THERMOREGULATION: DINOSAURS AND BEYOND

Thermoregulation

Ectotherms: obtain most of their heat from outside their body.
Endotherms: generate most of their heat internally.
Poikilotherms: allow their body temperature to vary widely.
Homeotherms: keep their body temperatures within a limited range.

Endotherms (mammals, birds) typically have metabolic rates 10x higher than Ectotherms (living amphibians and reptiles) of an equivalent size.
Endotherms consume 10x more food, and breathe in 10x more oxygen, than an equivalent sized ectotherm.
At present, animals with high metabolic rates (endotherms) also have body temperatures significantly higher than ambient temperatures (they are warm), and they don't let their body temperatures vary too much (they are homeotherms).

In contrast, animals with lower metabolic rates (ectotherms) have body temperatures not too much higher than ambient temperature (they are "cold"), and they let their body temperatures vary considerably (they are heterotherms).

Temperature Regulation in Modern Ectotherms

• Avoid climates where temperature vary widely or go outside the optimal range.
• Stay near water or near the equator (e.g., living amphibians)
• Behavioral thermoregulation: Use activity to control body temp.

Temperature Regulation in Modern Endotherms

• Turn up metabolic rate to keep the body uniformly warm.
• Insulate the body with hair, feathers or fat.
• Pant and sweat to cool off, shiver to keep warm.
• Use the ectotherm strategies as well.

Three Questions to consider:

Were dinosaurs ectotherms or endotherms?
Were dinosaurs homeotherms or poikilotherms?
Did dinosaurs have a high or a low metabolic rate?

I'll consider 10 different lines of evidence concerning dinosaur thermoregulation.
1) Dinosaurs had secondary palates.

The secondary palate separates allows the nasal openings to connect to the back of the throat, rather than dumping air from the nose directly into the front of the mouth.!
With a secondary palate, an animal can breathe and chew at the same time.!
Modern endotherms, that need lots of oxygen to run their high metabolic rates, all have secondary palates.!
This has led some to speculate that all animals with a secondary palate are endotherms.

Although all animals with a high metabolic rate probably require a secondary palate, but the converse does not apply.!
The ability to chew and breath simultaneously would probably benefit any organism that needs to keep its mouth shut for a long time while feeding.!

**Summary:** NO SUPPORT for warmth, a high metabolic rates, or homeothermy.

2) Erect Posture

Today, all endotherms have an upright posture.!
They position their legs under their bodies, rather than sprawled out to the side.!!
Some scientists have argued that an upright posture is a sign that the animal is an endotherm.!
As dinosaurs had upright posture, they have argued that dinosaurs were endotherms.!

*Why do endotherms have upright posture?*

Upright posture is necessary for an animal to have **stamina** - the ability to conduct sustained aerobic exercise.
Mammals and birds are capable of sustained aerobic exercise.
Living reptiles and amphibians have a low capacity for sustained exercise.!
They use **Ambush Tactics** to get prey; move fast, but only in short bursts.!!

**Aerobic Respiration** involves complete combustion of food to carbon dioxide and water.!! It is an extremely efficient way to use fuel, but it requires oxygen.

**Anaerobic Metabolism** (fermentation) also produces heat and energy, BUT:
- It has a lower energy yield than aerobic respiration.
- It is accompanied by a build up of acids and alcohols, which impede muscle function.
- It leads to an oxygen debt, as acids and alcohols must ultimately be fully oxidized.

So, anaerobic metabolism can't be sustained, it is good for sprinting, but animals must eventually stop to get oxygen.
Living reptiles and amphibians use anaerobic metabolism to fuel burst activity.!!
Reptiles and amphibians seem to have a limited ability to obtain oxygen to fuel sustained aerobic activity.

What is the source of this limitation on oxygen supply?

Dave Carrier discovered that reptiles can't breathe and walk at the same time. In amphibian and reptiles, the body undergoes lateral flexing during locomotion. During this flexing on land, air is pumped from side-to-side (from lung-to-lung), rather than in and out. To breath, reptiles must stop, then use their rib musculature to expand/contract the entire rib cage.

Living reptiles and amphibians are operating under an Evolutionary Constraint - they use the same muscles, in antagonistic ways, for walking and breathing.

How have animals accommodated this constraint?

Amphibians: mostly aquatic, propulsion from tail, land beasts suffered.
Modern reptiles: move in bursts, fast recovery following anaerobic bursts.
Pelycosaur Solution: Stiff back bone, propel body with rear limbs and just use front limbs as props! Body didn't bend during locomotion.
Archosaur/Therapsid Solution: Erect Posture. Put the limbs under the body. Move limbs forward and backward. Flex body vertically rather not laterally.

What does any of this have to do with temperature regulation?

