Series

Living in a physical world
IV.   Moving heat around

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1.   Introduction – why move heat?

We care about temperature. All too often we feel either too hot or too cold. Our appliances come with thermostats, cooling fans, and thermal protection switches. The temperatures of organisms yield lovely data via thermocouples, thermal imaging equipment, and all manner of other thermometers. Temperature anomalies signal trouble, from personal fevers to global climate change. But the diverse and complex physical phenomena underlying temperature pose perilous pitfalls for explanations of such data. Furthermore, we are easily misled by our intuitive sense, that of a large, terrestrial animal that maintains a steady body temperature close to the maximum it encounters. We too easily forget that net photosynthetic rates for plants commonly peak at lower temperatures and that some of the most productive marine waters are quite cold.

In this and the next essay, I want to look at the complexities of temperature and heat, asking what physical phenomena matter most, what options are open to organisms, what devices organisms use, and what as yet undemonstrated devices might yet be uncovered.

In few terrestrial habitats do organisms lack some thermal challenge. Where I live, in southeastern North America, temperatures range from about – 19° to 37°C, on the old Fahrenheit scale a variation of no less than on of up to 1000 W m^{-2}, and air movement can range from imperceptible to overwhelming. Breathing, a convective process, comes with the evaporation's inevitable heat transfer. Our own heat production adds an additional complication – a resting human generates about 80 watts; were an adult human to retain that energy, body temperature would rise by about a degree per hour.

Why not just accept a body temperature determined by the local interplay of such phenomena? As is so often the case, we can, at best, make educated guesses, recognizing in the present case that some bacteria, for instance, tolerate truly infernal heat. Still, laissez faire might make either chemical or physical trouble, or, quite likely, both. Nearly all enzymatically-catalyzed reactions depend severely on temperature. Rates typically double or triple for every 10° rise in temperature, whether one looks at individual reactions or the overall metabolic rates of animals that do not regulate their temperatures. (To calculate proper temperature effects, the Arrhenius equation and Arrhenius constants should be used instead of this so-called Q_{10}) On top of that, most enzymes, as proteins, denature with ever increasing rapidity as temperatures rise above around 40°C. For instance, one protein that denatures a marginally tolerable 4·4% per day at 40°C, cooks (to use the appropriate vernacular) at 46% per day at 46°C.

As bad, perhaps, temperature-dependence varies from enzyme to enzyme, so sequences of reactions might demand something beyond simple mass-action effects to coordinate their operation. That may underlie the notably limited temperature range tolerated by many organisms. Most non-regulating inhabitants of niches that do not vary much in temperature cannot withstand body temperatures more than a few degrees above or below that normal range – even when well above freezing and well below the point of severe protein denaturation. The extreme in sensitivity must be creatures such as ourselves that regulate body temperature closely. Such constancy typically brings a loss of ability to survive – even briefly and dysfunctionally – without it.

Most physical variables change less with temperature. That same 10°C rise in temperature (using 20° to 30° for the examples) decreases air density by about 3·4% and the surface tension of water (against air) about 2%. It decreases the thermal capacity of water (on a mole basis) a mere 0·04% but increases the diffusion coefficients of

ordinary gases in air by about 6%. One notes as a bench-mark that something proportional to the absolute temperature will increase by 3·4% for a 10° rise – as does the reciprocal of air density. For instance, Weis-Fogh (1961) showed that the tensile stiffness (Young's modulus) of the protein rubber of insect wing hinges, resilin, stiffens by just that 3·4% per ten degree rise.

But a few physical quantities vary more widely. The viscosity of water decreases by over 20% from 20° to 30°C. An animal accustomed to pumping blood at 35°, say a reptile basking in the sun, must expend twice as much energy (or pump half as much blood) if it plunges into water at 5° – unless, as in so-called multiviscosity motor oils, its blood has a peculiarly low dependence of viscosity on temperature. And any increase in blood viscosity at low temperatures might well compound the problems of the temperature-dependent decreases in basal metabolic rate and maximum metabolic capability. (The maximum matters more if the animal is active while in the water – a drop in basal rate will decrease the need to move blood.)

Compounding the problem, the diffusion coefficients of solutes increase with temperature in parallel with the decrease in solution viscosity. So for a given solute at different temperatures, the product of viscosity and diffusion coefficient will remain nearly constant. That recognition came as one of Einstein's great achievements during that *annus mirabilis*, exactly a century ago, as he linked the viscosity (m) in Stokes' law for small-scale flows with the diffusion coefficient (D) in the Sutherland-Einstein relation or Stokes-Einstein equation (Pais 1982):

$$D = \frac{RT}{N} \frac{1}{6pmr}, \tag{1}$$

where R is the gas-law constant, T the absolute temperature, N Avogadro's number, and r the radius of the solute molecules. (William Sutherland obtained the same result in the same year, hence Pais's suggestion of a hyphenated name.) So both biological transport processes, diffusion and convection, will be seriously impeded in liquid systems by a drop in temperature. At least if flow slows in proportion to viscosity, then Péclet numbers (ratios of convective to diffusive mass transfer: see Vogel 2004) will not change, and system geometries ought still be appropriate. Put less encouragingly, tinkering with system geometry cannot easily compensate for temperature change.

Nor do viscosity and diffusion coefficients mark the extremes. Once again looking at a rise from 20° to 30°C, the maximum concentration of water vapour in air (100% relative humidity) goes up from 17·3 to 30·4 g m^{-3} – a 75·6% increase. Put another way, water vapour makes up a mass fraction of 1·44% of saturated air at 20° and 2·61% at 30° – an increase of 81·6%. No wonder a lot of water condenses on a cool body in a hot, humid environment.

2. Heat-moving modes

How might a creature move heat from one place to another, whether shifting heat from one inside location to another, absorbing heat from its surroundings, or dumping heat onto those surroundings? A rather large array of options turn out to be available:

(i) *Radiation*: All objects above absolute zero radiate energy. A net radiative transfer of heat from warmer objects to colder ones occurs even if the objects are in a vacuum.

(ii) *Conduction*: Heat moves from warmer to colder parts of a material (or a contacting material) by direct transfer of the kinetic energy of its molecules.

(iii) *Convection*: Heat moves from warmer to colder places by direct transfer of the warmer material itself. Ordinarily its place is taken by either cooler material to close the cycle or yet more material from elsewhere.

(iv) *Phase change*: Vaporization takes energy, so it can absorb heat and leave a body cooler than otherwise. Fusion, likewise, takes energy, so melting a solid will cool either the rest of the solid or something else. Solid-to-gas change, sublimation, combines the two, absorbing even more energy.

(v) *Ablation*: The average temperature of an object of non-uniform temperature can be reduced by discarding some of its hotter-than-average portion, in effect exporting heat.

(vi) *Gas expansion cooling*: A contained gas exerts some pressure on the walls of its container; if it pushes those walls outward, thus doing work, either its temperature will drop or it will absorb heat.

(vii) *Cooling by unstressing an elastomer*: If an elastomer is stressed (stretching rubber, for instance), it warms. Elastic recoil as it is released cools the elastomer.

