HOT BLOOD

Breaking the Energy Barrier

Time flies by when you're the driver of a train, runs a children's lyric. And who can't remember the reverse as a child – the endless minutes of mind-numbing tedium in the back of a car, asking repeatedly, 'Are we there yet, Daddy?' I imagine most readers will also remember the distress of watching their ageing grandparents, or parents, slow down to a snail's pace, in the end sitting inscrutably as hours pass by like minutes. Both extremes are far removed from the tempo of our own world, the andante of an adult human being.

We don't need Einstein to tell us that time is relative. But what Einstein established rigorously for time and space is, as ever, more impressionistic in biology. As the celebrated wag Clement Freud had it: 'If you resolve to give up smoking, drinking and loving, you don't actually live longer, it just seems longer.'[1] Yet there is a real sense in which time rushes through childhood, and crawls through old age. It lies in our internal settings, our metabolic rate, the rate at which our hearts beat and our cells burn up food in oxygen. And even among adults there are striking differences between the active and the slovenly. Most of us shift slowly from one to the other. The rate at which we slow down, or indeed gain weight, depends much on our metabolic rate, which varies innately between individuals. Two people who eat the same and exercise equally will often differ in their tendency to burn off calories while at rest.

Nowhere is metabolic rate more significant than the difference between hot-blooded and cold-blooded creatures. While these terms make biologists cringe, they are vivid and meaningful to almost everyone, and convey as much as the slippery technical terms, like homeothermy and poikilothermy. It's a curious thing, but I've noticed there are few aspects of biology that we feel so chauvinistic about, we hot-bloods. The fury and spleen vented in journals, and online, about whether dinosaurs, for example, were hot-blooded or cold-blooded is hard to understand rationally: it is a visceral distinction, perhaps something to do with our dignity, whether we would rather be eaten by giant lizards, or clever, scheming, fast-moving beasts, against whom we must pit our wits to survive. We mammals still bear a grudge, it seems, for the time we spent as small furry animals, cowering underground in hock to the top preda-tors of the past. But then it was for 120 million years, which is a long time by any reckoning.

Hot blood is all about metabolic rate, all about the pace of life. Hot blood helps in its own right, for all chemical reactions speed up with rising tempera-ture, including the biochemical reactions that underpin life. Over the small range of biologically meaningful temperatures, from around 0°C up to 40°C in animals, the difference in performance is striking. Oxygen consumption, for example, doubles with every 10°C rise in temperature in this range, cor-responding to mounting stamina and power. So an animal at 37°C has twice the power of one at 27°C, and quadruple the power of an animal at 17°C.

But to a large extent, temperature misses the point. Hot-blooded animals are not necessarily any hotter than cold-blooded animals, for most reptiles are adept at absorbing the energy of the sun, warming their core body temperature up to levels similar to mammals and birds. Certainly, they don't maintain such high temperatures after dark; but then mammals and birds are often inactive at night too. They might as well save energy by lowering their core body temp-erature, but rarely do, at least not by much (although hummingbirds often pass into a coma to conserve energy). In our energy-conscious times, mammals ought to make environmentalists weep: our thermostat is jammed at 37°C, twenty-four hours a day, seven days a week, regardless of need. And forget alternative energy. We're in no way solar-powered, like lizards, but generate heat prodigiously by way of internal carbon-burning power stations, giving us

a giant carbon footprint too. Mammals are the original eco-hooligans.

You might think that running on full power through the night would give mammals a head start in the morning, but lizards don't waste much time raising their temperatures back to operational levels. The earless lizard, for example, has a blood sinus on top of its head, through which it can warm its whole body rapidly. In the morning, it pokes its head out of its burrow, keeping a wary eye out for predators, ready to duck back in if necessary, and after half an hour is usually warm enough to venture out. It's a pleasant way to start the day. Characteristically, natural selection is not content with only one function. If caught out, some lizards have a connection from the sinus to their eyelids, through which they can squirt blood at predators, such as dogs, which find the taste repugnant.

Size is another way to maintain high temperatures. You don't need to be a great white hunter to picture the hides of two animals stretched out as rugs on the floor. Imagine that one such hide is twice the length and breadth of the other. This means that the larger animal had four times more hide than the smaller beast ($2 \times 2 = 4$), but it would have been eight times heavier, as it also had twice the depth ($2 \times 2 \times 2 = 8$). Thus every doubling of dimensions halves the surface-to-weight ratio ($4 \div 8 = 0.5$). Assuming that each pound in weight generates the same amount of heat, larger animals have more pounds and so generate more internal heat.[2] At the same time, they lose heat more slowly because their skin surface is relatively small (in relation to internal heat generated). So, the bigger the animal, the hotter it gets. At some point, cold-blooded creatures become hot-blooded. Large alligators, for example, are technically cold-blooded, but retain heat long enough to be borderline hot-blooded. Even overnight, their core temperature only drops a few degrees, despite producing little internal heat.

Plainly many dinosaurs would have surpassed this size threshold comfortably, making them de facto hot-blooded, especially given the pleasantly warm ambient temperatures enjoyed by much of the planet in those halcyon days. There were no ice caps, then, for example, and atmospheric carbon dioxide levels were as much as tenfold higher than today. In other words, some simple physical principles mean that many dinosaurs would have been hot-blooded, regardless of their metabolic status. The giant herbivores may well have had

more trouble losing heat than gaining it; and some anatomical curiosities, like the great armoured plates of the stegosaurus, may have played a second role in heat dissemination, not unlike an elephant's ears.

But if it were as simple as that, there would have been no controversy about whether or not the dinosaurs were hot-blooded. In this limited sense they certainly were, or at least many of them were. For those who like mouth-filling terms, it's called 'inertial endothermy'. Not only did they maintain a high internal temperature, they generated heat internally, in the same way as modern mammals, through burning carbon. So in what broader sense were dinosaurs *not* hot-blooded? Well, some of them may well have been, as we'll see later, but to understand the real oddity of mammalian or avian hot blood we need to reverse the size trend to see what happens in smaller animals, below the 'hot-blood threshold'.

Think of a lizard. By definition, it is cold-blooded, which is to say, it can't maintain its internal body temperature overnight. While a large crocodile might come close, the smaller the animal, the harder it gets. Insulation, like fur or feathers, only helps to a point and can actually interfere with heat absorption from the surroundings. Dress up a lizard in a fur coat (and needless to say, earnest researchers have done exactly this) and the lizard gets steadily colder, unable to absorb the sun's heat so well, or to generate enough heat internally to compensate. This is far from the case with mammals or birds, and that brings us to the real definition of hot blood.

