

CYCLIC THERMAL ENERGY HARVESTING BY ORGANISMS

v1.0

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ABSTRACT

In principle, many animals could obtain significant metabolic energy direct from their environment, additional to that from food.

Photosynthesis requires a large area of modified skin and imposes behavioural constraints: few animals are photosynthetic.

An alternative is to use the Carnot cycle, exploiting temperature differences. The maximum efficiency with which work can be extracted is $\sim\Delta T/T$, where terrestrially $T\sim 300$ K: comparable to photosynthesis. For a cold blooded animal which moves frequently between environments at significantly different temperatures, this energy harvest could be substantial: its entire body can act as a thermal reservoir. The energy harvesting machinery might however be hard to spot, much as 'brown fat' in human adults was overlooked until recently. It could be based on any temperature-sensitive chemical equilibrium.

In the temperate and tropical oceans, animals could gain Carnot cycle energy very easily as they swim up and down through the thermocline during diel vertical migration. In so doing, they would transfer significant heat from near-surface waters to the mid-depths. Such behavior would be increasingly favored as surface waters become warmer, as has recently occurred. This could conceivably have contributed to the recent 'pause' in the anthropogenic greenhouse effect.

At the origin of life, diurnal thermal harvesting by non-motile organisms could evolve far more easily than photosynthesis, and might have preceded both photosynthesis and the use of external chemical energy.

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1. INTRODUCTION: THE BASIC PHYSICS

In human technology, the difficulty of turning sunlight into useful energy is reflected in the fact that the first practical solar cells were made only 60 years ago. By contrast heat has been successfully harnessed for centuries and hydraulic pressure for millennia. Biological systems also seem to find light harvesting no easy feat. Photosynthesis is at best a few percent efficient relative to the energy available in the full spectrum of sunlight. Even to achieve that is chemically very complicated.

Given that various photosynthesis pathways appear to have evolved independently many times, it would be surprising if direct harvesting of heat energy from thermal cycling had never been explored by evolution. Due to the simpler chemical machinery required, it might have been the first energy harvesting mechanism at the origin of life.

Cold-blooded animals which move between significantly different temperatures could gain such energy repeatedly, using their bodies as thermal reservoirs. Suppose the warmer environment has absolute temperature T_1 , the cooler T_2 , the animal's body mass is M with specific heat capacity c . The animal stays in the warm environment until its temperature approaches T_1 , then transfers to the cool. It circulates a working fluid between its body interior and e.g. a flap of skin which is at temperature T_2 . From basic thermodynamics, the maximum initial efficiency with which work can be done is $(1-T_2/T_1)$. As the process continues body temperature falls toward T_2 , so the average efficiency is half this: maximum work extractable is $\frac{1}{2}Mc(T_1-T_2)(1-T_2/T_1)$. If the difference $\Delta T=T_1-T_2$ is small compared to T_1 and T_2 , this approximates as $\frac{1}{2} Mc\Delta T^2/ T_1$.

The animal now returns to the warm environment and again circulates the working fluid. A second maximum quantity of work $\frac{1}{2}Mc\Delta T^2/T_1$ can be done as its body temperature tends back to its initial T_1 . Total maximum work is $Mc\Delta T^2/T_1 = \Delta T/T_1 \times$ the change in enthalpy of the animal's body from T_1 to T_2 .

The working fluid will probably be a chemical equilibrium whose equilibrium point varies substantially between T_1 and T_2 : a likely candidate would cause the production of high-energy chemicals such as sugars. This might be via the intermediate production of ATP, but ATP holds too little energy, ~ 112 J/g Gibbs free energy, to be useful for longer term storage. Whatever the details, the thermodynamics of the Carnot cycle sets the same upper bound for the energy harvest. The chemical machinery will not necessarily be easy to spot, just as brown fat in adult humans was overlooked until recently. Evolution has a huge choice of reactions to use, and the quantity of energy-containing chemical produced per cycle will likely be a fraction of a percent of the animal's body weight: in the examples below, energy harvest is ~ 1 J/g per temperature cycle, whereas sugars, oils and fats can store tens of kJ/g.

This paper points out some ecological niches and specific organisms in which the phenomenon might be discovered.