(viii) *Changing the composition of a solution*: Dissolving one substance in another – mixing two different liquids or dissolving a solute in a solvent – may either absorb or release heat.

Even without invoking ordinary chemical reactions or thermoelectric phenomena, we have at least eight modes of heat transfer, some of which can be divided further. All are reversible, and the last five can be used to move heat from something cool to something warm without doing violence to thermodynamics. Physics assuredly affords an abundance of possibilities that we should examine for biological relevance.

3. Radiative heat transfer

The temperature of an object determines the peak wavelength at which it either absorbs or emits radiation. How it behaves at (or near) that wavelength depends on its

emissivity and absorptivity; since these do not differ, we use single measure, most often called the emissivity. (Were the two unequal, an isolated system might spontaneously move from temperature uniformity to non-uniformity, thermodynamically unlawful.) Not only peak wavelength but radiant intensity depends on temperature, the latter quite strongly. The first operative relationship, making the necessary distinction between emissivities (the e's) at incoming and outgoing wavelengths, is the Stefan-Boltzmann law:

$$q = sS(e_2 T_2^4 - e_1 T_1^4), \tag{2}$$

where q is the rate of energy transfer, T_1 and T_2 the Kelvin temperatures of the objects involved in the radiative exchange, S the effective exposed area, and s the Stefan-Boltzmann constant, $5 \cdot 67 \times 10^{-8}$ W m^{-2} K^{-4}.

The second is Wien's law (sometimes the "Wien displacement law"), asserting an inverse relationship between surface temperature, T, and peak emission wavelength, l_{max}:

$$l_{max} = \frac{0 \cdot 0029}{T}. \tag{3}$$

(The constant assumes temperatures in Kelvin and wavelengths in meters.) Thus peak emission of the sun, at about 5800 K, occurs at 500 nm, roughly in the middle of our visual spectrum. A organism at 30°C or 303 K will emit with a peak a little under 10 μm, far out in the infrared.

The solar peak at 5800 K, perceived by us as yellow, implies that both the photosynthetic machinery of plants and the visual systems of animals make good use of solar radiation. That may mislead slightly, an artifact of the way we ordinarily plot intensity against wavelength. The energy represented by radiation varies inversely with wavelength, something we mention parenthetically when cautioning against the hazards of the ultraviolet. So a better picture emerges from a graph with a scale on its abscissa inversely proportional to wavelength and thus independent of energy content. Wavelength inverts to frequency (f), with the speed of light as conversion factor ($f = c/l$), so frequency would work. In practice, something called "wave number", the unadjusted reciprocal, $1/l$, replaces frequency. Then equal areas under a line represent equal amounts of energy, wherever the areas might be located – a curve tolerates simple integration for energy, what matters when considering the heating effect of radiation.

Figure 1 gives such a spectrum for direct overhead solar illumination at sea level (from Gates 1965), along
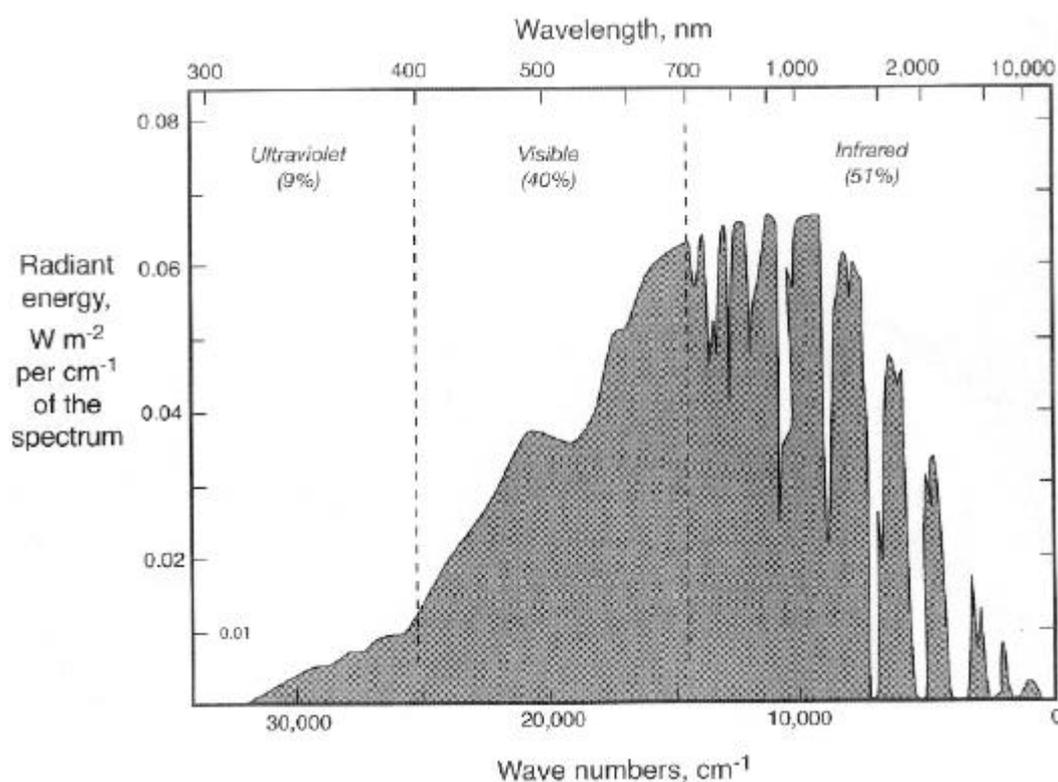

Figure 1.   Spectral distribution of solar illumination of the Earth's surface on a plot in which energy is uniformly proportional to area under the curve.

with some fractional divisions (the latter from Monteith and Unsworth 1990.) Most of the energy we receive does not come in the visible at all. Fortunately, the ultraviolet, makes up only a small component; infrared radiant energy actually exceeds visible radiant energy. (The various bands absorbed by water give the curve its jagged appearance in the infrared.) That infrared radiation can make trouble for terrestrial organisms.

Consider a leaf exposed to full sunlight. It must absorb solar energy to split water and fix carbon. Yet the photons of solar radiation at wavelengths beyond 700 nm are insufficiently energetic for that purpose. If absorbed, though, they will convert to heat. We rarely worry that leaves might get intolerably hot, but the possibility should not be dismissed. The 1000 W m^{-2} of an overhead sun imposes no small thermal load – enough to heat a thin leaf by over $2°\ s^{-1}$. By converting solar energy to a non-thermal form, photosynthesis might help, but its 5 W m^{-2} capture takes less than a per cent of the load. Leaves make a major dent in the problem by rejecting most of the infrared component of sunlight, reflecting or transmitting rather than absorbing about half the overall input. Photograph a tree with infrared-sensitive monochromatic film and a red filter to stop most of the visible light – the leaves will appear white (on a positive) against a starkly black sky.