Erect posture would allow sustained maintenance of a high metabolic rate (i.e., endothermy). All living warm-blooded animals (mammals and birds) have an erect posture. But as with a secondary palate, erect posture does not obligate an animal to have a high metabolic rate, it only makes it possible.

Summary: NO SUPPORT for warmth, a high metabolic rates, or homeothermy.

3) Bone Structure: two key observations

Some dinosaurs had extensively remodeled bone. Many living endotherms exhibit a high degree of bone remodeling, whereas many living ectotherms deposit bones in concentric bands that are not subsequently remodeled! When this pattern was first noted, it was thought that endotherms remodeled their bones to exploit stored nutrients to fuel their high metabolic rates!
Some baby dinosaurs had woven "fast growth" bone. Endotherms have peculiar type of woven bone that is indicative of rapid growth. Rapid growth is only possible in warm animals, as cellular activity and enzyme function often go faster at higher temperatures.

Problems with Bone Data

Subsequent observations have shown that remodeling is not uniquely associated with high metabolic rate. Bones remodel in response to applied stress. If dinosaurs stressed their bones extensively, which is likely given the high loads their bones must bear, they should show remodeling no matter what their metabolic rate.

Summary: NO SUPPORT for warmth, a high metabolic rates, or homeothermy from bone remodeling.

However, there is no doubt that young dinosaurs had woven bone, indicating that they had high growth rates. If crocodile babies are raised in high temperature incubators, they will grow fast and exhibit woven bone.

Summary: STRONG SUPPORT that baby dinosaurs were warm.

4) Predator/Prey Ratios

Because of their high metabolic rates, endotherms need more food than similar sized ectotherms. If we compare biomass of predator to prey, we should find a higher percentage of predators, if the predator are ectotherms than if predators are endotherms.

Although we can't compare herbivore biomass to plant biomass, we can attempt to compare carnivore biomass to herbivore biomass, however.

- Modern soil litter communities: 25% predator/75% prey
- Modern grassland mammal communities: 1% predator/99% prey
- Permian Pelycosaurs communities: 25% predator/75% prey
- Permian Therapsid and Triassic Archosaur communities: 10% predators/90% prey
- Mesozoic Dinosaur and Cenozoic mammal communities: <5% predators/95% prey

These observations would suggest that dinosaur carnivores, like mammal carnivores of the Cenozoic, were endotherms.
Problems with the approach

It is difficult to figure who is eating whom.!
We tend to lose smaller animals from the fossil record. This is a bias against prey.
Most fossil beds are attritional accumulations, representing the bodies piled up on a
landscape due to death over 100s of years.!
This line of reasoning only works for standing biomass, what is out there on the
landscape for any instant in time.!
Attritional accumulations may not accurately reflect standing biomass.!

Summary: NO SUPPORT for warmth, a high metabolic rates, or homeothermy

5) Relatives and descendents of Dinosaurs are endotherms

Pterosaurs, the next of kin of dinosaurs, and birds, descendents of dinosaurs, were both endotherms.!
If we assume the evolution is parsimonious, then we should assume that archosaur endothermy arose one time, on the branch leading from the last common ancestor with crocodile-like archosaurs and the common ancestor of pterosaurs and dinosaurs.!

More specifically, some dinosaurs are very closely related to birds, and they are endotherms.

Summary: WEAK-MODERATE SUPPORT for warmth, a high metabolic rate, and homeothermy, particularly in Theropod dinosaurs.

6) Some dinosaurs had feathers

In addition to their function in flight, feathers also serve as insulation for birds, holding in body heat.!
The presence of feathers in dinosaurs that clearly could not fly suggests that they were trying to control heat loss.

Summary: STRONG SUPPORT for warmth and a high metabolic rate in dinosaurs with feathers (only small theropods are known to have been feathered at this point).

7) Inertial Heating and Homeothermy

Dinosaurs had a large body volume, from which they generated heat, relative to the area of their skin, through which they lost heat.!
As a consequence, large dinosaurs should have heated up and cooled down very slowly, with body core temperatures only changing 1 to 2°C throughout the day.
A low surface-to-volume ratio also impedes heat loss, such that big dinosaurs would have been warmer than ambient temperatures, even if they had reptilian metabolic rates, even if we ignore the heat produced by veggies and food fermenting in the gut, which can be substantial.

**Temperature difference between the body and air for dinosaurs at four body sizes**

<table>
<thead>
<tr>
<th></th>
<th>50 kg</th>
<th>500kg</th>
<th>5t</th>
<th>50t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reptile Metabolism</td>
<td>0.2-0.4°C</td>
<td>0.7-1.4°C</td>
<td>2-4°C</td>
<td>6-13°C</td>
</tr>
<tr>
<td>Mammal Metabolism</td>
<td>3-5°C</td>
<td>7-15°C</td>
<td>20-50°C</td>
<td>60-140°C</td>
</tr>
</tbody>
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So, big dinosaurs would have been warm and homeothermic just because of size. A slight increase in metabolic rate would allow them to maintain temperature well above ambient.