Mammals and birds generate up to ten or fifteen times as much internal heat as a similarly sized lizard. They do so regardless of circumstances. Place a lizard and a mammal in suffocating heat and the mammal will continue to generate ten times as much internal heat, to its own detriment. It will have to go out of its way to cool down – drink water, plunge into a bath, pant, find shade, fan itself, drink cocktails, or switch on the air-conditioning. The lizard will just enjoy it. It's not surprising that lizards, and reptiles in general, fare much better in the desert.

Now try placing the lizard and the mammal in cold conditions, let's say close to freezing, and the lizard will bury itself in leaves, curl up and go to sleep. To be fair, many small mammals would do that too, but that's not our default setting. Quite the contrary. Under such conditions, we just burn up

even more food. The cost of living for a mammal in the cold is a hundred times that of a lizard. Even in temperate conditions, say around 20°C, a pleasant spring day in much of Europe, the gap is huge, around thirtyfold. To support such a prodigious metabolic rate, the mammal must burn up thirty times more food than a reptile. It must eat as much in a single day, every single day, as a lizard eats in a whole month. Given that there's no such thing as a free lunch, that's a pretty serious cost.

So there it is: the cost of being a mammal or a bird starts at around ten times the cost of being a lizard and is often far higher. What do we get for our expensive lifestyle? The obvious answer is niche expansion. While hot blood may not pay in the desert, it enables nocturnal foraging, or an active existence over winter in temperate climates, both of which are denied to lizards. Another advantage is brainpower, although it's hard to see why there should be a necessary relationship. Mammals certainly have far larger brains, relative to their body size, than reptiles. While a large brain is no guarantee of intelligence, or even quick wits, it does seem to be the case that a faster metabolism supports a bigger brain, without specifically dedicating resources to it. So if lizards and mammals both earmark, say, 3 per cent of their resources to the brain, but mammals have at their disposal ten times the resources, they can afford ten times more brain, and usually have exactly that. Having said that, primates, and especially humans, allocate a far greater proportion of their resources to brainpower. Humans, for example, dedicate around 20 per cent of resources to the brain, even though it takes up only a few per cent of our body. I suspect, then, that brainpower is little more than an added extra, thrown in at no extra cost, for a hot-blooded lifestyle. There are far cheaper ways of building bigger brains.

In short, niche expansion, nocturnal activity and added brainpower don't seem much payback for the serious metabolic costs of hot blood. Something seems to be missing. On the debit side, the costs of eating, eating, eating go well beyond bellyache. There is the serious cost of time and effort spent foraging, hunting or cropping vegetation, time vulnerable to predators or competitors. Food runs out, or becomes scarce. Plainly, the faster you eat, the faster you will run out of food. Your population shrinks. As a rule of thumb metabolic rate governs population size, and reptiles often outnumber mammals

by ten to one. By the same token, mammals have fewer offspring (though they can dedicate more resources to the few they have). Even lifespan varies with metabolic rate. Clement Freud was right about people but wrong about reptiles. They may live slow and boring lives, but they do live longer, in the case of giant tortoises for hundreds of years.

So hot blood exacts a cruel toll. It spells a short life, spent eating dangerously. It depresses the population size and the number of offspring, two factors that should be penalised ruthlessly by natural selection. In recompense we have the boon of staying up at night and hanging out in the cold. That seems a poor deal, especially if we go to sleep anyway. Yet in the great pantheon of life, we routinely give top billing to the mammals and birds. What exactly is it that we have but the reptiles don't? It had better be good.

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The single most compelling answer is 'stamina'. Lizards can match mammals easily for speed or muscle power, and indeed over short distances outpace them; but they exhaust very quickly. Grab at a lizard and it will disappear in a flash, streaking to the nearest cover as fast as the eyes can see. But then it rests, often for hours, recuperating painfully slowly from the exertion. The problem is that reptiles ain't built for comfort – they're built for speed.[3] As in the case of human sprinters, they rely on anaerobic respiration, which is to say, they don't bother to breathe, but can't keep it up for long. They generate energy (as ATP) extremely fast, but using processes that soon clog them up with lactic acid, crippling them with cramps.

The difference is written into the structure of muscle. There are various types of muscle, as we saw in Chapter 6. These vary in the balance of three key components: muscle fibres, capillaries and mitochondria. In essence, the muscle fibres contract to generate force, the blood capillaries supply oxygen and remove waste, while the mitochondria burn up food with oxygen to provide the energy needed for contraction. The trouble is that all of them take up valuable space, so the more muscle fibres you pack in, the less space there is left over for capillaries or mitochondria. A muscle packed tightly with fibres will have tremendous force, but soon runs out of the energy needed to fuel its

contraction. It's a choice with the most widespread consequences – high power and low stamina, or low power and high stamina. Compare a bulky sprinter with a lean distance runner, and you'll see the difference.

We all have a mixture of muscle types, and this mix varies according to circumstances: whether we live at sea level or altitude, for example. Lifestyle can also make a big difference. Train to be a sprinter and you will develop bulky 'fast-twitch' muscles, with lots of power but little stamina. Train to be a long-distance runner and you'll shift the other way. Because these differences also vary innately between individuals and races, they are subject to selection over generations, if the circumstances dictate. That's why the Nepalese, East Africans and Andean Indians have a good many traits in common – traits that lend themselves to life at high altitude – whereas lowlanders are heavier and bulkier.

According to a classic paper in 1979 by Albert Bennett and John Ruben, then at the University of California, Irvine, such differences lie at the root of hot blood. Forget temperature, they said: the difference between hot-blooded and cold-blooded creatures is all about stamina. Their idea is known as the 'aerobic capacity' hypothesis, and even if it's not entirely right, it changed the way the whole field thought about life.

The aerobic capacity hypothesis makes two claims. First, selection is not for temperature but for increased activity, which is directly useful in many circumstances. As Bennett and Ruben put it themselves:

> The selective advantages of increased activity are not subtle but rather are central to survival and reproduction. An animal with greater stamina has an advantage that is readily comprehensible in selective terms. It can sustain greater levels of pursuit or flight in gathering food or avoiding becoming food. It will be superior in territorial defence or invasion. It will be more successful in courtship or mating.

That much seems incontestable. An interesting refinement of the idea, from the Polish zoologist Pawel Koteja, places the emphasis on intensive parental care, associated with feeding the young lasting for months or years, which sets mammals and birds apart from cold-blooded animals. Such

investment requires very substantial stamina, and can have a big impact on survival at the most vulnerable time in an animal's life. Regardless of the exact reasons, though, it is the second part of the aerobic capacity hypothesis that is the more problematic and interesting: the link between stamina and rest. There is a necessary connection, say Bennett and Ruben, between the maximal and the resting metabolic rate. Let me explain.