That white 'colour' should be regarded as something special. Ordinary pigments, fabrics, animal skin and fur – all absorb infrared and thus look black. Among biological objects, are leaves unique in this respect? Unfortunately, radiative processes have drawn little attention from physiologists other than those concerned with terrestrial vascular plants. Bird eggs reflect most – sometimes over 90% – of the near-infrared. Bakken *et al* (1978) showed the independence of an egg's visible colour (commonly cryptic) from its infrared reflectivity, and the basis of the latter, the use of pigments other than the melanin typical of vertebrates. The shells and opercula of desert snails may also reflect most of the sun's direct infrared load (Yom-Tov 1971). And the spacing of the laminae in the cuticle of some iridescent red algae (from micrographs of Gerwick and Lang 1977) hints at infrared reflection; these organisms (*Iridaea* and others) can be exposed to both air and full sunlight at low tide. Still, one suspects investigative inattention rather than biological rarity. Some practical technology might come from knowing a bit more – adding a truly white roof could reduce the internal temperature of a sun-lit house in a hot place, and a truly white-crowned hat might provide shade with less concomitant heat.

The common lack of coincidence between visible colour and overall solar radiant energy absorption needs emphasis. Leaves and egg shells absorb little; fur of almost any colour absorbs a lot. That may deprive us of an easy visual assessment, but it permits organisms to decouple colour as seen by prey, predators, and conspecifics from effective radiant colour.

In addition to receiving solar radiation, organisms exchange infrared radiation with their more immediate surroundings, with intensities and wavelengths set by the Stefan-Boltzmann (eq. 2) and Wien (eq. 3) relationships. Ultimately, what matters is net transfer, something easy to forget when incoming greatly exceeds outgoing. One feels warmed on the side of the body that faces an surface above skin temperature, such as a stove, even when surrounded by air at a uniform temperature. Normally the temperatures and emissivities of organisms and their immediate surroundings are similar, so no great net heat transfer usually occurs. An exception is an open sky – a very large 'object' at a low effective temperature. According to Nobel (1999), with clean air, the effective temperature of a clear night sky may be as low as 220 K (– 53°C); with cloud cover that may rise to 280 K (+ 7°C). Thus something with a surface temperature of 30°C can radiate 3·6 times as much energy to a clear sky as it receives in return.

That asymmetry can be noticeable and significant. Ever since I became bald, I can feel whether a night sky is clear or cloudy without looking up, at least with no wind blowing. If I stand still for a few seconds beneath a clear sky, I get a particular tingle in my scalp. Of more consequence is radiation from foliage. On clear, windless nights, condensation often forms frost on low plants even when the atmosphere well above the ground remains above the freezing point – the foliage radiates sufficient energy to the sky to drop its temperature and, by conduction and convection, that of the air in its immediately vicinity, below freezing. The phenomenon can damage freeze-sensitive crops; prevention schemes include cover-

Table 1. Thermal conductivities of a variety of materials. Imagine heat transfer (W K^{-1}) through a rectangular slab of material oriented normal to heat flow. The linear dimension, m^{-1}, represents slab thickness (m^1) over slab area (m^2).

Material	Conductivity (W $m^{-1}\ K^{-1}$)
Copper	385·0
Steel	46·1
Glass	1·05
Water	0·59
Skin	0·50
Muscle (meat)	0·46
Adipose tissue (human fat)	0·21
Wood (typical, dry)	0·20
Soil (inverse with air fraction)	0·25 to 2·0
Fur	0·024 to 0·063
Air	0·024

ings, sufficient wetting to overwhelm the temperature drop from the radiant emission, or (at least formerly) burning smoky fires, not to heat the crop but to obscure the sky.

One small tree may take action to avoid exposure to that cold night sky. *Albizzia julibrissin*, sometimes called the silk tree, is native to China but well established as an ornamental in the US southeast. Its doubly compound leaves with a few hundred leaflets give it a vaguely fern-like appearance. The leaves seem to have three distinct postures. In the shade, both leaves and leaflets extend horizontally; a light shining down on a leaf is almost fully intercepted. In the sun, the rachis of the leaf remains horizontal, but leaflets shift to near-vertical so the leaf casts only a minimal shadow (Campbell and Garber 1980 describe the motor responsible). At night, the entire leaf bends down to near-vertical, with the individual leaflets folded against the rachis – the leaf then looks like the tail of a horse. I suspect that the orientation in direct sunlight reduces exposure to a point source of radiation while the complete folding at night reduces exposure to a distributed radiation sink.

Postural control of solar irradiation has been documented for many terrestrial animals, mainly insects and lizards. Many of these either assume postures that minimize solar input, as in a leaf that takes up a vertical orientation during the heat of the day, or postures that maximize solar input – or both. Many insects absorb sunlight in preflight warm-ups that raise body temperatures well above ambient, taking advantage of their small size and consequently high surface-to-volume ratios. Wings often assist as shields against simultaneous convective cooling. (Heinrich 1996 gives an engaging account of the thermal devices of insects.) Lizards, larger, capitalize on their sit-and-wait predation mode to engage in more leisurely thermal basking.

Some mammals as well control solar radiation. A ground squirrel (*Xerus inauris*) that inhabits hot, dry areas of southern Africa, for instance, turns its back to the sun when conditions get especially challenging. That puts it in position to use its tail as a parasol to provide local shade. Bennett *et al* (1984), who describe the behaviour, calculate that the squirrel can thereby increase daytime foraging episodes from about 3 to 7 h.

Organisms may adjust emission as well as absorption. At the long wavelengths corresponding to their surface temperatures, desert plants have slightly higher emissivities than do plants from temperate regions, which are slightly higher than those from rain forest (Arp and Phinney 1980). All values, though, are high, most above 0·95. In general, at long wavelengths foliage, with emissivities of 0·96 to 0·98, emits more effectively than non-vegetated surfaces, typically about 0·91 (Kant and Badarinath 2002). What remains uncertain is whether the difference can confer a biologically significant additional heat loss.

Reradiation to the sky may underlie the peculiarly large and well-vascularized ears of many desert animals – jack rabbits (*Lepus* spp) in particular. As Schmidt-Nielsen (1964) points out, these animals are too small to cool by evaporating water, and most lack burrows as mid-day retreats. With air temperatures at or even above body temperature, their large ears look paradoxical. But by feeding in open shade, with hot ears exposed to a much colder sky (at an effective temperature of perhaps 13°C), an animal could off-load a large amount of heat.

4.   Conductive heat transfer

The formal rules for conduction of heat parallel those for diffusion. Fourier's law (eq. 5) renames the variables in Fick's law (eq. 4), using energy transferred per unit time (q) instead of mass transfer rate (m/t), temperature difference ($T_1 - T_2$) in place of concentration difference ($C_1 - C_2$), and thermal conductivity (k) rather than diffusion coefficient (D):

$$\frac{m}{t} = DS\left(\frac{C_1 - C_2}{x}\right), \tag{4}$$

$$q = kS\left(\frac{T_1 - T_2}{x}\right). \tag{5}$$

Here S is the area over which transfer takes place and x the distance mass or heat has to move. In each process, a gradient – concentration or temperature – provide the impetus.

