The furnace within

Why do we waste so much energy keeping our body thermostat cranked up to 37? **Nick Lane** tackles the mystery of warm-bloodedness

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IF YOU stopped eating today, you wouldn't survive more than two months. A crocodile, on the other hand, might live for a year or more. Why the difference? You waste most of the food you eat generating heat.

The evolution of warm-bloodedness, or endothermy, is one of life's great mysteries. Sure, there are some advantages – staying active in the cold, keeping young cosy and warm, and avoiding having to go out into the open to soak up heat from the sun.

The thing is, you could get much the same advantages by turning up the heat only when and where in the body it is needed, as many animals do. So why keep the furnaces burning 24/7, as most birds and mammals do? Staying warm – which for birds means 40 °C on average – comes at a price. Some warm-blooded animals have to eat as much in one day as similarly sized reptiles do in a month, a dangerous and time-consuming strategy.

Biologists have long struggled to understand why we mammals and our feathery cousins are warm-blooded. The standard explanation is that it evolved in small carnivores to enable an active, predatory lifestyle. Last year, however, a radical new idea was put forward: warm blood evolved not in carnivores but in herbivores, as a way of balancing their nutrient requirements. Though it is early days, this idea could explain not only why we have such an apparently wasteful lifestyle, but also some long-standing mysteries about the dinosaurs (see "Why did dinosaurs grow so big?", page 44).

In mammals and birds, heat is generated mainly by the visceral organs such as the liver and the brain. These organs are usually larger than their counterparts in cold-blooded animals (ectotherms), and their cells contain up to five times as many food-burning factories, the mitochondria. As a result, they generate heat continuously, keeping the entire body warm all the time.

This is extraordinarily wasteful, especially when you consider that many other animals have evolved more efficient strategies. For example, leatherback turtles conserve the heat they generate when swimming to keep their body temperature 10 °C or more above that of seawater, allowing them to forage in much colder waters than other turtles (*Comparative Biochemisty and Physiology A*, vol 147, p 323). Swordfish selectively warm their eyes and brain while hunting, while some sharks and tuna keep their long-distance swimming muscles well above the water temperature. Even a few insects, such as the hawkmoth, can generate heat when it's needed.

So why do most mammals and birds turn the thermostat to maximum all the time? The leading explanation was put forward three decades ago by zoologists Albert Bennett of the University of California, Irvine, and John Ruben of Oregon State University. They proposed that the evolution of endothermy was all about stamina. They noted that mammals and birds have a high aerobic capacity compared with other animals, which provides their muscles with lots of oxygen and keeps that supply going for long periods. As a result, they are able to sustain exertion for longer, whether chasing prey or fighting competitors. Nobody disagrees with that. Bennett and Ruben, however, went on to argue something more contentious: that high aerobic capacity inevitably leads to a high metabolic rate at all times. In other words, selection for stamina leads to endothermy.

Not so many people agree with that. There's no obvious reason why the two should be linked: aerobic capacity depends on the cardiovascular system and muscles whereas the resting metabolic rate depends mostly on the brain and visceral organs. On top of that there are a few reptiles, such as monitor lizards, which have high aerobic capacity but a low resting metabolic rate. Some mammals and birds achieve much the same by dropping their body temperature when inactive or when hibernating. The aerobic capacity hypothesis has never really been proved or disproved, despite quite a few attempts to do so (*Physiological and Biochemical Zoology*, vol 77, p 982).

There are other contradictions too. The theropod dinosaurs – the group that includes velociraptors – certainly had a high aerobic capacity. Most researchers agree that they lie on the evolutionary line to birds. But were they endotherms?

Ruben insists the answer is no, even though his own aerobic capacity hypothesis predicts a link. He agrees that the theropods were capable of great speed and exertion, but thinks they still had a slow resting metabolism. His conclusion is based on the fact that they lack so-called respiratory turbinates, elaborate whorls of bone or cartilage in the nasal passages of birds and mammals that reduce water loss through breathing, which is a big problem when you have a fast metabolism.

So if there isn't necessarily a link between stamina and warm blood, then why did it evolve at all? Enter Marcel Klaassen and Bart Nolet of the Netherlands Institute of Ecology. They study stoichiometry – how animals get enough of the various nutrients they need. Herbivores have a well-recognised problem here: how to get enough nitrogen, which ›

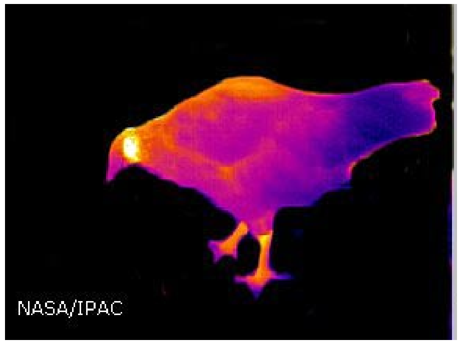
WARM-BLOODED OR COLD-BLOODED?