2. MARINE ANIMALS

It has recently been suggested that, based on acoustic data from the Malaspina cruise, the estimated biomass of large mesopelagic fishes in the temperate and tropical oceans between 40°N and 40°S should be raised from ~ 1 billion tonnes (4 tonnes/ km^2 ocean) to ~ 10 -100 billion tonnes (40-400 tonnes/ km^2 ocean).^[1]

Mesopelagic fish tend to be diel vertical migrators: the data from ^[1](Figure 1) suggest they will transit a temperature difference typically $> 20^\circ\text{C}$. Animal tissue has specific heat ~ 3.5 J/g $^\circ\text{C}$, so an animal whose body experiences temperature change 20°C has enthalpy change 70 kJ/kg. $\Delta T/T = 20/300 = 6.7\%$, so up to 4.7 kJ/kg of this could ideally be extracted into chemical energy per cycle. A real system might do perhaps

half as well, storing 2.35 kJ/kg bodyweight in the animal's tissue. Muscle ultimately converts this chemical energy to mechanical work at ~30% efficiency^[2] to do work 700 J/kg bodyweight.

A temperature change from 27°C to 7°C causes 5 g/litre seawater density change. The ideal minimum work needed to transport 1 litre of water at the lower temperature up 500m, then 1 litre of water at the higher temperature down 500m, through a region of continuous density change, is 25 J. Assuming fish swimming efficiency 50%, 50 J muscle work is done per diel cycle.

Thus there is a 14:1 favourable ratio of muscle work made available to muscle work required for the operation.

The strategy generates 0.56 kcal/kg body tissue. From Kleiber's law^[3], a 1 kg poikilotherm requires ~0.5 kcal/hr = 12 kcal/day. Such an animal would get only ~5% of its energy from thermal harvesting. However Kleiber's law is an approximation which would apply to a 'typical' fish swimming up to several times its body length each second. Diel vertical migration takes place at a far more modest pace. Since energy expenditure is proportional to the cube of swimming rate, it is quite conceivable that mesopelagic fish using this strategy would have energy consumption ~10% that implied by Kleiber's law, and could get half their energy from thermal cycling. More would be unlikely as the fish needs to eat to gain biomass, and will obtain some energy from this.

Energy consumption scales as $\text{bodyweight}^{0.75}$: a larger animal could generate half its energy by thermal cycling even if its energy consumption is closer to that predicted by Kleiber's law. Large fish such as rays and skates have a flat body plan with high surface area that would be ideal for rapid intentional temperature change by heat exchange despite their large size. Animals such as basking sharks might conceivably be sunbathing to raise their body temperature for maximum thermal harvest. A colleague points out that sailed fish might be able to increase their rate of heat exchange by deploying their sails, and that small sharks often rest on the seabed in very shallow water during the daytime, which should maximize their body temperature.^[4]

The thermal harvesting hypothesis could help explain the discrepancy between the large quantity of fish observed acoustically, and the smaller quantity previously predicted by food web models. ^[11]

If some marine organisms do indeed harvest thermal energy as they traverse the thermocline, for the thermodynamic reasons described they must transport hundreds of times more thermal energy downward than they output as muscle work. As an illustration, to export 1 W/m^2 heat downward requires thermocline-traversing marine animals to do only 700 W muscle work per square kilometre. This is easily ecologically feasible: about one horsepower.

In terms of mass, each 1 kg diel vertical migrator transports 70 kJ/day. To export 1 MW/km^2 heat energy, 86 GJ/day, 1,200 tonnes/km² of fish would be required. This is about three times the upper limit of the Malaspina fish mass estimate. However it is interesting to speculate on the role of soft-bodied motile organisms such as jellyfish and salps. With body mass $\sim 95\text{-}98\%$ water, thermal harvesting could explain why it makes sense for a motile organism to drag so much water around with it. Hard data on both total jellyfish biomass and individual jellyfish movements in warmer waters are at present almost totally lacking, but a dry biomass comparable to that of the mesopelagic fish could export 10-20 \times more energy.

