and so uses power $P = Dv \propto m^{2/3} v^3$. This power is used to change the animal's potential energy, so $P = mgv \propto mv$, hence $v \propto m^{1/6}$. Therefore, the distance that a mammal can dive is $d = vt$, where t is how long it can stay under water, which we know from above to be $t \propto m^{1/4}$, so $d \propto m^{5/12} \sim m^{1/2}$.

Here's a related question: how far can a mammal swim horizontally? Clearly, it still uses power at a rate $P \propto m^{2/3} v^3$ due to drag. But the power that it can supply is proportional to m, so $v \propto m^{1/9}$, hence the swimming distance is $d = vt \propto m^{13/36} \sim m^{1/3}$.

5.3. **Speed on flat ground.** Let's consider first a cyclist: how fast can a human cycle on flat ground? For simplicity, let's just think in terms of l rather than the more accurate m (this will have the effect of making the exponents easier; you can also try to do it with m to see if it makes any real difference).

Assume that the bicycle and its rider scale together and that air drag is the only relevant external force. Then a cyclist moving at speed v experiences a drag force $D \propto l^2 v^2$ and so requires power $P = Dv \propto l^2 v^3$. However, the rate at which power can be delivered is proportional to the rate of oxygen intake and hence to l^2. Thus, equating these, we obtain $v \propto l^0$.

Is there a similar argument for running on flat ground? Because the characteristic speed of a runner is considerably lower than that of a cyclist, it is likely that it is no longer air resistance that is the relevant

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[3]Of course, as you know from experience, the drag force when going through water is much stronger than that going through air.

limitation, but rather that of something more internal, say, the speed of leg movement. But we have already looked at this, so by appealing to this previous result, we can argue that $v \propto l^0$ also.

5.4. **Speed up a steep hill.** How fast can a human cycle up a steep hill? As before, the power supplied is $P \propto l^2$. However, for a sufficiently steep hill, the relevant force is now gravity instead of air resistance. At a maintained maximum speed, the kinetic energy of the cyclist is constant, hence all power is used to change the potential energy, i.e., $P = mgu \propto l^3 u$, where u is the climbing speed of the cyclist. Thus, $u \propto l^{-1}$.

What about running? It is reasonable that a runner's uphill speed be limited by his power output, so we can apply the same argument to get $u \propto l^{-1}$ here as well.

There is a lesson in here somewhere: if you find yourself getting chased by a hungry T-rex, find a steep hill and run up!

5.5. **Walking-running transition.** How fast can an animal walk? We refer here to walking, as opposed to running, in a somewhat technical manner: at least one leg must always be in contact with the ground.

The argument that we will use is a bit on the creative side. Approximate an animal as a rimless spoked wheel of mass m and spoke length l. For such a wheel moving transversely at speed v, a point at the tip of a spoke experiences a centrifugal acceleration[4] $a = v^2/l$. If $a < g$, then the wheel will have at least one spoke on the ground at all times, thus representing walking; if $a > g$, then there will be periods for which no spokes will touch the ground, thus representing running. Therefore, the transition speed is attained at $a = g$, for which $v \propto l^{1/2}$.

It is important to note here that this analysis is extremely approximate; for instance, I would not bet on the depedence $v \propto l^{1/2}$ with much confidence at all. However, the mathematics is simple and illustrative, and the model gives some physical intuition about why we might expect a walking-running transition speed.

In real life, this transition does indeed exist but generally depends more on matters of energetics. More precisely, below a certain speed, walking is more efficient, and above it, running is more efficient[5]; most animals are found to spontaneously switch from walking to running when they exceed this limit.

5.6. **Parachute size.** How big does a parachute need to be to produce a safe landing? For a parachute of area A, the drag experienced at speed v is $D \propto Av^2$. Thus, at terminal velocity, $D = mg \propto l^3$, so $v^2 \propto l^3/A$, hence the kinetic energy at impact is $K = mv^2/2 \propto l^6/A$. As before, the work that can be done by a body in resisting the impact is $W \propto l^3$. Therefore, the threshold for a safe landing is given by $K = W$, for which $A \propto l^3$.