If big dinosaurs had mammalian or avian metabolic rates, however, they would have boiled!

**Summary**: STRONG SUPPORT for warmth and homeothermy coupled with a low metabolic rate in large dinosaurs

8) **Oxygen isotope thermometer?**

The $^{18}$O to $^{16}$O ratio of a mineral, such as apatite in bones and teeth, is determined by the isotopic composition of the water from which it forms and by the temperature at which it forms.

Reese Barrick and Bill Showers have attempted to take the "temperature" of different bones from dinosaur bodies.

They assume that the water in a single individual will be the throughout the body (a fair assumption).

If they get the similar oxygen isotope ratios in different body parts, then these parts probably formed at the same temperature (i.e., the animal was a homeotherm).

If they get different oxygen isotope ratios in different bones, the animal was a heterotherm.

Because, today, all strongly homeothermic animals are also endotherms, they argue that demonstration of homeothermy would also imply that the animal was an endotherm.

**Observations**:  

They've examined big theropods, big ornithopods, and baby ornithopods, and in all cases, have found little evidence for temperature variations among skeletal parts.

They have argued that all these animals were homeotherms.
Problems with approach:

Animal body temperatures may not vary because animals live in places where the ambient temperature is invariant. It's hard to know what Mesozoic climates were like, but all available evidence suggests the climate was much more moderate, with reduced seasonal temperature extremes and overall higher mean annual temperatures. Also, as noted above, large size may render big animals functional homeotherm despite the fact that they have a low metabolic rate.

Summary: MODERATE SUPPORT for homeothermy in adult theropods and ornithopods and baby ornithopods.

9) Nasal Volume

Animals with high metabolic rates breathe in and out 10x as much as ectotherms with low metabolic rates. As a consequence, they must modify their nasal regions to warm the air on the intake and prevent water loss on exhalation. Mammals and birds do this by expanding the nasal region above the secondary palate, and filling it with fine bones that are covered with highly vascularized tissue.

If we take the cross-sectional area of the nasal volume in the snouts of modern endotherms, we discover that it is 10x larger than the area in an equivalent sized ectotherm. In the end, this is a simple reflection of the difference in metabolic rates between these types of organisms.

John Ruben and his colleagues at Oregon State University have analyzed the snout areas of several different types of dinosaurs, including small theropods. They discovered that these dinosaurs fall on the ECTOTHERM nose area line. They don't seem to have noses modified for the high ventilation rates required by endothermy.

Problems with the method:

The only way this type analysis might fail is if dinosaurs had some other system for recapturing water and warming air, perhaps using regions in their throats rather than regions in their nose.
10) Four Chambered Heart

Mammals and birds have a four-chambered heart, so that they can effectively segregate
highly-oxygenated blood arriving from the lungs from poorly-oxygenated venous blood
arriving from the rest of the body.!
Ectothermic animals, that have lower oxygen utilization rates, lack such complicated and
efficient systems for pumping blood.!
Recently, a group of workers, including Barrick and Showers, have discovered the
fossilized remains of a heart inside the chest of an ornithopod dinosaur.!
They used CAT scans to demonstrate that the heart had four-chambers.!
They conclude that the animal was an endotherm.

*Problems with the method:*
All endotherm may have a four-chambered heart, but the converse need not be true.

**BOTTOM LINE ON DINOSAURS**

**Dinosaur babies** were warm and homeothermic (3,8).!
Since they had no inertial heating (7), they probably achieved this state with a high metabolic rate, though we can't
completely rule out that they lived in warm climates.

**Small theropod dinosaurs** were warm (5,6).!
Since they had no inertial heating (7), they too probably had high metabolic rates, though
their low nasal volume (10) is a problem that must ultimately be addressed.

**Large theropods** were homeotherms, either by inertia or a high metabolic rate.

**Large sauropods and ornithopods** were almost certainly warm and homeothermic, but
with arelatively low metabolic rates (7).!
As they grew from babies to adults, they slowed down their metabolic rate.
!
!
**What about the organisms we've considered?**

**Ancient Amphibians:** live near equator or water, certainly ectotherms.

**Pelycosaurs:** near equator or water, very likely ectotherms.
Some suggestion of problems with heat (e.g., sail may be used to pick up or shed heat
rapidly from large body).

**Therapsids:** secondary palate and upright posture suggest greater stamina.!
Live far from equator.!
On the way to higher metabolic rates?