The only additional variable of concern is specific heat, usually given as c_p, which establishes a proportionality for a given material between energy input relative to mass and change in temperature. Water has a fairly high specific heat, 4·18 kJ kg^{-1} K^{-1} at ordinary temperatures; for air c_p is 1·01 kJ kg^{-1} K^{-1}, for soils c_p is typically (but not inevitably!) about 1·0 to 1·5 kJ kg^{-1} K^{-1}. Organisms, mostly water, rarely deviate much from its temperature-stabilizing high value.

For conduction through a slab of material, heat transfer varies inversely with thickness – as in eq. 5; for gain or loss from a solid body, rates (for most geometries) run inverse with the square of linear dimensions. And just as some diffusive step underlies every case of transfer of mass by bulk flow (as noted in Vogel 2004), conduction plays some role in all convective processes. (Advantage can sometimes be taken of that practical equivalence of diffusion and conduction. One can serve as proxy for the other, usually conductive heat transfer for diffusion, capitalizing on the greater ease of measuring temperature than chemical concentration – as, for instance, done by Hunter and Vogel 1986.)

In conduction lies the greatest divergence between heat transfer in nature and in human technology. Humans have access to metals, materials of high conductivity; non-human nature uses no metallic materials, either within organisms or in their surroundings. Metallic and non-metallic materials differ by orders of magnitude; table 1 gives a sampling of values. Between the low values of conductivity and its severe distance discount, conduction can play no great role in moving significant amounts of heat over appreciable distances in living systems. Again, consider a leaf in sunlight and nearly still air. The center of the leaf gets hotter than its margins because the latter make better thermal contact with the convective updraft induced by the hot leaf itself. Were the leaf made of metal, peak temperature would be lower – lateral conductance would move heat down the temperature gradient from center to edges. But a leaf is mainly air, water, and cellulose; and it cannot move enough heat to affect that temperature gradient, unlike the metallic heat sinks with which we protect heat-intolerant semiconductors (Vogel 1984).

Thus one should not (as have several studies) use radiantly-heated metallic models to study the thermal behaviour of leaves. Those models will have lower center and average temperatures; perhaps more importantly, as a result of their lateral heat transfer they will approach the condition referred to in books on heat transfer as "constant temperature" rather than "constant heat flux". Unfortunately, those books reflect our metallic culture, so most of their formulas assume that unbiological near-constancy of temperature. Metal models are handy, but they must be heated in the middle rather than everywhere with a thickness of metal chosen to give the center-to-edge temperature gradient of real leaves.

In a sense pure conduction represents a gold standard for minimal heat transfer. Thus fur works by reducing convective air movement enough for overall transfer to approach the value for conduction in air. And heat exchangers (about which more in the next essay) drive the heat transfer due to blood circulation down toward the value for conduction in isolated tissue.

Nonetheless, a few organisms do employ conductive heat transfer as more than a short-distance link between a flowing fluid and an adjacent surface. Our elderly house cat rests on dry straw in the garden on cool days; on hot days he shifts to bare soil or pavement that never gets direct sunlight. The pattern is common among medium and large-size domestic animals with soft enough flesh and fur for effective contact with the substratum. More specific use of heat earthing has been documented in a desert rodent, the antelope ground squirrel (*Ammospermophilus leucurus*). For a diurnal desert animal it is especially small, which means that it heats up rapidly when foraging in the summer sun – 0·2 to 0·8°C min⁻¹. A squir-

rel deals with this heat load by tolerating brief bouts of hyperthermia (sometimes exceeding 43°C) and returning to its burrow as often as every 10 min. In the burrow, it loses heat rapidly by pressing itselfs against the walls, which are about 10°C cooler than its body (Chappell and Bartholomew 1981).

5. Convective heat transfer

Conduction poses few analytic problems, with reliable equations and only the peculiarities of biological geometries to complicate things. Radiative exchange may be less familiar, but, likewise, we can rely on straightforward rules. But whether looking at thermal phenomena within or around our creatures, we can rarely ignore convective transfer. And no such tidiness characterizes convection. While the textbooks for engineering courses (I particularly value Bejan 1993) provide reliable explanations, the equations they cite must be viewed warily. Most provide no more than rules of thumb, many presume conditions quite different from what organisms encounter, and even the first figure of their three-significant-figure constants may diverge from our reality. To list a few of the complicating aspects of convection:

(i) Internal versus external convection. We move lots of heat by pumping blood and other fluids through our various pipes and internal channels; flows of air and water around us transfer heat between ourselves and the environment. The basic phenomenon may be the same, but the practicalities depend strongly on whether the solid object surrounds the fluid or vice versa.

(ii) Flows may be laminar or turbulent, with major differences for heat transfer. In most laminar flows (such as in our capillaries) convection carries heat only with the overall flow – conduction drives transfer normal to the direction of flow. By contrast, the internal mixing of turbulent flow provides a major avenue for cross-flow transfer, and the thermal conductivity of the fluid loses most of its importance. For internal flows through circular pipes, the shift from laminar to turbulent occurs at a reasonably sharp value (2000 ± 1000) of a single variable, the so-called Reynolds number, *Re*:

$$Re = \frac{\mathbf{r}lv}{\mathbf{m}}, \tag{6}$$

where $\mathbf{r}$ and $\mathbf{m}$ are the fluid's density and viscosity, l the diameter of the pipe or width of the channel, and v its average flow speed. External flows may have a similarly sharp transition, but the location of the transition depends a lot on texture and geometry – between *Re*'s of about 20 and 200,000, with l now taken as a variously defined characteristic length of the object in the flow.

(iii) Convection can be driven by density differences within the fluid – "free convection" – or it may be driven by some external current – "forced convection." Unlike the previous distinctions, regimes can be mixed. Another dimensionless number, the Grashof, *Gr*, provides an index of the intensity of free convection:

$$Gr = \frac{\boldsymbol{r}g\boldsymbol{b}(\Delta T)l^3}{\boldsymbol{m}^2}. \tag{7}$$

The only new variable is $\boldsymbol{b}$, the volumetric thermal expansion coefficient; its value for liquid water is about $0{\cdot}3 \times 10^{-3}$ K^{-1}. All gases have about the same value of $\boldsymbol{b}$. Since their volumes vary directly with the absolute temperature, $\boldsymbol{b} = 1/T$; at 20°C, $\boldsymbol{b} = 3{\cdot}4 \times 10^{-3}$ K^{-1}. Free convection mainly matters for external flows. It can be laminar or turbulent with a transition from former to latter at a Grashof number of about 10^9.

In substantial winds, for very large objects, for objects well above or below ambient temperature, forced convection will dominate the picture. But what of a small organism exposed, say, to sunlight in nearly still air? Another dimensionless index provides a rough-and-ready criterion, the ratio of the Grashof number to the square of the Reynolds number. In effect, this looks at the ratio of buoyant force to inertial force; viscous force, affecting both components, cancels out. Thus

$$\frac{Gr}{Re^2} = \frac{g\boldsymbol{b}\Delta(T)l}{\boldsymbol{r}v^2}. \tag{8}$$

Some sources give the following rules of thumb. For ratios below about $0{\cdot}1$, forced convection predominates and free convection can be ignored. For ratios above about 16, free convection predominates and the effects of whatever wind might be present can be ignored. Higher thermal expansion coefficients, larger differences in temperature between organism and surroundings, and larger size raise the value and favour free convection; denser fluids and more rapid flows favour free convection, all intuitively reasonable.