5.7. **Size of a spiderweb.** What is the maximum size of a spiderweb? Assume that the total volume of material that can be put into the web is $V \propto l^3$, and let A be the cross-sectional area of each strand. Since each strand must be able to support the weight of the spider, we have $A \propto mg \propto l^3$. Now let $d \propto l$ be the spacing in between adjacent strands, and let r be the linear dimension of the web, which we may assume to be in the shape of a square for simplicity. Then the total volume of web material is $V = Ar(r/d) = Ar^2/d \propto l^2 r^2$. But $V \propto l^3$, so $r \propto l^{1/2}$.

5.8. **Vocal frequency.** How does the frequency of sound produced by an animal scale? We need to know a little bit more physics here, but basically the frequency of sound produced is determined by the resonant frequency of the animal's vocal cords, whose resonant wavelength is proportional to l. Therefore, the frequency is $f \propto l^{-1}$.

We can also use this in a more direct application: what vocal frequency does a bat use? The linear dimension of the smallest object that a bat needs to resolve is about $d \sim 10^{-3}$ m for an insect. Then $f = c/\lambda$, where $c \sim 100$ m/s is the speed of sound in air and $\lambda \sim d$ is the wavelength used, so $f \sim c/d \sim 10^5$ s^{-1}.

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[4]For the picky among you, note that this is *not* centripetal acceleration!

[5]You can actually gauge this efficiency by measuring oxygen consumption in a controlled environment.

5.9. **Travel distance of a grazing animal.** How far must a grazing animal travel in order to collect enuogh food? Consider an animal walking along a strip of length L and width w. Clearly, $w \propto l \propto m^{1/3}$ as the animal can only graze from an area proportional to its size, so assuming that the energy density of grass is uniform on this strip, we have the power input $P \propto Lw \propto Lm^{1/3}$. Therefore, assuming that metabolism is the only power expenditure, $P \propto m^{3/4}$, so $L \propto m^{5/12}$.

5.10. **Liquid films on plant stems.** Some plants in water use spaced hairs along its stem to maintain an air film through surface tension. How does this spacing vary with water depth? The force on the air film is due to hydrostatic pressure, which is proportional to h, the depth of the water. Thus, for a given surface tension constant γ, we have $h \propto n\gamma$, where n is the linear density of hairs. But this is just $n \propto d^{-1}$, where d is the hair spacing, so $d \propto \gamma/h$.

5.11. **Time to boil an egg.** How long does it take to cook an egg? Suppose that an egg at temperature $T = T_0$ is submerged in a heat bath at temperature $T = T_1$. Heat transfer is governed by the diffusion equation

$$\frac{\partial T}{\partial t} = k\nabla^2 T,$$

which is a differential equation and, in particular, a *partial* differential equation, which in general can be quite nasty[6].

We won't need to know very much about what this equation actually means, but let me just try and give you a sense of its flavor. The term $\partial T/\partial t$ on the left-hand side is called a derivative and expresses a ratio of differences (that's what you can think of ∂ as standing for), in this case the difference in the temperature over the difference in time—in other words, the rate at which temperature is changing.

As for the term on the right, let's just consider $\nabla^2 T$ for now. In multiple dimensions, the operator ∇^2 is a little complicated, but in one dimension (i.e., along a line), we can write this as

$$\nabla^2 T = \frac{\partial^2 T}{\partial x^2} = \frac{\partial}{\partial x}\left(\frac{\partial T}{\partial x}\right),$$

where x is the spatial variable (e.g., position along a line). The term $\partial T/\partial x$ we already know how to interpret: it tells us how the temperature changes over space. The outer $\partial/\partial x$ now acts on $\partial T/\partial x$ to give us how the spatial derivative itself changes over space; in other words, it is a *second-order* spatial derivative. Finally, the constant k simply tells us how the units of $\partial T/\partial t$ and $\nabla^2 T$ relate.