The maximal metabolic rate is defined as the amount of oxygen consumed at full tilt, when we can push ourselves no further. It depends on many things, including fitness and, of course, genes. The maximal metabolic rate depends ultimately on the rate of oxygen consumption by the end-users, the mitochondria in the muscles. The faster they consume oxygen, the faster the maximal metabolic rate. But even a cursory reflection makes it plain that many factors must be involved, all of them interrelated. It will depend on the number of mitochondria, the number of capillaries supplying them, the blood pressure, the size and structure of the heart, the number of red blood cells, the precise molecular structure of the oxygen-transporting pigment (haemoglobin), the size and structure of the lungs, the diameter of the wind pipe, the strength of the diaphragm, and so on. If any one of these features is deficient, the maximal metabolic rate will be lower.

Selection for stamina, then, equates to selection for a high maximal metabolic rate, which boils down to selection for a whole suite of respiratory characters.[4] According to Bennett and Ruben, a high maximal metabolic rate somehow 'pulls up' the resting metabolic rate. In other words, an athletic mammal with lots of stamina has a high *resting* metabolic rate by default: it continues to breathe in plenty of oxygen, even while lying down doing nothing at all. They argued their case empirically. For whatever reason, they said, the maximal metabolic rate of all animals, whether mammal, bird or reptile, tends to be about ten times greater than the resting metabolic rate. Thus selection for high maximal metabolic rate drags up the resting metabolic rate too. If the maximal metabolic rate rises tenfold, which is the recorded difference between mammals and lizards, the resting metabolic rate also rises tenfold. And by that stage, the animal generates so much heat internally that it becomes, in effect, accidentally 'hot-blooded'.

The idea is pleasing and makes intuitive sense, but on closer examination

it's very hard to work out quite why the two *need* to be linked. Maximal metabolic rate is all about getting oxygen out to the muscles, but at rest muscles contribute little to oxygen consumption. Instead, the brain and visceral organs – the liver, pancreas, kidneys, intestines, and so on – play the most important role. Exactly why the liver needs to consume lots of oxygen, just because the muscles do, is not clear. It is at least possible to imagine an animal that has a very high aerobic capacity and a very low resting metabolic rate, a kind of souped-up lizard that combines the best of both worlds. And it may be that this is exactly what the dinosaurs were. It's a bit of an embarrassment, frankly, that we still don't know why the maximal and resting metabolic rate tend to be linked in modern mammals, reptiles and birds, or if the link can be broken in some animals.[5] Certainly, very athletic mammals, like the pronghorn antelope, have very high aerobic capacities, around sixty-five times higher than their resting metabolic rates, implying that the two can be disconnected. The same applies to a few reptiles. The American alligator, for example, has an aerobic capacity at least forty times higher than its resting rate.

Be that as it may, there are still some good reasons to think that Bennett and Ruben are right. Perhaps the strongest relates to the source of heat in most hot-blooded animals. There are many ways to generate heat directly, but most hot-blooded animals don't bother: their heat production is an indirect consequence of metabolism. Only small mammals that lose heat rapidly, like rats, generate heat directly. Rats (and the young of many other mammalian species) make use of a specialised tissue known as brown fat, which is chock full of hot mitochondria. The trick they use is simple enough. Normally, mitochondria generate an electrical current, composed of protons, across their membrane, and this is used to generate ATP, the energy currency of the cell (see Chapter 1). The whole mechanism requires an intact membrane that acts as an insulator. Any leak in the membrane short-circuits the proton current, dissipating its energy as heat. And that's exactly what happens in brown fat – protein pores are deliberately inserted into the membrane, rendering it leaky. Instead of ATP, these mitochondria generate heat instead.

So if heat is the primary objective, the solution is leaky mitochondria. If all the mitochondria are rendered utterly leaky, as in brown fat, all the energy in food is converted into heat directly. It's simple and quick, and doesn't take up

a lot of space, because a small amount of tissue generates heat efficiently. But that's not what normally happens. There's little difference in the degree of mitochondrial leakiness between lizards, mammals and birds. Instead, the difference between cold-blooded and hot-blooded creatures lies mostly in the size of the organs and the number of mitochondria. For example, the liver of a rat is much bigger than that of a similarly sized lizard and it's packed with far more mitochondria. In other words, the visceral organs of hot-blooded creatures are effectively turbocharged. They consume vast quantities of oxygen, not to generate heat directly, but to boost performance. Heat is merely a by-product, only later captured and put to good use with the development of external insulation, like fur and feathers.

The onset of hot-bloodedness in the development of animals today lends support to the idea that hot blood is more about turbocharging visceral organs than heat production. The evolutionary physiologist Frank Seebacher, at the University of Sydney, has begun looking into which genes underpin the onset of hot blood in embryonic birds, and finds that a single 'master gene' (which encodes a protein called PGC1α) powers up the visceral organs by forcing their mitochondria to proliferate. Organ size, too, can be controlled quite easily, by adjusting the balance between cell replication and death, via similar 'master genes'. The long and short of it is that turbocharging the organs is not genetically difficult to do – it can be controlled by just a handful of genes – but it's energetically extremely costly, and will only be selected if the payback is worth it.

The broad scenario of the aerobic capacity hypothesis, then, looks convincing. There's no doubt that hot-blooded animals have far more stamina than cold-bloods, typically ten times the aerobic capacity. In both mammals and birds, this soaring aerobic capacity is coupled to a turbocharged resting metabolism – large visceral organs, with high mitochondrial power – but little deliberate attempt to generate heat. To me at least, it makes some sort of intuitive sense that a high aerobic capacity should be coupled to a boosted support system. And the idea is readily testable. Breed for high aerobic capacity, and the resting metabolic rate should follow suit. At the very least the two should correlate, even if causal relationships are hard to prove.

There's the rub. Since the hypothesis was proposed, nearly thirty years

ago, there have been many attempts to verify it experimentally, with mixed success. There is indeed a general tendency for resting and maximal metabolic rates to be linked, but little more than that, and there are many exceptions to the rule. It may well be that the two *were* linked in evolution, even if such a link is not strictly necessary in physiological terms. Without a more specific idea of evolutionary history, it's hard to say for sure. But as it happens, this time the fossil record might actually hold the key. It may be that the missing link lies not in physiology, but in the vicissitudes of history.

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Hot blood is all about the power of the visceral organs like the liver. Soft tissues don't survive the ravages of time well, though, and even fur is rarely preserved in the rocks. For a long time, then, it was hard to tease out the origins of hot blood in the fossil record, and even today angry controversy is rarely a stranger. But reappraising the fossil record in light of aerobic capacity is a more feasible task, since much can be gleaned from skeletal structure.

The ancestors of both mammals and birds can be traced back to the Triassic age, beginning 250 million years ago. The period came hot on the heels of the greatest mass extinction in the entire history of our planet, the Permian extinction, which is thought to have wiped out about 95 per cent of all species. Among the few survivors of that carnage were two groups of reptiles, the *therapsids* ('mammal-like reptiles'), ancestors of modern mammals, and the *archosaurs* (from the Greek 'ruling lizards'), the ancestors of birds and crocodilians, as well as dinosaurs and pterosaurs.