By this criterion, mixed regimes cannot be ignored. Consider, yet again, a sun-lit broad leaf on a tree. A leaf 10 cm across will encounter a mixed regime at wind speeds between about $0{\cdot}04$ and $0{\cdot}5$ m s^{-1}. The lower figure is less than ambient wind ever gets for more than a few seconds in full sun. If nothing else, differential heating of ground and other foliage will generate that much convection. The higher figure, about our perceptual threshold for air movement, will nearly cool a leaf to air temperature – stronger winds make little further difference, and overheating ceases to be hazardous.

For that leaf, then, the only significant regime is a mixed one, the regime least amenable to anything other

than direct measurements. Some years ago, a local engineering graduate student, Alexander Lim (1969), compared published formulas for mixed free and forced convection with measurements under conditions a leaf might encounter. He found even greater deviations than we expected, with discrepancies typically around 50% – in both directions. And he controlled variables that in nature would confound things even further. For instance, free convection carries air vertically, while forced convection need not be horizontal, since it includes not just ordinary wind but the upward free convection of adjacent leaves.

The main generalization one might make is that free convection will be insignificant for very small systems and a major consideration only for quite large ones. As Monteith and Unsworth (1990) point out, a cow might lose heat by free convection when the wind drops below about 1 m s^{-1}. Similarly, a camel, need not wait for a gentle breeze to dump heat convectively at night that it had acquired during the previous day. Judging from photographs of thermal updrafts around standing humans (using a technique which visualizes differences in air density), our large size permits some self-induced free convection. Still, even barely perceptible air movements help us avoid overheating when we work hard under hot and humid conditions. On yet larger scales free convection becomes yet more important; together with spatially irregular heating of the ground it produces the ascending thermal tori in which birds such as hawks and vultures soar.

6. Conduction versus convection

For biological systems, made of low conductivity materials, pure conduction with zero convection represents a kind of gold standard for minimal internal heat transfer. A warm human increases convective transfer by vasodilation of capillaries in the skin and the associated larger blood vessels – body temperature becomes less spatially variable. When cold, one reduces blood flow to the extremities, setting up internal temperature gradients closer to those of conducting systems. But we humans remain convection-dominated, reflecting both our high aerobic capacity and warm-climate ancestry.

How might one determine the relative importance of conduction and convection in an intact, living animal? Measuring blood flow will not give reliable results since heat exchangers (about which more in the next essay) can decouple heat flow from mass flow. A simple scaling argument suggests at least one possible approach – it adopts the rationale for circulatory systems of the Nobel laureate physiologist August Krogh (1941), merely substituting heat for oxygen.

If heat content depends on volume ($\propto l^3$) and heat loss depends on surface area ($\propto l^2$), then the rate of heat loss relative to volume will vary inversely with a typical linear dimension ($\propto l^{-1}$). That should happen where heat moves much more readily within the organism than to or from the organism. If, conversely, heat loss depends on the distance between core and periphery ($\propto l^1$), then the rate of heat loss relative to volume will vary inversely with the square of linear dimensions ($\propto l^{-2}$). That will happen when heat transfer to and from the organism presents less of a barrier than transfer within the organism. Muscle, fat, and other biological materials have low thermal conductivities (table 1 again), while circulating liquids make fine heat movers. So the first situation (loss $\propto l^{-1}$) will characterize convection-dominated cases, the second (loss $\propto l^{-2}$) conduction-dominated cases.

One needs only scaling data, at least at this crude level of judgment. Measurements of core body temperatures as equilibrated animals are heated or cooled will suffice, at least for ectothermic animals – temperature tracks heat loss per unit volume if heat capacity remains constant. Can such an easy model apply, or do confounding factors overwhelm it?

As a quick test, I created two sets of heat-transferring systems, one predominantly convective and the other exclusively conductive. Each set consisted of six ordinary laboratory beakers, of nominal capacities from 50 to 1000 ml, with each beaker filled to a depth equal to its internal diameter. A thermometer supported by a piece of corrugated paperboard extended down to the center of each beaker, as in figure 2. One set contained pure water while the other was filled with water plus 1% agar – the small amount of agar suffices to immobilize the water, preventing the free convection of self-stirring without significant effect on its specific heat. The twelve beakers were equilibrated overnight in an incubator at 49°C, moved at time zero to a room at 25°C, and their temperatures recorded every 5 min. Free convection stirred the water-filled beakers enough to make deliberate stirring unnecessary, and room air movement sufficed to minimize external resistance. Figure 3 shows the results, with log-log slopes satisfyingly close to the predicted values. An analogous exercise in which the beakers warmed after equilibration at 7°C gave much the same result – immobilizing the water gave greater reductions in the rate of temperature change in larger systems.

So this simplest of scaling rules can place systems on a spectrum from pure conduction to predominant convection. As an example, we might look at some old data for cooling lizards. For a variety of cooling varanids, Bartholomew and Tucker (1964) found a scaling exponent of – 1·156 (tripling their mass-based number), just a bit
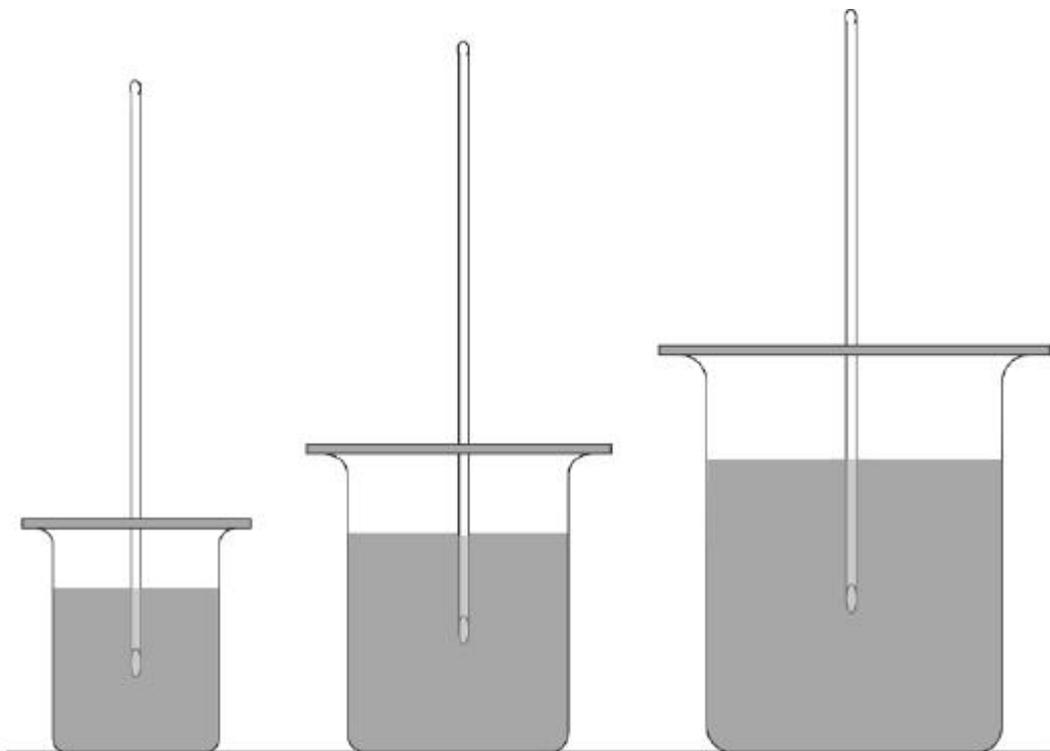