The theory of differential equations is very interesting, but we don't really need any of that here. From a scaling perspective, things are pretty easy: in going from T_0 to T_1, the left-hand side is like $\partial T/\partial t \propto (T_1 - T_0)/t$, and the right-hand side like $k\nabla^2 T \propto (T_1 - T_0)/l^2$, where l is the size of the egg. Therefore, setting these equal, the time needed to cook an egg is roughly $t \propto l^2$.

According to Dr. Jansons, who taught me this particular example, this *actually works* fairly well! You can use chicken eggs to figure out what the proportionality constant is, then extrapolate to find how long you'd have to cook, say, an ostrich egg for—you know, in case you ever run into that problem.

5.12. **Pine tree trunk shape.** How does the trunk shape of a tree vary with height? In particular, let us consider a pine tree, which typically has a mass of foliage near the canopy and nowhere else. We approach this problem by assuming that the trunk shape is determined by static load, i.e., the tree mass at any point must be able to support the tree mass above it. To do this, we're going to need to know some calculus, which, unfortunately, I'm not going to be able to teach here, so proceed at your own risk!

Let $A(h)$ be the cross-sectional area of the tree, where $0 \leq h \leq H$ is the height above ground, and let W_0 be the weight of the foliage. Then the weight that must be supported at height h is

$$W(h) = W_0 + \rho \int_h^H A(h)\ dh,$$

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[6]This may look scary now, but in a few years, especially if you take an applied mathematics, physics, or engineering curriculum, you will rock at stuff like this. So if you want to know what all these funny little symbols mean, don't cop out now—do maths and science in college!

where we have assumed, for simplicity, a uniform density ρ. The support force, on the other hand, is $F(h) = \alpha A(h)$ for some proportionality constant α. Setting $F(h) = W(h)$ and differentiating gives

$$\frac{A'(h)}{A(h)} = -\frac{\rho}{\alpha},$$

so $A(h) = A_0 \exp(-\rho h/\alpha)$, where $A_0 = A(0)$ is the cross-sectional area of the tree base. In fact, A_0 and W_0 are related, as may be seen by considering the equality $F(H) = W(H)$, which gives

$$A_0 = \frac{W_0 e^{\rho H/\alpha}}{\alpha}.$$

If we assume that the tree trunk is circular with radius $R(h)$, then equivalently

$$R(h) = R_0 e^{-\rho h/(2\alpha)}, \quad R_0 = \sqrt{\frac{W_0 e^{\rho H/\alpha}}{\pi \alpha}}.$$

Does this exponential profile remind you of anything?—something in Paris, perhaps? While obviously the details are different, the general principle behind the design of the Eiffel Tower is the same assumption of static load, which gives rise to the same exponential form seen here.

6. Concluding perspective

Using very simple mechanical arguments, we've seen some remarkable examples of how certain activities fundamentally depend (or not!) on size. In my opinion, among the most striking of these are:

- The height that an animal can jump is independent of size.
- Small animals can lift proportionally more weight than large animals.
- There is an upper limit to the size of a flying animal.
- There is a critical size above which it is impossible to survive a high drop.

Even still, there is much that we have not even touched on. For instance, a simple consideration of heat generation and loss explains why you hardly ever see any small animals in cold regions; and a more sophisticated analysis of oxygen requirements and delivery explains why insects have to be small (and also why they were much bigger in the prehistoric past). In fact, earlier just this week, I read a letter in Science that explains why long-necked dinosaurs, such as *Barosaurus* and *Brachiosaurus*, had to keep their heads and necks low, as opposed to the usual nine meters above the chest that museums seem to prefer for display, on the basis of the exorbitant cardiac forces and energies that would be required to circulate blood to a head held so high (hint: dinosaur heart attacks!).

It has been a joy writing these notes, and I hope that, from them, you have gained an intuitive sense of the relevant forces in biology at the organismal level and how they interact. There are two major themes that I hope you will take away with you.