Given the later rise and dominance of the dinosaurs, it's perhaps surprising that the therapsids were the most successful group in the early Triassic. Their descendants, the mammals, shrank down in size and descended into holes before the onslaught of the dinosaurs. But earlier on in the Triassic, easily the most dominant species was *Lystrosaurus* ('shovel-lizard'), a pig-sized herbivore with two stumpy tusks, a squat face and a barrel chest. Quite what manner of life the lystrosaurs led is ambiguous. For many years they were pictured as amphibious beasts, a small reptilian hippo, but they are now thought to have lived in more arid climates, and purported to have burrowed holes, a common

therapsid trait. We'll return to the significance of this later; but what is plain is that the lystrosaurs dominated the early Triassic in a way never seen again.[6] It's said that, for a period, 95 per cent of all terrestrial vertebrates were lystrosaurs. As the American poet and naturalist Christopher Cokinos put it: 'Imagine waking up tomorrow, walking across the continents and finding, say, only squirrels.'

The lystrosaurs themselves were herbivores, perhaps the only herbivores of that age, and feared no predators at the time. Later in the Triassic, a related group of therapsids called the *cynodonts* (meaning 'dog-teeth') began to displace the lystrosaurs, which finally fell extinct at the end of the Triassic 200 million years ago. The cynodonts included both herbivores and carnivores and were the direct forebears of the mammals, which emerged towards the end of the Triassic. The cynodonts showed many signs of high aerobic capacity, including a bony palate (separating the air-passages from the mouth, to allow simultaneous breathing and chewing), a broad chest with a modified rib cage and probably a muscular diaphragm. Not only that, but their nasal passages were enlarged, enclosing a delicate latticework of bone, known as 'respiratory turbinates'. The cynodonts might even have been covered in fur, but still laid eggs like reptiles.

It looks likely, then, that the cynodonts already had a high aerobic capacity, which must have given them great stamina; but what about their resting metabolic rate? Were they hot-blooded too? According to John Ruben, respiratory turbinates are one of the few reliable indications of an elevated resting metabolism. They restrict water loss, which can be very substantial during sustained heavy breathing, as opposed to short bursts of activity. Because reptiles have such a low resting metabolic rate, they breathe very gently when at rest and have little need to restrict water loss. As a result, no reptiles are known to have respiratory turbinates. In contrast, almost all true hot-blooded creatures do have turbinates, although there are a few exceptions including primates and some birds. Plainly turbinates help, even if they're not absolutely necessary, and their presence in fossils is as good a clue as any to the origin of hot blood. When coupled with the likely presence of fur (inferred rather than observed in fossils), it looks as if the cynodonts really did evolve hot blood somewhere along the line to the mammals.

But for all that, the cynodonts soon found themselves on the back foot, ultimately pressed into a cowering, nocturnal existence by the all-conquering archosaurs, in a late 'Triassic takeover'. If the cynodonts had evolved hot blood already, what about their vanquishers, a group that soon evolved into the first dinosaurs? The last survivors of the archosauran age, crocodiles and birds, are cold- and hot-blooded, respectively. At some point en route to the first birds, the archosaurs evolved hot blood. But which ones, and why? And did they include the dinosaurs?

Here the situation is more complex, and at times furiously controversial. Birds, like dinosaurs, attract passionate views that barely even masquerade as science. Long seen as related in some way to the dinosaurs, especially a group called the theropods that includes *Tyrannosaurus rex*, birds were redesignated squarely within the theropod line by a succession of systematic anatomical (cladistic) studies, dating back to the mid 1980s. The big conclusion was that birds are not merely related to the dinosaurs, they *are* dinosaurs, specifically avian theropods. While most experts are persuaded, a vociferous minority, led by distinguished paleo-ornithologist Alan Fedducia, at the University of North Carolina, maintain they derive from an earlier uncertain group that branched off before the evolution of theropods. In this view, birds are not dinosaurs; they are unique, a class unto themselves.

As I write, the latest in this long line of studies is also the most colourful, and relates to proteins rather than morphological traits. The amazing discovery, in 2007, by a team at Harvard Medical School led by John Asara, is that an exceptionally preserved bone from *T. rex*, some 68 million years old, still contains fragments of collagen, the main organic component of bone. The team succeeded in sequencing the amino acids in a few fragments, then piecing them together to give a sequence for part of the *T. rex* protein. In 2008, they compared this with equivalent sequences in mammals, birds and alligators. The sequences were short, and so potentially misleading, but on the face of it, the closest living relative of *T. rex* is the humble chicken, followed closely by the ostrich. Unsurprisingly, the reports were greeted by a chorus of approval in the newspapers, delighted to know finally how a *T. rex* steak would taste. More to the point, the collagen study broadly corroborates the cladistic picture of birds as theropod dinosaurs.

The other major source of rancour in the avian world is feathers. Feduccia and others have long maintained that feathers evolved for flight in birds, imparting to them a disturbingly miraculous sense of perfection. But if feathers evolved for flight, they certainly should not be found among non-avian theropods like *T. rex*. According to Feduccia, they're not; but a parade of feathered dinosaurs has marched out of China over the last decade. While some of these are a bit dubious, the majority of experts, again, are convinced that flightless theropods did indeed sport feathers, including a small ancestor of *T. rex* itself.

The alternative view, that the 'feathers' are not what they seem, but actually squashed collagen fibres, smacks of special pleading. If they were merely collagen fibres, it's hard to explain why they should be found mostly in a single group of theropods known as raptors, a group including *Velociraptor*, made famous by the film *Jurassic Park*. Or why they should look the same as the feathers of fully fledged birds, preserved in the same strata. Not only do the feathers look like feathers, but some raptors, notably *Microraptor*, could apparently glide between trees aided by feathers sprouting copiously from all four limbs (or, for want of a better word, wings). I find it hard to believe that these beautifully preserved feathers are not feathers; and even Feduccia is relenting. Whether the gliding arboreal flight of *Microraptor* has any bearing on the origins of flight in birds proper, or in their closest relative, *Archaeopteryx*, is a moot point.

The conclusion that feathers evolved in theropod dinosaurs, before the origin of flight, is backed by studies of the embryonic development of feathers in birds, and especially their relationship to the skin of embryonic crocodiles. Crocodiles, remember, are living archosaurs, the ruling lizards that first appeared back in Triassic times. The crocodiles and dinosaurs (including birds) started diverging in the mid-Triassic, around 230 million years ago. Yet despite this ancient divergence, crocs already held within them the 'seeds' of feathers; even today they retain exactly the same embryonic skin layers that develop into feathers in birds, as well as the selfsame proteins, called 'feather keratins', naturally light, flexible and strong.