Figure 2.   The arrangement of beakers and thermometers used to obtain the scaling data of figure 3.

greater than what we would expect for convection-dominated systems. By contrast, Bartholomew and Lasiewski (1965) reported an exponent of -1.881 for Galapagos marine iguanas suddenly immersed in cold water, just short of what we anticipate for conduction-dominated systems. During dives, heart rates slow, but no more so than for the varanids. Somehow they must reroute their blood so it carries little heat peripherally. (Whether in air or water, the iguanas reheat much more rapidly.)

Cooling slowly makes adaptive sense for reptiles that bask on warm, sunny, shoreline rocks and then plunge into fairly cold water to feed. Charles Darwin gives a fine descriptions of iguana and its behaviour in *The Voyage of HMS Beagle* (1845) ("a hideous looking creature") as well as in his diaries (unoriginally, "imps of darkness"). Not that these iguanas do anything unprecedented. Immersed reptiles quite commonly heat faster than they cool, with the ratio increasing with body size, as noted by Turner (1987) and consistent with our scaling exponents.

One caveat. For systems surrounded by minimally moving air – insulated systems, the external resistance to heat transfer can approach the internal resistance. Thus reducing internal resistance by preventing convection within the system may not decrease the exponent for loss relative to size as much as expected. A somewhat unnatural comparison illustrates the effect. Turner (1988) gives

heat loss exponents of -1.8 for infertile eggs cooling in water, nearly the -2.0 of our model, but only -1.2 when cooling in still air.

7. Heat transfer by evaporation and condensation

Vaporization of a liquid (or sublimation of a solid) provides a particularly effective heat transfer mechanism, especially if the liquid has a high heat of vaporization, as does water. Indeed, the value most often found in non-biological sources, 2.26 MJ kg^{-1}, presumes boiling at 100°C and understates the case; at a more biologically reasonable 25°C, water's heat of vaporization is 2.44 MJ kg^{-1}, about 8% higher.

Several conditions, though, limit its use by organisms. The atmosphere into which water vaporizes must not be water-saturated, at least at the temperature of the evaporating surface (which, as our skin commonly is, may be above ambient temperature). Evaporation itself will reduce the temperature of the evaporating surface (again, as with our skin). And a copious supply of water must be available. A succulent plant, some lore to the contrary, cannot store enough water for significant evaporative cooling in a warm, dry habitat. Hard-working humans, cooling evaporatively as we do, must consume water at a great rate. At a metabolic rate of 400 W (a minimal esti-
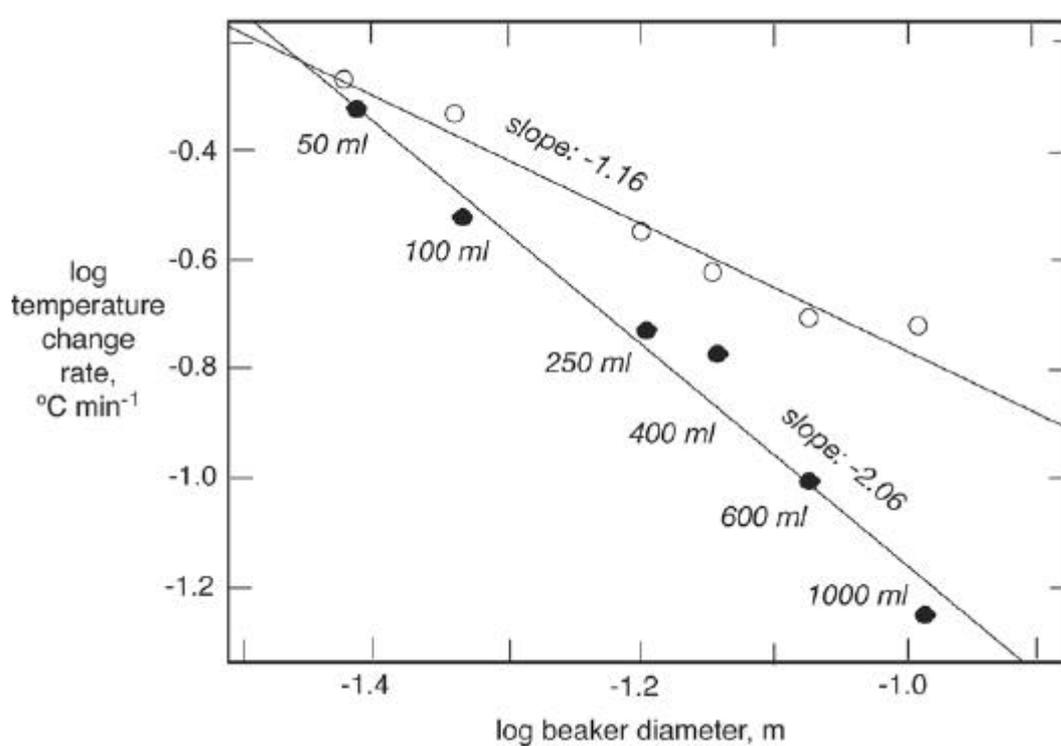

Figure 3. Log cooling rate versus log beaker diameter for water-filled (slope = -1.16) and water-plus-agar filled beakers (slope = -2.06). The slopes represent the exponent *a* in the expression (cooling rate $\propto$ diameter^a).

mate for a labourer working at 100 W output), dissipating metabolic heat by evaporation, our main mechanism, would take 0·6 l h^{-1}, or almost 5 liters for an 8 h working day.

Few small animals can rely on evaporative cooling as a principal mode during sustained activity – it demands too great a volume of water for the surface area exposed to a hot environment or for their metabolic rates (which scale nearly with surface area). Fortunately their higher surface-to-volume ratios improve the efficacy of convection. Not unexpectedly, they seem more often concerned with water conservation, with devices that reduce respiratory water loss and so forth.

Among animals that cool evaporatively, two routes play major roles; each has its points. Evaporation from skin (predominant in humans, cattle, large antelopes, and camels) takes advantage of the skin's large surface area. The concomitant vasodilation improves convective loss as well. On the debit side, cutaneous evaporation inevitably causes a loss of salt, which then becomes a particularly valuable commodity for herbivores active in hot climates. In addition, its requirement for exposed external surface conflicts with the presence of fur or plumage that might reduce heat loss under other circumstances.