The first, which we have already emphasized, is that size is a fundamental determinant of ability. There is typically an optimal size for any given activity, and animals of all sizes compromise on what they can and cannot do. For example, large animals, like humans, cannot afford to fall off of high ledges, while small animals, like insects, cannot afford to get wet. In thinking about the implications of size for different animals, we can understand what restrictions physics imposes on them, and how and why they operate in the way that they do.

The second, which we have only implicitly touched on but which you are likely to encounter again and again, is that the story of size is really the story of the fight between surface area and volume. We have already seen an example of this in flight, in which the force of gravity grows as the mass of the animal and hence its volume, while the power available to counter gravity grows only as its area, namely the area that it has available for absorption of oxygen and food. Since the volume grows faster than the surface area, much of biological complexity is really about how to, essentially, get more area out of a given size. It is for this very reason that we have such coiled and convoluted intestines, as well as why our brains have so many folds and ridges. Indeed, as Haldane aptly put it: "The higher animals are not larger than the lower because they are more complicated. They are more complicated because they are larger" [2].

I leave you now with a famous short essay written by Haldane in the 1920s, entitled "On Being the Right Size" [2]. Enjoy the wonderful British prose, and the (somewhat courageous) generalization to politics at the end:

The most obvious differences between different animals are differences of size, but for some reason the zoologists have paid singularly little attention to them. In a large textbook of zoology before me I find no indication that the eagle is larger than the sparrow, or the hippopotamus bigger than the hare, though some grudging admissions are made in the case of the mouse and the whale. But yet it is easy to show that a hare could not be as large as a hippopotamus, or a whale as small as a herring. For every type of animal there is a most convenient size, and a large change in size inevitably carries with it a change of form.

Let us take the most obvious of possible cases, and consider a giant man sixty feet high—about the height of Giant Pope and Giant Pagan in the illustrated Pilgrim's Progress of my childhood. These monsters were not only ten times as high as Christian, but ten times as wide and ten times as thick, so that their total weight was a thousand times his, or about eighty to ninety tons. Unfortunately the cross sections of their bones were only a hundred times those of Christian, so that every square inch of giant bone had to support ten times the weight borne by a square inch of human bone. As the human thigh-bone breaks under about ten times the human weight, Pope and Pagan would have broken their thighs every time they took a step. This was doubtless why they were sitting down in the picture I remember. But it lessens one's respect for Christian and Jack the Giant Killer.

To turn to zoology, suppose that a gazelle, a graceful little creature with long thin legs, is to become large, it will break its bones unless it does one of two things. It may make its legs short and thick, like the rhinoceros, so that every pound of weight has still about the same area of bone to support it. Or it can compress its body and stretch out its legs obliquely to gain stability, like the giraffe. I mention these two beasts because they happen to belong to the same order as the gazelle, and both are quite successful mechanically, being remarkably fast runners.

Gravity, a mere nuisance to Christian, was a terror to Pope, Pagan, and Despair. To the mouse and any smaller animal it presents practically no dangers. You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away, provided that the ground is fairly soft. A rat is killed, a man is broken, a horse splashes. For the resistance presented to movement by the air is proportional to the surface of the moving object. Divide an animal's length, breadth, and height each by ten; its weight is reduced to a thousandth, but its surface only to a hundredth. So the resistance to falling in the case of the small animal is relatively ten times greater than the driving force.

An insect, therefore, is not afraid of gravity; it can fall without danger, and can cling to the ceiling with remarkably little trouble. It can go in for elegant and fantastic forms of support like that of the daddy-longlegs. But there is a force which is as formidable to an insect as gravitation to a mammal. This is surface tension. A man coming out of a bath carries with him a film of water of about one-fiftieth of an inch in thickness. This weighs roughly a pound. A wet mouse has to carry about its own weight of water. A wet fly has to lift many times its own weight and, as everyone knows, a fly once wetted by water or any other liquid is in a very serious position indeed. An insect going for a drink is in as great danger as a man leaning out over a precipice in search of food. If it once falls into the grip of the surface tension of the water—that is to say, gets wet—it is likely to remain so until it drowns. A few insects, such as water-beetles, contrive to be unwettable; the majority keep well away from their drink by means of a long proboscis.

