Mammal body size and heart energy efficiency: An inverse relationship

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A groundbreaking study undertaken by researchers from the University of Pretoria's (UP) Faculty of Veterinary Science has revealed that the heart operates with declining energy efficiency as body size increases among mammals.

This means that larger mammals have hearts that lose relatively more energy as heat, rather than directing that energy to the blood so that it circulates around the body. A tiny shrew, therefore, has a more efficient heart than that of a large elephant. The implication is that eventually an upper limit on body size will be reached, where the heart is so inefficient at pumping blood, that it is no longer viable to do so. A gigantic 100-tonne sauropod, or any large-sized member of the dinosaur group Sauropoda, may represent this upper limit on body size.

The UP-led study, which was published today in the *Proceedings of the Royal Society B*, was conducted in collaboration with scientists from the University of Adelaide and Monash University in Australia, and the University of British Columbia in Canada.

The researchers assessed the hearts of mammals across a broad range of body size – from a shrew to an elephant, as well as many species in between – and realised they could use the relative densities of capillaries and mitochondria in the walls of the heart to determine the metabolic power of the cardiac tissue. "Capillaries and mitochondria are important because they are involved in the supply and consumption of fuel and oxygen that generate the energy the heart needs to pump blood around the body," Dr Ned Snelling, experimental physiologist at UP, explains.

The researchers found that the densities of the capillaries and mitochondria in the walls of the heart decrease in larger mammals. Dr Snelling explains that this was expected because heart rate also decreases with body size. "A large elephant may have a heart rate of about 30 beats per minute, but a tiny shrew can have a heart rate of well over 1 000 beats per minute!"

The scientists then compared the metabolic power of the heart against its mechanical power, which is measured as the energy imparted to the blood as it is pushed through the major vessels. They were surprised to discover a mismatch between the heart's metabolic power and its mechanical power. Because this mismatch increases with body size, it means the heart appears to operate with a declining efficiency in larger mammals than in smaller ones.

The implication is that as mammals increase in body size, they appear to be investing disproportionately more metabolic power into the heart, relative to the mechanical power imparted to the blood exiting the heart. "In terms of energy, larger mammals put more in, but get less out," Dr Snelling says. In larger mammals, the heart appears to become less efficient at using energy in the fuel delivered to the cells of the heart (primarily fatty acids) and converting it into energy in the blood exiting the heart (primarily blood pressure). In other words, the heart becomes less "energy efficient" in larger mammals with larger hearts.

"The heart is a bit like the motor in a car: it uses fuel and oxygen to make it run and do work for us, but a lot of that energy is wasted as heat, and it does no work for us," Dr Snelling explains. "Just like larger motors in larger cars appear less efficient, so too do larger hearts in larger mammals."

The researchers wanted to put more precise values on this decline in energy efficiency. By taking known values from humans, they showed that across the body size range of their data, the efficiency of the heart decreases from 44% in a 2g shrew to 19% in a six-tonne elephant. "By cautious extrapolation, we can estimate that a sauropod, weighing 100 tonnes or more, would have operated a heart with an efficiency in the region of only 15 to 17%," Dr Snelling says. This means that of all the energy used by the heart, only this small percentage is imparted to the blood so that it flows around the body. The rest is lost as heat.

The scientists do not know at what body size the efficiency of the heart might become so poor that it is no longer viable. They suggest that because of the complexity with which animals interact with their environment, there is unlikely to be an exact cut-off body weight, but rather a broad body weight range where the benefits of being big no longer pay off. That range probably overlaps to include the 100-tonne body size of the gigantic sauropods.

Dr Snelling says that for centuries, scientists and philosophers have been debating the maximum possible size of animals. "In the 1600s, Galileo Galilei argued that the 100-tonne blue whale could reach its size only because it is supported by water. But in the early 1900s, doubt was cast on this idea after palaeontologists unearthed a gigantic sauropod dinosaur, the 70-tonne *Brachiosaurus*. More recently, parts of other colossal sauropods have been uncovered, and some estimates place these species in the vicinity of 70 to 100 tonnes."

The traditional theory has been that 100 tonnes must be close to the maximum size that is physically possible, at least for land animals, because larger weights could not be supported by the strength of the bones and the forces of the muscles. "In effect, larger animals would be crushed by their own body weight," Dr Snelling adds. "Therefore, it is likely that gigantic sauropods were so restricted by their own weight that they struggled to move and could walk only at a slow, lumbering pace. But when you're this big, who is going to chase you? The disproportionate burden of gravity on larger animals is evident even today – it explains how a mouse can gallop, leap and jump, whereas an elephant can do none of these things."

The new research offers an alternative possibility: that it is declining energy efficiency of the heart that imposes an upper limit on body size.

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