The feather keratins are found mostly in some embryonic layers of crocodile skin that slough off after hatching to expose their scales (and remnants

are found in the adult scales too). Birds have similar scales on their legs and feet, likewise exposed when the outer skin layers slough off after birth. According to Lorenzo Alibardi, a specialist in the evolutionary development of feathers at the University of Bologna, feathers grow from the same embryonic layers that are sloughed off when scales form. The embryonic scales elongate into tubular filaments, or barbs. These are hollow hair-like structures, with living walls formed from embryonic skin layers, which can sprout branches anywhere down their length.[7] The simplest feathers, down feathers, are basically tufts of barbs attached to the same spot, whereas flight feathers are formed from barbs that fuse into a central rachis. The living walls of barbs lay down keratin before degenerating to uncover a branching structure composed of keratin: a feather. Not only do the growing feathers co-opt existing skin layers and proteins, but even the genes needed are found in crocodiles, and so presumably were present in their shared archosaurian ancestors. Only the developmental programmes changed. The close embryological relationship between feathers and scales is betrayed by the (very) odd mutation that causes scales to erupt into feathers, which sprout from the legs of birds. Nobody has found a feathered crocodile yet, though.

From this perspective, prototype feathers are virtually bursting to get out of the skin of even the earliest archosaurs, so it's little surprise that theropods began sprouting 'epidermal appendages', probably ranging from bristles (like those of pterosaurs) to simple branching structures, akin to downy feathers. But what were they used for, if not flight? There are many plausible answers, by no means mutually exclusive, including sexual display, sensory functions, protection (barbs magnify size as well as potentially pricking like a porcupine) and, of course, insulation. The riot of feathered theropods certainly raises the possibility that they were hot-blooded, as their living relatives the birds.

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Other evidence, too, squares with the idea of theropods as an active group of dinosaurs, at least implying that they had stamina. One feature is the heart. Unlike lizards and most other reptiles, crocodilians and birds all have powerful hearts with four chambers. Presumably, then, the four-chambered heart

was a trait inherited by all archosaurs, and therefore the dinosaurs too. A four-chambered heart is significant because it splits the circulatory system in two. Half supplies the lungs, the other half the rest of the body. This offers two important advantages. First, blood can be pumped at high pressure to the muscles, the brain, and so on, without damaging the delicate tissues of the lungs (leading to pulmonary oedema and probable death). Plainly, a higher blood pressure can support more activity, as well as far greater size. Large dinosaurs could never have pumped blood all the way up to their brains without the four-chambered heart. Second, splitting the circulatory system in half means there is no mixing of oxygenated with deoxygenated blood: oxygenated blood returns from the lungs and is immediately pumped at high pressure to the rest of the body, delivering maximal oxygen to the places of need. While the four-chambered heart doesn't necessarily imply hot blood (crocodiles are cold-blooded, after all), it's verging on the impossible to attain a high aerobic capacity without one.

The respiratory system of theropod dinosaurs also looks to have been similar to that of birds and could have supported high rates of activity. Bird lungs operate differently from our own, and are more efficient even at low altitudes. At high altitudes the difference is breathtaking. Birds can extract two or three times as much oxygen from rarefied air as mammals. That's why migrating geese can fly thousands of feet above the top of Everest, while mammals gasp for breath at much lower altitudes.

Our own lungs are built like a hollow tree, with air entering via the hollow trunk (the trachaea), and then following one of the branches (tracheoles) that lead into blind-ending twigs. The twigs don't end in sharp points, though, but in semi-inflatable balloons, the alveoli, which are riddled with tiny blood capillaries in their walls, the sites of gas exchange. Here the haemoglobin in the red blood cells gives up its carbon dioxide and picks up oxygen, before being spirited back off to the heart. The entire balloon system is inflated then deflated like bellows, through breathing, powered by muscles in the rib cage and diaphragm. The inescapable weakness is that the whole tree ends in dead spaces, where air barely mixes, just in the place fresh air is most needed. And even when fresh air does arrive, it has already mixed with the stale air on its way out.

Birds, in contrast, have a beautifully modified reptilian lung. The standard reptilian lung is a simple affair: just a big bag, really, divided by blade-like sheets of tissue, called septa, which partition the central cavity. Like the mammalian lung, the reptilian lung functions like bellows, either through expanding the rib cage, or, in the case of the crocodile, by way of a piston-like diaphragm attached to the liver and drawn back by muscles that fix on to the pubic bone. That makes the crocodile lung a bit like a syringe, where the diaphragm is equivalent to an airtight plunger that is drawn back to fill the lung. While this is quite a powerful method of breathing, the birds have gone even further and turned half of their bodies into a sophisticated one-way system of interconnecting air sacs. Rather than entering the lungs directly, air first flows into the air-sac system and eventually exits via the lungs, giving a continuous through-flow of air that eliminates the problem of dead space in our own blind-ending alveoli. Air flows past the septa (likewise refined in birds), during both inspiration and expiration, via the movement of lower ribs and the rear air-sac system – crucially, birds have no diaphragm. What's more, air flows one way, whereas blood flow is in the opposite direction, setting up a 'countercurrent' exchange that maximises gas transfer (see Fig. 8.1).[8]