Of course tall land animals have other difficulties. They have to pump their blood to greater heights than a man, and, therefore, require a larger blood pressure and tougher blood-vessels. A great many men die from burst arteries, greater for an elephant or a giraffe. But animals of all kinds find difficulties in size for the following reason. A typical small animal, say a microscopic worm or rotifer, has a smooth skin through which all the oxygen it requires can soak in, a straight gut with sufficient surface to absorb its food, and a single kidney. Increase its dimensions tenfold in every direction, and its weight is increased a thousand times, so that if it is to use its muscles as efficiently as its miniature counterpart, it will need a thousand times as much food and oxygen per day and will excrete a thousand times as much of waste products.

Now if its shape is unaltered its surface will be increased only a hundredfold, and ten times as much oxygen must enter per minute through each square millimetre of skin, ten times as much food

through each square millimetre of intestine. When a limit is reached to their absorptive powers their surface has to be increased by some special device. For example, a part of the skin may be drawn out into tufts to make gills or pushed in to make lungs, thus increasing the oxygen-absorbing surface in proportion to the animal's bulk. A man, for example, has a hundred square yards of lung. Similarly, the gut, instead of being smooth and straight, becomes coiled and develops a velvety surface, and other organs increase in complication. The higher animals are not larger than the lower because they are more complicated. They are more complicated because they are larger. Just the same is true of plants. The simplest plants, such as the green algae growing in stagnant water or on the bark of trees, are mere round cells. The higher plants increase their surface by putting out leaves and roots. Comparative anatomy is largely the story of the struggle to increase surface in proportion to volume. Some of the methods of increasing the surface are useful up to a point, but not capable of a very wide adaptation. For example, while vertebrates carry the oxygen from the gills or lungs all over the body in the blood, insects take air directly to every part of their body by tiny blind tubes called tracheae which open to the surface at many different points. Now, although by their breathing movements they can renew the air in the outer part of the tracheal system, the oxygen has to penetrate the finer branches by means of diffusion. Gases can diffuse easily through very small distances, not many times larger than the average length traveled by a gas molecule between collisions with other molecules. But when such vast journeys—from the point of view of a molecule—as a quarter of an inch have to be made, the process becomes slow. So the portions of an insects body more than a quarter of an inch from the air would always be short of oxygen. In consequence hardly any insects are much more than half an inch thick. Land crabs are built on the same general plan as insects, but are much clumsier. Yet like ourselves they carry oxygen around in their blood, and are therefore able to grow far larger than any insects. If the insects had hit on a plan for driving air through their tissues instead of letting it soak in, they might well have become as large as lobsters, though other considerations would have prevented them from becoming as large as man.

Exactly the same difficulties attach to flying. It is an elementary principle of aeronautics that the minimum speed needed to keep an aeroplane of a given shape in the air varies as the square root of its length. If its linear dimensions are increased four times, it must fly twice as fast. Now the power needed for the minimum speed increases more rapidly than the weight of the machine. So the larger aeroplane, which weighs sixty-four times as much as the smaller, needs one hundred and twenty-eight times its horsepower to keep up. Applying the same principle to the birds, we find that the limit to their size is soon reached. An angel whose muscles developed no more power weight for weight than those of an eagle or a pigeon would require a breast projecting for about four feet to house the muscles engaged in working its wings, while to economize in weight, its legs would have to be reduced to mere stilts. Actually a large bird such as an eagle or kite does not keep in the air mainly by moving its wings. It is generally to be seen soaring, that is to say balanced on a rising column of air. And even soaring becomes more and more difficult with increasing size. Were this not the case eagles might be as large as tigers and as formidable to man as hostile aeroplanes.