Transfer of thermal energy in sacs of water which move to and fro but remain effectively sealed could explain how heat energy is transferred vertically, without also transferring man-made isotopes and chemicals such as tritium and CFCs, whose concentrations are measured to monitor vertical ocean water movement and mixing. Thus a high vertical energy export rate by this method would not contradict the known concentration data, resolving a potential anomaly.

Thermal harvesting organisms will tend to thrive and increase as surface waters become warmer, as has recently occurred, due to the greater efficiency of energy harvest possible as the $\Delta T/T$ ratio increases. This could at least partially explain the anomaly of the current global warming 'pause'. While not really a pause, a present slowdown in surface level

warming appears to be due to thermal energy passing from shallow ocean water to the mid-depths at an unprecedentedly high rate.^[5]

If this bio-feedback from ocean surface warming is a real effect, it is of some importance, because the deep oceans have sufficient heat capacity to store centuries' worth of anthropogenic greenhouse energy before warming appreciably. Total current anthropogenic radiative greenhouse forcing^[6] is $\sim 2.5 \text{ W/m}^2$, and would be balanced by a drawdown of $\sim 5 \text{ W/m}^2$ in the temperate and tropical oceans. An even larger drawdown is ecologically conceivable. This negative feedback could have been damping rapid surface temperature changes for hundreds of millions of years.

3. LAND ARTHROPODS

Insects and other arthropods can move from sun to shade very easily, and heat and cool very rapidly, due to their small size. Insect energy consumption will vary enormously with species and life cycle stage, but a thermal cycle contribution could be significant in many cases.

Beetles might plausibly use their elytra as thermal reservoirs for this purpose. Often coloured black, which gives optimal absorption and emission of radiant energy, the elytra temperature could be cycled very rapidly by moving in and out of direct sunlight, without affecting the insect's core body temperature. These organs are normally assumed to serve as wing protective cases, but have always seemed to me disproportionately massive structures for a flying insect to carry for this purpose.

Arthropods which spend a long time in a non-motile state, such as a pupa in a chrysalis, could harvest energy from the diurnal thermal cycle at a time no other source is available to them.

A colleague observed that on the Canadian farm where she spent her youth, monarch butterflies hang their chrysalises beneath milkweed whose shadow forms an intricate pattern of light and shade.^[4] As the sun tracks across the sky, such a chrysalis would likely switch between full sun and full shade many times a day, providing a correspondingly large number of thermal cycles.

4. LAND REPTILES

Alligators are often observed to sunbathe in the morning, enter water in the middle of the day to cool, then sunbathe again in the afternoon. An alligator's body temperature can vary by 14°C in a single day, twice as much as its average diurnal temperature varies over a year, strongly suggesting that it is deliberately maximising short-term thermal cycling.^[7]

Taking a more typical cycle as 10°C, the animal has 40 J/g more thermal energy in its body tissue at the higher temperature than the lower. $\Delta T/T = 10/300 = 3.3\%$, so up to 1.3 J/g of this could ideally be extracted into chemical energy. A real system might do perhaps half as well, storing 0.65 J/g in the animal's tissue: a twice daily cycle produces 1.3 J/g

A 70 kg alligator produces 72 kcal/day metabolic energy^[8], 4.3 J/g. Thus thermal cycling could produce 30% of the animal's total energy requirement for around half of each year.

Large crocodylians, by contrast, appear to have near-homeothermic body temperatures.^[9]

Among small reptiles, the lizard *Ameiva Exsul* cycles its body temperature by ~7°C many times a day by shifting from sun to shade.^[10] However Kleiber's Law suggests that with mass < 100g, it will need too much energy for cyclic thermal harvesting to be of significant use.

5. BIRDS

The peacock's tail famously puzzled Darwin, and evidence for its value as a sexual ornament is not unequivocal.^[11] An arrangement of bird feathers could be alternately sun-heated and air-cooled in the shade in the same way as suggested above for the beetle's elytra. The mass of any bird's feathers is typically greater than that of its skeleton, a high fraction of its total body weight, and the feathers are thin and can be deployed in a large surface area to both warm (if exposed to the sun) and cool (if shaded and exposed to the wind) very rapidly.