The question that has divided the field in acrimony for decades is, what kind of lungs did the theropods have? Piston lungs, like crocodiles, or through-flow lungs, like birds? The air-sac system in birds invades not only the soft tissues of the abdomen and chest but also the bones, including the ribs and spine. It has long been known that the theropods have hollows in their bones in the same places as birds. The incendiary palaeontologist Robert Bakker used this finding, among others, to reconstruct dinosaurs as active hot-blooded animals in the 1970s, a revolutionary view that inspired Michael Crichton's book, and later the film, *Jurassic Park*. John Ruben and colleagues, though, reconstructed theropod lungs differently, much closer to crocodiles, with a piston diaphragm arguably identifiable in one or two fossils. Ruben doesn't deny the existence of air pockets in theropod bones, just their purpose. They were not there to provide ventilation, he said, but for other reasons: to reduce weight or aid balance in bipedal animals, perhaps. The dispute grumbled on, incapable of proper resolution without new data, until the publication of a landmark paper in *Nature*, in 2005, by Patrick O'Connor and Leon
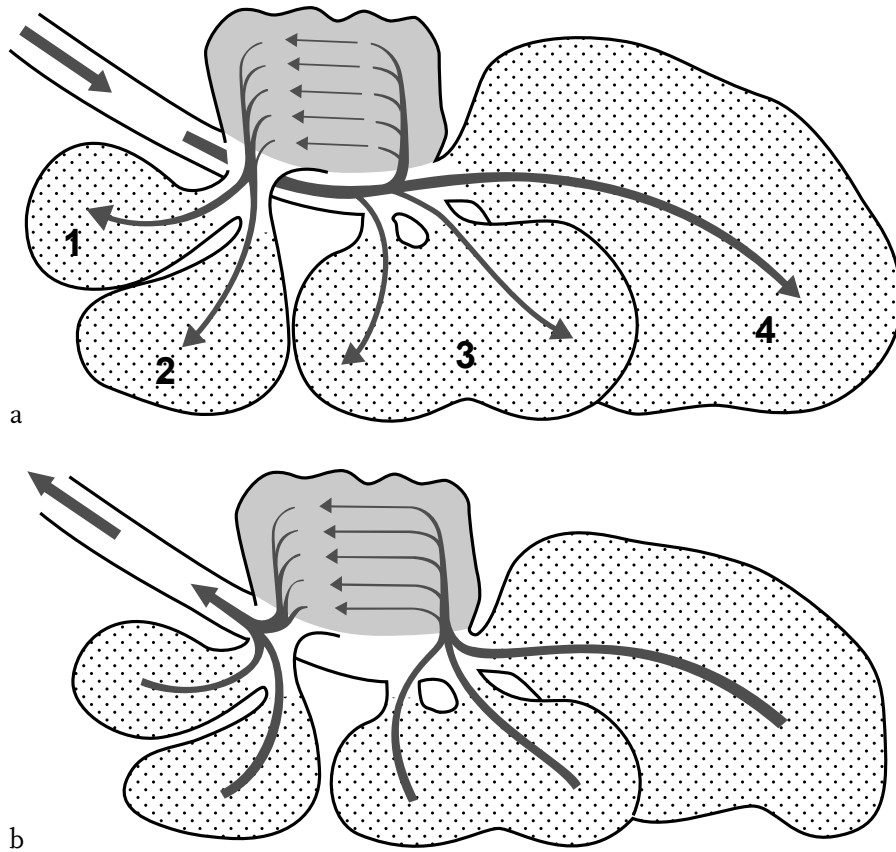
Figure 8.1 Air flow through bird lungs during (a) inspiration and (b) expiration. 1: clavicular air sac; 2: cranial thoracic air sac; 3: caudal thoracic air sac; 4: abdominal air sac. Air flows continuously in the same direction through the lung, while blood flows the other way, giving a highly efficient counter-current exchange of gases.

Claessens, then at Ohio University and Harvard, respectively.

O'Connor and Claessens started out conducting a thorough examination of the air-sac systems of several hundred living birds (or rather, as they said, 'salvage specimens' taken from wildlife rehabilitators and museums). They injected the air sacs of these birds with latex, to get a better sense of pulmonary anatomy. Their first realisation was that the system is even more pervasive than they had appreciated, occupying not only parts of the neck and

chest, but also much of the abdominal cavity, from where it invades the lower spine, a detail that was critical to interpreting the skeletal anatomy of theropods. This rear (caudal) air sac is the real driving force behind the whole pulmonary system of birds. During breathing, it becomes compressed, squeezing air into the lungs from behind. On expanding again, the caudal air sac sucks in air from the connecting air sacs in the chest and neck. In the lingo, it's an *aspiration pump*. It works a bit like bagpipes, in which pumping the bag streams a continuous airflow through the chanter.

O'Connor and Claessens went on to apply their findings to the bone structure of fossil theropods, including a superb skeleton of *Majungatholus atopus*, a theropod only distantly related to birds. While most studies have focused on the bone structure of the upper vertebrae and the ribs, they looked for hollows in the lower spine, as evidence of abdominal air sacs in theropods, and duly found them, in exactly the same place as in birds. Not only that, but the anatomy of the spine, rib cage and sternum met the specifications of an aspiration pump: the greater flexibility of the lower ribs and sternum allows compression of a caudal air sac, able to ventilate the lungs from behind as in birds. All in all, there can be little doubt that the theropod dinosaurs really did have an aspiration pump like that of birds – the most efficient system of breathing in all vertebrates (see Fig. 8.2).

So theropods had feathers, four-chambered hearts and air sacs coupled to through-flow lungs, all of which suggest they lived active lives, requiring stamina. But did their stamina lead inevitably to proper hot blood, as argued by the aerobic capacity hypothesis, or were they a halfway house, intermediate between modern crocodiles and birds? While their feathers suggest insulation, and so hot blood, they could have served other purposes instead; and further evidence, including the respiratory turbinates, is more ambiguous.[9]

Birds, like mammals, mostly possess respiratory turbinates, yet they are not composed of bone like the mammalian variety, but cartilage, which does not preserve well. Thus far, there's been no sign of turbinates in theropods, though few fossils are well enough preserved to judge. More tellingly, however, John Ruben notes that the turbinates in birds are invariably associated with enlarged nasal passages. Presumably, the delicate scrollwork of turbinates impedes airflow to a degree, which can be offset by enlarging the
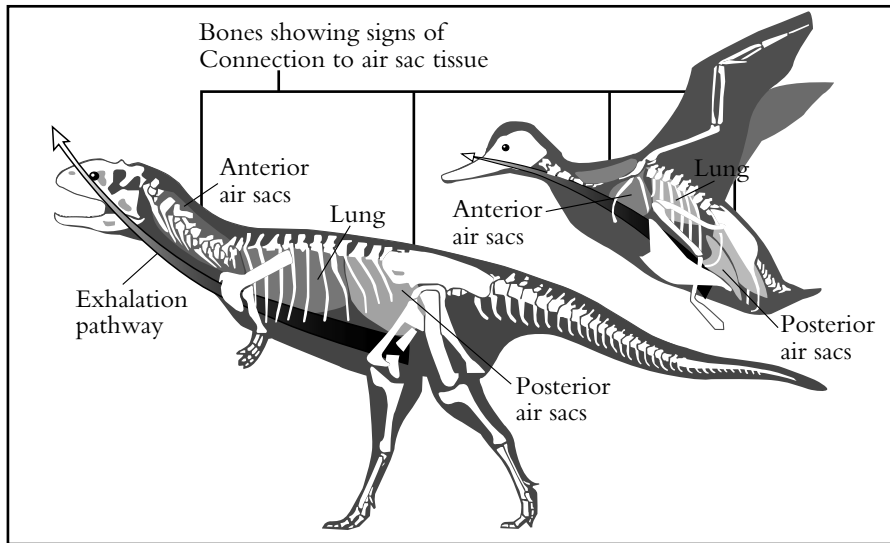
Figure 8.2 Reconstruction of the air-sac system in a dinosaur like *Majungatholus atopus* compared with modern birds. In both cases, the lung is supported by anterior and posterior air-sacs, the traces of which are exactly analogous to birds in dinosaur bones. The air-sacs work like bellows to move air through the rigid lung.

passages. But the theropods don't have especially large nasal passages, and that implies that the apparent absence of turbinates is real, not merely a preservation artefact. If they didn't have turbinates, could they have been hot-blooded? Well, we don't have turbinates, and we are hot-blooded, so the answer technically is yes; but it does raise some questions.