The old dichotomy between warm and cold blood is now seen as too simplistic to deal with the many and varied ways animals control their body temperature. Here are some examples:

- **Naked mole rats don't control their own temperature but adopt that of their burrows - usually a constant 30 °C. They are the only known ectothermic mammals**
- **A few insects, such as the apache cicada, sweat: exuding moisture cools their bodies by a few degrees**
- **The Indian python and some other snakes shiver while incubating eggs, warming themselves by up to 8 °C**
- **Most bats and a few birds let their body temperature fall while roosting, often to that of the ambient temperature. If it gets too cold they switch on the heat again**
- **Monotremes (platypuses and echidnas) maintain a temperature of 32 °C, well below the 37 °C norm for placental mammals. For most marsupials it is 35 °C**
- **Hyraxes are poor at maintaining a constant temperature and resort to reptile-like behaviour such as basking to keep warm**

Couldn't the food that warm-blooded animals burn to stay toasty be put to better use?

Infrared images reveal where body heat leaks out, and which creatures are the hottest



NASA/IPA

they need for making proteins, DNA and RNA. Essentially, if you only eat leaves, you get too much carbon and not enough nitrogen. Some reptiles are herbivores but it is not a common lifestyle and those that are cheat, says Robert Espinoza of California State University, Northridge. "From time to time most herbivorous lizards eat bugs or small vertebrates," he says. "It undoubtedly helps them overcome nutrient deficits."

Last year, Klaassen and Nolet suggested that the nitrogen issue could explain why birds and mammals evolved warm blood (*Ecology Letters*, vol 11, p 785). "If one bucket of leaves gives you a fifth of your daily nitrogen needs," says Klaassen, "then all you need to do is eat five buckets. What do you do with all the excess carbon? Burn it off. That's endothermy."

He thinks that resting metabolic rate might have risen in animals switching to a herbivorous diet. "A theropod that turned to herbivory would benefit from warm blood. It's possible that a diet of leaves could have given rise to endothermy in the first place."

One objection to this idea is that it appears self-defeating: a higher metabolism leads to a higher turnover of proteins and so a greater absolute demand for nitrogen. Modern birds and mammals have to consume about four times as much nitrogen per day as a similar-sized reptile, Klaassen and Nolet calculated.

However, there's a pay-off in terms of the kinds of foods an endotherm can survive on. An endothermic herbivore might have to eat more, but Klaassen and Nolet calculate it can survive on food that contains only a half to a quarter as much nitrogen per mouthful as an ectotherm.

You might also think there are simpler ways of getting rid of excess carbon, but in fact endothermy is a very neat solution. Turning excess carbon into a gas that can be breathed out is a simple way of getting rid of it.

What's more, the molecular changes required look relatively simple. According to Frank Seebacher at the University of Sydney in Australia, developing chicks start generating their own heat when their cells produce more mitochondria under the influence of a protein called PGC-1alpha. A similar switch could easily have occurred in evolution, in mutants that happened to make a bit more PGC-1alpha.

Other possible solutions, such as selectively absorbing nitrogen-rich compounds from the gut, would require the evolution of entirely new mechanisms, and animals that did this

WHY DID DINOSAURS GROW SO BIG?

Sauropod dinosaurs such as apatosaurus are the largest animals ever to walk on land. The heaviest weighed up to 100 tonnes and the longest might have measured as much as 60 metres from head to tail.

Why they became so big is a long-standing conundrum. In 2002, Jeremy Midgley, an ecologist at the University of Cape Town, South Africa, suggested that it was down to deficiencies in their diet.

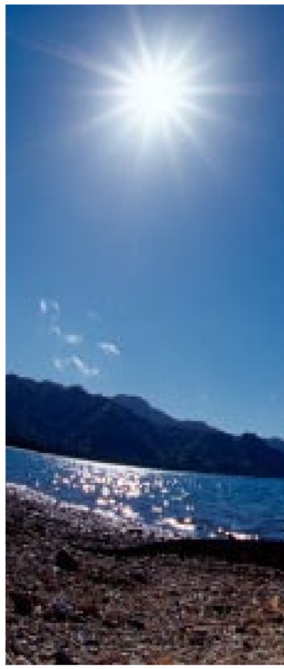
In the Jurassic, herbivorous dinosaurs had a serious problem getting enough nitrogen, Midgley argues. "The average nitrogen content of most plants living then was typically lower," he says. "And then the carbon dioxide levels were much higher, maybe 10 times today's. That suppresses the nitrogen content of plants even more."