It is normally assumed that a fully grown feather is effectively dead tissue which does not exchange material with the rest of the bird's body. But if

the energy from thermal cycling is converted into hydrocarbons in situ, the energy stored in fats and oils is ~25-40 kJ/g: an unnoticeably tiny amount of oil flowing from the feather back into the bird's skin could convey the energy harvested. Alternatively, the secretions from the uropygial gland might be converted to a chemically more energetic form before being combed off the feather and eaten.

While the peacock's tail could be a formidable energy-harvesting array, many birds with more ordinary plumage spend a considerable portion of their daylight perching time adjusting areas of feathers with respect to the sun. The usual assumption is that the purpose of this behavior is to cause parasites to congregate so the bird can easily remove them, but it could also be to maximise energy harvesting by thermal cycling.

A colleague points out that while the extreme of the male peacock's tail may indeed serve principally as a sexual ornament, and may have been further enhanced by selective breeding by humans, the fantail of the American wild turkey, which comprises black feathers suitable for maximum absorption and emission of radiant energy, could comprise a purer example of a thermal harvesting organ.^[4]

6. DINOSAURS

Ancient cold-blooded animals could have harvested thermal energy. In particular the sail of Dimetrodon could have helped this animal to cycle its body temperature rapidly: any blood circulated through it could be heated and/or cooled by adjusting the angle of the sail with respect to sun and wind. Some modern lizards have a similar sail-like feature.

Dinosaurs were likely warm-blooded. However, external features of dinosaur anatomy otherwise puzzling to explain could be thermal harvesting organs. Significant masses of external bone which could be exposed to the sun and wind for thermal cycling include the back plates of stegosaurus, the tail club of ankylosaurids, and the head ornamentation of many dinosaurs.

Large warm-blooded dinosaurs could nevertheless not have used thermal cycling nearly as effectively as creatures which could either thermally

cycle their entire body mass, like alligators, or thermally cycle a substantial part of their body mass very rapidly, like birds. This might help explain why, when dinosaurs became extinct, these lineages survived.

7. NON-MOTILE ORGANISMS

Particularly in regions where the ground surface temperature undergoes a large diurnal cycle, static organisms which have energy needs beyond carbon fixation might use thermal harvesting. This applies to plants which manufacture sugars for animal lures such as fruits or nectar, or high-energy fuel for their seeds as contained in nuts. Organisms incapable of photosynthesis such as fungi might also use this energy source.

The energy might be harvested as previously described, using the diurnal temperature cycle. Alternatively, a spatially extended organism can span a range of temperatures at a single instant: for example a tropical or desert plant with deep roots will have a large temperature differential between its above-ground and below-ground portions at the hottest part of the day and coldest part of the night. Chemicals circulated in its sap could readily perform thermal harvesting. Cacti, tubers and trees are all plausible candidates.

8. ORIGIN OF LIFE

Cyclic thermal harvesting could evolve far more easily than either photosynthesis or the use of external chemical energy. Temperature affects essentially every chemical equilibrium between reactants. Even stationary organisms, or ones which drift randomly, experience temperature variations: for example the diurnal temperature cycle. Thermal cycling might be the original form of energy gathering, used by the first lifeforms.

Thermal harvesting mechanisms in modern animals might or might not be related to such ancient ones. Either way, functional harvesting mechanisms of ancient origin or non-functional remnants might be found in single-celled organisms or larger ones. Almost any part of the kingdom

of life, with the possible exception of mammals because almost their entire body mass is homeothermic, can harvest thermal energy in the right circumstances.

9. CONCLUSIONS

The cyclic thermal harvesting hypothesis can be tested with comparatively simple experiments.

Behavioural observations and tests could be suggestive, and easiest to do in the first instance.

Measurement of the internal and external temperature of a freely moving animal at high time frequency is now technically straightforward, and could be strongly indicative.

The actual mechanism of energy harvesting may be more challenging to study. The 'working fluid' (not necessarily a fluid) need be only a fraction of a percent of the animal's body mass, and the energy stored per cycle is likewise a fraction of a percent of a typical animal's total energy store.

If the hypothesis is correct, a significant portion of the energy available to life on earth may come not from photosynthesis, but from cyclic thermal harvesting. The implications, theoretical and practical, will be enormous.

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