Ruben himself believes that theropods *did* have high aerobic capacity, but not hot blood, despite his own aerobic capacity hypothesis stipulating that the two must be linked. And while we don't yet know enough to say for sure, the consensus position, insofar as there is one, is that theropods probably had a raised resting metabolism, but not yet true hot blood. That at least is the story of the fossils, but there is more in the rocks than fossils, including a record of ancient climates and atmospheres. And there was something about the air in the Triassic that places quite a different spin on the fossil record. It helps to explain not only the high aerobic capacity of cynodonts and theropods, but also why the dinosaurs sprang to dominance.

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Most discussions of physiology take place in a historical void: an unspoken assumption that the past was the same as the present, selection pressures as unchanging as gravity. But they are not, as the great extinctions attest. And the greatest of all extinctions came at the end of the Permian age, some 250 million years ago, the immediate curtain-raiser to the irresistible rise and rise of the ruling lizards and the ensuing age of the dinosaurs.

The Permian extinction is often regarded as one of life's great mysteries – apart from anything else, that helps attract grant monies – but the environmental background has been sketched out in broad brushstroke. It was not, in fact, one mass extinction, but two, separated by nearly 10 million years, an age of desperate decline. Both extinctions corresponded in time to prolonged volcanic unrest, the most extensive outpourings of lava in the history of the earth, burying vast areas, almost continental, beneath deep basalt. The lava flows eroded to form a stepped terrain known as 'traps'. The first of the volcanic episodes forged the Emeishan traps in China, around 260 million years ago, followed 8 million years later by a second, even greater outpouring, that produced the Siberian traps. Critically, both the Emeishan and Siberian volcanic flows erupted through strata containing carbonate rocks and coal. That's significant because the intensely hot lava reacts with carbon to release massive quantities of carbon dioxide and methane, each and every eruption for thousands of years.[10] And that changed the climate.

There have been lots of attempts to oust the killer behind the Permian extinctions, with strong cases made for global warming, ozone depletion, methane release, carbon dioxide suffocation, oxygen deprivation, hydrogen sulphide poisoning, and so on. The only case more or less ruled out is meteorite impact; there's little evidence of an impact like the one that finally brought the curtains down on the long reign of the dinosaurs, nearly 200 million years later. All the rest of the list, though, are more than plausible, and the big advance in the last few years has been the recognition that all of them are intimately and irrevocably linked. Any volcanic episode on the scale of the Emeishan traps sets in motion a train of circumstances that unfurls with inexorable momentum, a progression to chill the heart. Similar trains of

interdependence threaten our own world today, though not, as yet, in a way that begins to compare.

The volcanoes belched methane and carbon dioxide high into the stratosphere, along with other noxious gases, which damaged the ozone layer and ultimately warmed and dried the world. The arid lands spread across the vast continent of Pangaea. The great coal swamps of the preceding periods, the Carboniferous and Permian, dried out, and began to blow in the winds, their carbon consumed by oxygen, drawing down the vitality of the very air. Over 10 million years, oxygen levels plunged, a crash in slow motion, from 30 per cent, to a trough below 15 per cent. The combination of warming waters (limiting the solubility of oxygen), falling atmospheric oxygen, and high carbon dioxide choked life from the seas. Only bacteria thrived, a poisonous sort that once dominated our planet in the age before plants and animals, spewing out the toxic gas hydrogen sulphide in oceanic quantities. The seas turned black and lifeless. Gas belching from the deadening oceans corrupted the air still further, suffocating animals on the shores. And then, only then, came the final hammer blows of fate, the eruption of the great Siberian traps, a death-knell striking once and again over 5 million years. For those 5 million years or more, little stirred in the seas or on land; and then began the first glimmers of recovery.

Who survived? The answer, curiously, is much the same at sea as on land: those that were the best at breathing, those that could cope with low oxygen, high carbon dioxide, and a nasty mix of noxious gases. Those that were equipped to gasp for breath and yet still remain active, those that lived in holes, in burrows, in slime, in bogs, in sediments, those that scavenged their living in places where nothing else wanted to be. A thousand thousand slimy things lived on, and so did we. And that's why it's significant that the first land animals to recover after that great dying were the lystrosaurs, those burrowers with barrel chests, muscular diaphragm, bony palate, widened air passages and respiratory turbinates. They emerged, panting, from their rancid burrows, and colonised the empty continents like squirrels.

This amazing story, written in the chemistry of the rocks, goes on for millions of years – it was the stamp of the Triassic age. The toxic gases disappeared, but carbon dioxide soared, ten times higher than today. Oxygen

remained stubbornly below 15 per cent, the climate endlessly arid. Even at sea level, animals gasped for oxygen, a mouthful of air as thin there as at high altitudes today. This was the world of the first dinosaurs, hauling themselves on to their hind legs, freeing their lungs from the constraints of sprawling lizards that can't walk and breathe at once. Couple that with air sacs and an aspiration pump, and the rise of the dinosaurs begins to look inevitable, a story plotted out in convincing detail in an important book, *Out of Thin Air*, by palaeontologist Peter Ward, at the University of Washington. Archosaurs displaced cynodonts, says Ward (and I believe him), because the septate lung held within it the secret of success, an unknowable, latent ability to transform into the wonderful through-flow lungs of birds. The theropods were the only animals alive that didn't need to pant all the time. They had little need for turbinates.

And so stamina was no added extra, but a lifesaver, a ticket with the winning number to survive through terrible times. But this is where I part company with Ward, reluctantly. I agree that high aerobic capacity must have been critical to survival, but would it really have dragged up resting metabolic rate too? Ward implies this (by citing the aerobic capacity hypothesis), but that's not what happens today when animals live at high altitude. On the contrary, muscle mass tends to fall and wiry builds win. Aerobic capacity might be high, but resting metabolic rate does not rise in synchrony; if anything, it falls. Physiology in general is parsimonious in hard times, not profligate.

Back in the Triassic, with survival at a premium, did animals really raise their resting metabolic rate unnecessarily? That sounds counterintuitive at the least. The theropods seem to have raised their aerobic capacity without needing to become fully hot-blooded, at least at first. And yet the vanquished cynodonts apparently did become hot-blooded. Did they do it to compete, with little hope of success, against the formidable archosaurs? Or did it help them to remain active as they shrank down in size and took to the nights? Both are perfectly credible possibilities, but there's another answer I like even better, an answer that may shed some light on why the dinosaurs did precisely the reverse, burgeoning into giants the like of which the world has never seen again.