How does getting big help? As an animal's body size rises, its metabolic rate falls, along with the growth rate. Why this is so is controversial but it does affect nitrogen requirements: the lower an animal's metabolism and the slower its growth rate, the less protein and DNA it has to make, and thus the less nitrogen it will need per mouthful.

Juvenile sauropods must have supplemented their diet with a little meat, and perhaps fungi. Once they had become truly gigantic, however, they could survive solely on low-nitrogen leaves, Midgley believes.

Solving one dietary problem might have created another, though. Jim Elser, an expert in ecological stoichiometry at Arizona State University, Tempe, suspects that giant sauropods had problems getting enough phosphorus.

To support their weight, giants need relatively larger bones than smaller animals. This means they need relatively more phosphorus, because bones are made of hydroxyapatite, a phosphorus mineral. Large and fast-growing plants have a higher phosphorus content, so the giant sauropods may have been able to get enough of this element by eating the leaves of large trees.



Komodo dragons are one reason we need a new theory for the origins of warm blood

> "If one bucket of leaves gives you a fifth of your daily nitrogen needs, then all you need to do is eat five. What do you do with the excess carbon? Burn it off"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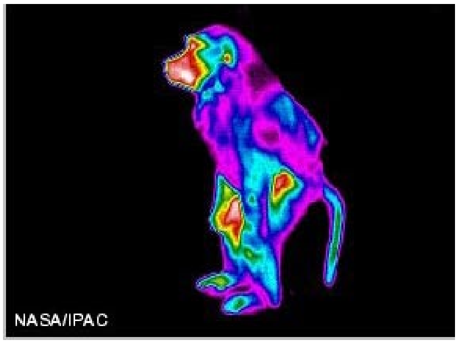
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would need to eat and excrete a lot of food from which they derive no benefit at all. Burning it, by contrast, produces a useful waste product: heat.

What the fossils tell us

It's an ingenious idea, says Jim Elser, an expert in ecological stoichiometry at Arizona State University in Tempe. Nitrogen balance is a major – if often overlooked – driving force in the behaviour of animals today, and Klaassen's idea shows how important it might have been in the past, Elser says. "But whether nitrogen balance was important in the origin of endothermy can only be answered from the fossil record."

So what do the fossils say? For the ancestors of birds it appears that the switch to endothermy took place around 140 million years ago, at the start of the Cretaceous. This was the period when nitrogen-rich flowering plants were beginning to take over. Atmospheric carbon dioxide levels started to fall, largely because the more developed root systems of flowering plants weather rocks faster, a process that removes CO_2 from the atmosphere. Over the Cretaceous, levels of CO_2 halved, from about 10 times pre-industrial levels to around 5 times.

Falling CO_2 would have made plants slightly richer in nitrogen, weight for weight. For some dinosaurs that would have made a herbivorous way of life possible. The rise of flowering plants coincides with the first examples of theropod dinosaurs turning vegetarian, such as *Falcarius utahensis*. Crucially, that dinosaur is part of a group quite closely related to the birds. A grand scenario, then, might see the rise of flowering plants and the evolution of warm blood as smaller dinosaurs – including the ancestors of birds – turned to herbivory.

Unfortunately, existing fossils provide no conclusive evidence. "There's little we can say at the moment about metabolic rates in *Falcarius* or its kin," says Scott Sampson from the Utah Museum of Natural History in Salt Lake City, one of the discoverers of *Falcarius*, "The skull of *Falcarius* is known only from fragments, so we cannot yet get a measure of the volume of the nasal cavity or whether it had turbinates."


REINHARD DIRSCHERT/GETTY

Much the same applies to the early mammals. Their ancestors, dicynodonts and cynodonts, certainly had a high aerobic capacity, and probably evolved warm blood sometime during the Triassic, over 200 million years ago. There are signs of both fur and turbinates in cynodonts, for example. But some were herbivores and others were carnivores, and it's not clear which gave rise to warm-blooded mammals.

Klaassen is the first to admit that his idea will take some proving. "Most theories argue that hot blood evolved in smaller carnivores, and that may be true. If so, then the rise of endothermy might have facilitated herbivory as a way of life; it became a lot more feasible once hot blood had already evolved," he says. Even this would represent a major shift in thinking.

"It's plausible that getting enough nitrogen could have been an impetus to the evolution of endothermy in the first place," Klaassen continues. It might not be as flashy as the idea that warm blood evolved to support a fast predatory lifestyle, but we may have vegetables to thank for our inner warmth. ■

Nick Lane is an honorary reader at University College London. His forthcoming book *Life Ascending: The ten great inventions of evolution* will be published in April 2009 by Profile