Respiratory evaporation entails no salt loss, but it requires pumping air across internal surfaces, which costs energy and produces yet more heat. And the CO_2 loss in excess breathing drives up the pH of the blood. Animals such as dogs, goats, rabbits, and birds that use respiratory evaporation beyond that associated with normal gas exchange reduce both problems by panting – shallow breaths repeated at rates matching the natural elastic time constants of their musculoskeletal systems (Crawford 1962; Crawford and Kampe 1971).

Some mammals (rats and many marsupials) cool evaporatively by licking their fur and allowing the saliva to evaporate; the mode, though, is not used during sustained activity. Some large birds (vultures, storks, and others) squirt liquid excrement on their legs when their surroundings get hot (Hatch 1970), augmenting evaporative cooling. A few insects with ample access to water (nectar and sap feeders) derive clear benefit from evaporative cooling for dumping the heat produced by flight muscles despite their low surface-to-volume ratios – some cicadas, sphingid moths, and bees in particular (Hadley 1994; Heinrich 1996).

What about leaves? Again, many do get well above ambient temperature, pushing what look like lethal limits. Plants with broad leaves, the ones likely to run into thermal trouble, evaporate water ('transpire') at remarkable rates. Leaf temperatures calculated (from admittedly crude formulas) by Gates (1980) point up the thermal consequences of that evaporation. He assumes a wind of 0·1 m s^{-1} (as noted earlier, about as still as daytime air gets), solar

illumination of 1000 W m^{-2} (again, an overhead unobstructed sun), an air temperature of 30°C, a relative humidity of 50%, and a leaf width of 5 cm. If reradiation were the only way the leaf dissipated that load, it would equilibrate (recall eq. 2) at a temperature of about 90°C. Allowing convection as well drops that to a still stressful 55°C. A typical level of evaporation cools the leaf to   – hot but not impossibly so for a worst-case scenario. Evaporation cools leaves; it could not do otherwise. Typically broad leaves dissipate about as much energy evaporatively as they do convectively.

Less clear than its thermal consequences is the thermal role of this transpirative water loss. Plant physiologists (see, for instance, Nobel 1999) generally regard the loss as an inevitable byproduct of the acquisition of CO_2 – a leaf with openings (stomata) that admit inward diffusion of CO_2 will permit outward diffusion of water. CO_2 makes only about 0·03% of the atmosphere, and the diffusion coefficient of CO_2 is well below that of H_2O. So a lot of water must vaporize for even a modest input of the crucial carbon upon which plants depend. A representative value for water-use efficiency (Nobel 1999) is about 6 g CO_2 per kg H_2O. Functioning leaves have to lose water, whatever the thermal consequences. Indeed, transpiration sometimes depresses leaf temperatures 10°C or more below ambient. The situation resembles evaporative heat loss from our breathing, something of minor use (since we do not pant) for an excessively warm human but a distinct liability for one stressed by cold.

But that view cannot be wholeheartedly embraced. Water-use efficiencies vary widely. The extreme values come from measurements on those species (6 or 7% of all vascular plants) that only open their stomata at night, when temperatures are lower and relative humidities higher. They fix CO_2 as organic acids; decarboxylation the next day provides the input for photosynthesis. The trick can push water-use efficiency up an order of magnitude. So the adaptive significance of evaporative water loss from leaves remains uncertain. The question has drawn little attention – plant physiologists have worried less than have animal physiologists about primary – adaptive – versus secondary functions of multifunctional processes.

If evaporation cools, then condensation heats. Under at least one condition organisms may use condensation as a significant heat source. On cold, clear, calm nights, radiative cooling, as noted earlier, often drops leaf temperatures below both the local air temperature and the local dew point – the term "dew point" comes from the resulting condensation. It provides a major water source for some low desert plants. Sometimes water vapour condenses as frost; where that happens the heat of sublimation, greater by 13% at 0°C than the heat of vaporization, becomes the relevant factor. Condensation as dew or frost should offset some of that radiative cooling; again,

the practical significance is uncertain. Frost *per se* causes little trouble – what damages plants is internal ice formation signalled by its appearance.

A wide variety of arthropods have been shown capable of condensing water from the atmosphere. In none does it seem to be such a simple physical process – the required temperature differences just do not occur, nor would they be likely in animals as small as ticks, fleas, and mites. Nor is a vapor-saturated atmosphere necessary – the minimum humidity can be as low as 50%. In none of these animals does condensation appear to confer any specific thermal benefit – obtaining liquid water is the pay-off (Hadley 1994).

A recent report implies a thermal role for still another form of phase change, one whose novelty may only reflect oversight. According to Dunkin *et al* (2005), a large fraction of dolphin blubber consists of fatty acids with melting points just below body temperature. The apparent thermal conductivity of the blubber of both young dolphins and pregnant females is well below that of human fat (as in table 1), and heat flux measurements suggest heat absorption by phase change as the mechanism.

8. Other modes – known and unknown

So far, we have only looked at half the heat transfer modes mentioned at the start – radiation, conduction, convection, and phase change. Some of the others can be either dismissed outright or their insignificance easily argued. Early spacecraft used *ablative cooling* when reentering the atmosphere. Animals, as noted, do void saliva and excrement, but the subsequent evaporation of the liquid from deliberately wetted skin or fur does far more to get rid of body heat than does ablation itself.

You can use *gas expansion cooling* to make excessively hot food or drink palatable by pursing lips and exhaling air that has been compressed by your thoracic muscles – air temperature can be dropped into the mid 20's according to a quick measurement on a cooperative colleague. But the muscle-powered compression-expansion sequence heats you more than it cools the food. Useful heat transfer by *stressing and unstressing elastomers* seems unlikely, even if the imperfect resilience of bio-

logical materials might be used (as in pre-flight warm-up in insects or in our shivering) as a small supplement to muscular heat generation. Similarly, transferring significant amounts of heat by *dissolving or extracting solutes* is unlikely, even though organisms commonly manipulate the composition of solutions.

What ought not be casually dismissed are novel combinations of the various heat transfer mechanisms. As an example of an unknown but biologically plausible scheme, consider a so-called heat pipe (figure 4), a device that combines phase change and convection. A liquid vaporizes at the warm end, absorbing heat. Vaporization produces a pressure difference that drives gas toward the cool end. There it condenses, releasing heat. Liquid then returns to the warm end by capillarity through some wicking material lining the pipe. A few uncommon bits of human technology use heat pipes since they can achieve effective conductivities orders of magnitude greater than that of copper bars of the same dimensions, but they have never become household items.