<p style="text-align:center">✴</p>

Vegetarians, in my experience, have a bad tendency to be holier than me; or perhaps it's just my carnivorous sense of guilt. But according to a quietly significant paper that slipped into a quietly obscure journal, *Ecology Letters*, in 2008, the vegetarians may have a lot more to be smug about than I've given them credit for. If it weren't for vegetarians, or rather their ancestral herbivores, we may never have evolved hot blood, and the fast pace of life that goes with it. The paper is by Marcel Klaassen and Bart Nolet at the Netherlands Institute of Ecology and it takes a splendidly numerate (technically 'stoichiometric') line on the difference between meat and greens.

Say the word 'protein' and most people think about a mouth-watering steak; and there is indeed a very strong connection in the mind, arising no doubt from our endless cookery shows and dieting manuals, between proteins and meat. Eat meat for proteins, and if you're a vegetarian make sure you eat plenty of nuts, seeds and pulses. Vegetarians, by and large, are more aware of dietary composition than meat-eaters. We need to eat proteins to ensure that we get enough nitrogen in our diet, which is needed for making fresh proteins for ourselves, as well as DNA, both rich in nitrogen. We actually have very little problem maintaining a balanced diet, even if we're vegetarian, but then we are hot-blooded: we eat a lot, by definition. Klaassen and Nolet point out that this is not at all true for cold-blooded animals. They don't eat a lot, by definition, and that gives them an interesting problem.

Very few contemporary lizards are herbivores, and of all the 2,700 species of snake not a single one is herbivorous. Of course, some lizards are herbivores, but they tend to be either relatively large, like iguanas, or given to greater activity, and higher body temperatures, than carnivorous lizards. Unlike the meat-eaters, which are quick to lower their body temperature and slump into a dormant state if need be, herbivorous lizards are far less flexible and have to soldier on. This has traditionally been ascribed to the difficulties of digesting plant materials, achieved with the aid of gut microbes able to ferment obstinate plant material, a process that works much better at higher temperatures. According to Klaassen and Nolet, though, there may be another reason, relating to the nitrogen content of typical plant matter. They

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performed an inventory of dietary nitrogen and confirmed that herbivorous lizards do indeed have a serious problem.

Imagine eating only greens, lacking in nitrogen. How can you get enough nitrogen in your diet? Well you could try to eat more widely, scavenge a little, eat seeds, and so on, but even then you will probably fall short. Or you could simply eat more. If you consume only, say, a fifth of your daily nitrogen needs by eating a bucket of leaves, then all you need to do is eat five buckets. If you do that you'll be left with a surplus of carbon, which plant matter is rich in, and you'll need to get rid of it somehow. How? Just burn it, say Klaassen and Nolet. A strictly herbivorous diet is perfectly attainable for hot-blooded animals, because we burn off bucket-loads of carbon all the time; but it's always problematic for cold-blooded animals. And in this context we might do well to look again at the lystrosaurs, which were herbivores, and the cynodonts, which were a mixture of herbivores and carnivores. Might it be that hot blood evolved in the cynodonts because they had a high aerobic capacity, a prerequisite of survival in those thin times, coupled with a diet rich in greens? Once hot blood had evolved in these early herbivores, they might easily have taken advantage of the extra energy to recover quickly, to roam for miles over the arid Triassic lands in search of food or in flight from predators. Predators had less of a dietary need for hot blood, perhaps, but they had to compete with those turbocharged herbivores on equal terms. Perhaps they needed hot blood just to keep up with the flight of the vegetarian Red Queen.

But what of the colossal dinosaurs, the most famous herbivores in history? Did they follow an alternative strategy to attain the same ends? If you eat five buckets of leaves but don't burn it off constantly, you could simply store it somewhere: get bigger, become a giant! Not only do giants have more 'storage capacity', they also invariably have a lower metabolic rate, which equates to a slower turnover of proteins and DNA, lowering the dietary need for nitrogen. So there are two plausible ways of coping with a diet rich in greens: larger size coupled with slower metabolism, or smaller size coupled with faster metabolism. It's revealing that these are exactly the strategies adopted by herbivorous lizards today, although they may be precluded from attaining a true hot-blooded state by their inherently low aerobic capacity. (How these lizards survived the Permian extinction is another question for another place.)

But why, then, did the dinosaurs get so big? The question has never been answered pleasingly despite many attempts. According to a throwaway line in a 2001 paper by Jared Diamond and his colleagues, the answer might conceivably lie in the high carbon dioxide levels at the time, which probably induced greater primary productivity, that is, faster plant growth. What Diamond's insight lacked, though, was the perspective on nitrogen provided by Klaassen and Nolet. High carbon dioxide levels do indeed induce greater productivity, but they also lower the nitrogen content of plant matter, a field of research that has grown up around concerns about the effect that rising carbon dioxide levels, in our own age, might have on feeding the planet. And so the problem facing the cynodonts and the dinosaurs was even more acute then than it is today: to get enough nitrogen in their diet, they needed even more greens. Strict vegetarians would have needed to eat gargantuan quantities.

And perhaps this explains why the theropods didn't need hot blood. They were carnivores, and so didn't face a nitrogen-balance problem. But unlike panting cynodonts, obliged to compete on equal terms with turbocharged herbivores, the theropods were above all that. They had super-efficient aspiration-pump lungs and they could catch anything that moved.

It wasn't until later, in the Cretaceous era, that the odd raptor turned to vegetarianism. And one of the first, as it happens, was a maniraptoran called *Falcarius utahensis*, described formally in *Nature* in 2005 by a team from Utah and informally by one of the authors, Lindsay Zanno, as 'the ultimate in bizarre, a cross between an ostrich, a gorilla and Edward Scissorhands'. But it was a *bona fide* missing link – half raptor, half herbivore – and lived around the time of the first tasty flowering plants, a time of unprecedented enticement to a vegetarian way of life. But from our point of view in this chapter, perhaps the most significant fact about *Falcarius* is that it was part of a group, the maniraptorans, from which birds are thought to have evolved. Could it be that the evolution of hot blood in birds, too, was linked with a shift in diet to vegetarianism, and so a greater dietary need for nitrogen? It's not totally implausible.

This chapter is closing on a speculative note. But speculation is easily dressed up as hypothesis, once described by Peter Medawar as an imaginative leap into the unknown; and that is the basis of all good science. There is much

here that remains to be examined or tested, but if we want to unravel the reasons for our fast-paced way of life, we may need to look beyond the principles of physiology, and into the story of life itself – to a time in the history of our planet when extreme circumstances played a magnified role. Perhaps this is history, more than science, in that events didn't need to be so, they just happened that way. If the Permian extinction had never happened, or its prolonged low-oxygen aftermath, would high aerobic capacity ever have been a matter of life and death? Would life have bothered to go beyond the primitive reptilian lung? And if a few of these aerobically charged animals had not turned vegetarian, would hot blood exist? Perhaps this is history, but reading that remote past is a science in its own right, one that can only enrich our understanding of life.