But it is time that we pass to some of the advantages of size. One of the most obvious is that it enables one to keep warm. All warmblooded animals at rest lose the same amount of heat from a unit area of skin, for which purpose they need a food-supply proportional to their surface and not to their weight. Five thousand mice weigh as much as a man. Their combined surface and food or oxygen consumption are about seventeen times a man's. In fact a mouse eats about one quarter its own weight of food every day, which is mainly used in keeping it warm. For the same reason small animals cannot live in cold countries. In the arctic regions there are no reptiles or amphibians, and no small mammals. The smallest mammal in Spitzbergen is the fox. The small birds fly away in winter, while the insects die, though their eggs can survive six months or more of frost. The most successful mammals are bears, seals, and walruses.

Similarly, the eye is a rather inefficient organ until it reaches a large size. The back of the human eye on which an image of the outside world is thrown, and which corresponds to the film of a camera, is composed of a mosaic of rods and cones whose diameter is little more than a length of an average light wave. Each eye has about a half a million, and for two objects to be distinguishable their images must fall on separate rods or cones. It is obvious that with fewer but larger rods and cones we should see less distinctly. If they were twice as broad two points would have to be twice as far apart before we could distinguish them at a given distance. But if their size were diminished and

their number increased we should see no better. For it is impossible to form a definite image smaller than a wave-length of light. Hence a mouse's eye is not a small-scale model of a human eye. Its rods and cones are not much smaller than ours, and therefore there are far fewer of them. A mouse could not distinguish one human face from another six feet away. In order that they should be of any use at all the eyes of small animals have to be much larger in proportion to their bodies than our own. Large animals on the other hand only require relatively small eyes, and those of the whale and elephant are little larger than our own. For rather more recondite reasons the same general principle holds true of the brain. If we compare the brain-weights of a set of very similar animals such as the cat, cheetah, leopard, and tiger, we find that as we quadruple the body-weight the brain-weight is only doubled. The larger animal with proportionately larger bones can economize on brain, eyes, and certain other organs.

Such are a very few of the considerations which show that for every type of animal there is an optimum size. Yet although Galileo demonstrated the contrary more than three hundred years ago, people still believe that if a flea were as large as a man it could jump a thousand feet into the air. As a matter of fact the height to which an animal can jump is more nearly independent of its size than proportional to it. A flea can jump about two feet, a man about five. To jump a given height, if we neglect the resistance of air, requires an expenditure of energy proportional to the jumper's weight. But if the jumping muscles form a constant fraction of the animal's body, the energy developed per ounce of muscle is independent of the size, provided it can be developed quickly enough in the small animal. As a matter of fact an insect's muscles, although they can contract more quickly than our own, appear to be less efficient; as otherwise a flea or grasshopper could rise six feet into the air.

And just as there is a best size for every animal, so the same is true for every human institution. In the Greek type of democracy all the citizens could listen to a series of orators and vote directly on questions of legislation. Hence their philosophers held that a small city was the largest possible democratic state. The English invention of representative government made a democratic nation possible, and the possibility was first realized in the United States, and later elsewhere. With the development of broadcasting it has once more become possible for every citizen to listen to the political views of representative orators, and the future may perhaps see the return of the national state to the Greek form of democracy. Even the referendum has been made possible only by the institution of daily newspapers.

To the biologist the problem of socialism appears largely as a problem of size. The extreme socialists desire to run every nation as a single business concern. I do not suppose that Henry Ford would find much difficulty in running Andorra or Luxembourg on a socialistic basis. He has already more men on his pay-roll than their population. It is conceivable that a syndicate of Fords, if we could find them, would make Belgium Ltd or Denmark Inc. pay their way. But while nationalization of certain industries is an obvious possibility in the largest of states, I find it no easier to picture a completely socialized British Empire or United States than an elephant turning somersaults or a hippopotamus jumping a hedge.

References

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