By contrast, heat pipes should be highly advantageous in nature inasmuch as organisms are made of materials of such low thermal conductivities. Having only water as a working fluid, though, imposes a serious limitation. Admittedly, water has a nicely high heat capacity. And the concentration of vapour at saturation is strongly temperature-dependent; recall the 81·6% increase in mass between 20° and 30°C that was mentioned earlier. But pressure-driven bulk flow from warm to cool end cannot drive vapour movement as it does in systems where nothing dilutes the substance that evaporates and condenses. Rough calculations suggest that diffusion, the obvious alternative, will not move enough water vapour over distances greater than about a millimeter. So such a system needs some local stirring of the gas phase – cross-flow thermal gradients, continuous flexing of the pipe, or something else.

Where in organisms might we find heat pipes? Air-filled passages with hydrophilic inner surfaces are not rare. I wonder about the insides (the spongy mesophyll) of small, succulent leaves. Several colleagues, Catherine Loudon and Thomas Daniel, suggest that insects might
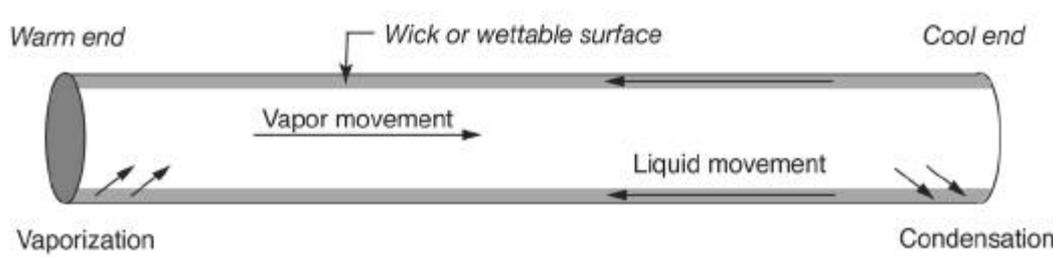
Figure 4. The operation of a heat pipe, with heat flow from left to right.

use the mechanism to move heat from flight muscles through their tracheal systems.

So the ease with which we measure temperature may all to easily obscure the complexity of thermal phenomena in general and the thermal behaviour of organisms in particular. Designing proper experiments challenges our ingenuity. For instance, putting an organism in a temperature-controlled chamber may not come close to mimicking the thermal character of a habitat of the same temperature. The walls will not behave like open sky, and the heat source will be unlikely to resemble the sun. The air movement needed to assure constant temperature will probably be unrealistically high – for instance for studying thermally stressed leaves. Or it may be unrealistically low – for, say, looking at the insulation fur provides for a mammal in the open. Beyond these difficulties lie the problems associated with the continuous variation in environmental temperatures, insolation levels, wind speeds, and so forth in nature.

Put in these terms, the obstacles appear daunting. I prefer to view the situation in a different light. Physical complexity instigates biological diversity, not just in phylogenetic terms, but as diversity of clever designs and devices awaiting elucidation. And identifying what nature does begins by recognizing the physical possibilities.

References

Arp G K and Finney D E 1980 Ecological variations in the thermal IR emissivity of vegetation; *Environ. Exp. Bot.* **20** 135–148

Bakken G S, Vanderbilt V C, Buttemer W A and Dawson W R 1978 Avian eggs: thermoregulatory value of very high near-infrared reflectance; *Science* **200** 321–323

Bartholomew G A and Lasiewski R C 1965 Heating and cooling rates, heart rate, and simulated diving in the Galapagos marine iguana; *Comp. Biochem. Physiol.* **16** 575–582

Bartholomew G A and Tucker V A 1964 Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards; *Physiol. Zool.* **37** 341–354

Bejan 1993 *Heat transfer* (New York: John Wiley)

Bennett A F, Huey R B, John-Alder H and Nagy K A 1984 The parasol tail and thermoregulatory behaviour of the cape ground squirrel *Xerus inauris*; *Physiol. Zool.* **57** 57–62

Campbell N A and Garber R C 1980 Vacuolar reorganization in the motor cells of *Albizzia* during leaf movements; *Planta* **148** 251–255

Chappell M A and Bartholomew G A 1981 Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer; *Physiol. Zool.* **54** 215–223

Crawford E C 1962 Mechanical aspects of panting in dogs; *J. Appl. Physiol.* **17** 249–251

Crawford E C and Kampe G 1971 Resonant panting in pigeons; *Comp. Biochem. Physiol.* **A40** 549–552

Darwin C 1845 *Journal of researches into the natural history and geology of the countries visited during the voyage of H M S Beagle under the command of Capt. Fitz Roy R N* (London: J Murray)

Dunkin R C, McLellan W A, Blum J E and Pabst D A 2005 The ontogenetic changes in the thermal properties of blubber from Atlantic bottlenose dolphin *Tursiops truncatus*; *J. Exp. Biol.* **208** 1469–1480

Gates D M 1965 Energy, plants, and ecology; *Ecology* **46** 1–13

Gates D M 1980 *Biophysical ecology* (New York: Springer-Verlag)

Gerwick W H and Lang N J 1977 Structural, chemical and ecological studies on iridescence in *Iridaea* (Rhodophyta); *J. Phycol.* **13** 121–127

Hadley N F 1994 *Water relations of terrestrial arthropods* (San Diego: Academic Press)

Hatch D E 1970 Energy conserving and heat dissipating mechanisms of the turkey vulture; *Auk* **87** 111–124

Heinrich B 1996 *The thermal warriors: strategies of insect survival* (Cambridge: Harvard University Press)

Hunter T and Vogel S 1986 Spinning embryos enhance diffusion through gelatinous egg masses; *J. Exp. Mar. Biol. Ecol.* **96** 303–308

Kant Y and Badarinath K V S 2002 Ground-based method for measuring thermal infrared effective emissivities: implications and perspectives on the measurement of land surface temperature from satellite data; *Int. J. Remote Sensing* **23** 2179–2191

Krogh A 1941 *The comparative physiology of respiratory mechanisms* (Philadelphia: University of Pennsylvania Press)

Lim A T 1969 *A study of convective heat transfer from plant leaf models*, MS Thesis, Duke University, Durham NC, USA

Monteith J L and Unsworth M 1990 *Principles of environmental physics* (Oxford: Butterworth-Heinemann)

Nobel P S 1999 *Physicochemical and environmental plant physiology*, 2nd edition (San Diego: Academic Press)

Pais A 1982 *Subtle is the lord–: the science and the life of Albert Einstein* (New York: Oxford University Press)

Schmidt-Nielsen K 1964 *Desert animals* (Oxford: Oxford University Press)

Turner J S 1987 The cardiovascular control of heat exchange: consequences of body size; *Am. Zool.* **27** 69–79

Turner J S 1988 Body size and thermal energetics: how should thermal conductance scale?; *J. Thermal Biol.* **13** 103–117

Vogel S 1984 The thermal conductivity of leaves; *Can. J. Bot.* **62** 741–744

Vogel S 2004 Living in a physical world I. Two ways to move material; *J. Biosci.* **29** 392–397

Weis-Fogh T 1961 Thermodynamic properties of resilin, a rubber-like protein; *J. Mol. Biol.* **3** 648–667

Yom-Tov Y 1971 Body temperature and light reflectance in two desert snails; *Proc. Malacol. Soc. London* **39** 319–326