Opinion piece

Raising the sauropod neck: it costs more to get less

The long necks of gigantic sauropod dinosaurs are commonly assumed to have been used for high browsing to obtain enough food. However, this analysis questions whether such a posture was reasonable from the standpoint of energetics. The energy cost of circulating the blood can be estimated accurately from two physiological axioms that relate metabolic rate, blood flow rate and arterial blood pressure: (i) metabolic rate is proportional to blood flow rate and (ii) cardiac work rate is proportional to the product of blood flow rate and blood pressure. The analysis shows that it would have required the animal to expend approximately half of its energy intake just to circulate the blood, primarily because a vertical neck would have required a high systemic arterial blood pressure. It is therefore energetically more feasible to have used a more or less horizontal neck to enable wide browsing while keeping blood pressure low.

Keywords: dinosaur; sauropod; blood pressure; circulation; neck; feeding height

Sauropod dinosaurs continue to arouse the interest of biologists, primarily because of their enormous size and exceptionally long necks. Recent work has revealed that they were fast-growing animals with elaborate lung structure—characteristics associated with high metabolic rates (Sander & Clauss 2008) and consistent with evidence for endothermy in basal archosaurs and dinosaurs (Seymour *et al.* 2004). A high demand for food and the long necks have reasonably prompted many palaeontologists to assume that at least some species browsed in tall trees, as the Mesozoic analogues of giraffes. The necks of certain species were exceptionally long, for example, in excess of 9 m in *Mamenchisaurus*, and, when rearing, the head would have been more than 11 m above the heart (McIntosh *et al.* 1997). Recent reconstructions of *Barosaurus* in the American Museum of Natural History in New York and *Brachiosaurus* in the Museum for Natural History in Berlin have placed the head approximately 9 m above where the heart must have been, in the body cavity near the lungs. Each metre is equivalent to 78 mm Hg blood pressure, because the densities of blood and mercury are 1.055 and 13.534 g cm⁻³, respectively. Thus the static blood column alone would produce 700 mm Hg at heart level. To induce flow, it is reasonable to add perhaps 50 mm Hg, giving a mean systemic arterial blood pressure of 750 mm Hg. The immense physiological problems

associated with such hypertension, including high perfusion pressure throughout the body (Hohnke 1973) and excessively large, strong or thick hearts (Seymour 1976), have been proposed. Despite attempts to invent auxiliary hearts in the neck (Bakker 1978; Choy & Altman 1992) or the siphon principle (Hicks & Badeer 1992; Badeer & Hicks 1996) to avoid the problem, it remains highly doubtful that such structures could have evolved or even functioned (Millard *et al.* 1992; Seymour & Lillywhite 2000).

With measurements of the range of tensions exerted by real cardiac muscle (Seymour & Blaylock 2000), it was estimated that a heart weighing 5 per cent of the body weight was necessary to produce 700 mm Hg arterial blood pressure below an upright *Barosaurus* neck (Seymour & Lillywhite 2000). According to the law of Laplace (Mirsky 1974), this heart would have had walls five times thicker, and 15 times heavier, than expected for a similarly sized animal that produced only 100 mm Hg. Aside from the space problems and mechanical disadvantages of such a grossly thick heart, the energy requirements would have been enormous. However, the magnitude of this energy cost has not been appreciated.

The present approach to the problem does not rely on the knowledge of heart size or strength, but involves an estimate of the energy cost of the heart, based on two axiomatic relationships between metabolic rate, blood flow rate and blood pressure. First, the Fick principle states that an animal's rate of oxygen consumption (aerobic metabolic rate) is equal to the rate of blood flow (cardiac output) from the left ventricle multiplied by the difference in oxygen content between the arterial and venous blood (Ruch & Patton 1974). Because oxygen content differences are similar in mammals regardless of size, metabolic rate is proportional to blood flow rate (Calder 1996). Second, it is well established that the rate of work done by the left ventricle is proportional to the product of blood flow rate and mean arterial blood pressure (Li 2000). It follows that the energy demand by the heart is a constant proportion of metabolic rate, if the blood pressure is constant.

Cardiac work rate averages approximately 10 per cent of the metabolic rate in small mammals that have a mean arterial blood pressure of approximately 100 mm Hg, but there is an indication that the percentage increases in larger species (Loiselle & Gibbs 1979; Wang *et al.* 2001). One reason for the increase is that blood pressure increases according to the vertical distance above the heart in mammals, because the heart must not only circulate the blood, but also support the column of blood above it (Seymour & Blaylock 2000). Although cardiac work rate has not been measured in adult giraffes, it is expected to be approximately 18 per cent of the metabolic rate, because its blood pressure is approximately two times higher than the mammalian mean (Goetz *et al.* 1960; Van Citters *et al.* 1966) and its myocardium is at least two times thicker (Goetz & Keen 1957).

Thus an animal that must produce 750 mm Hg would be expected to show a cardiac work rate some 7.5 times higher than the one that produced 100 mm Hg (figure 1). A sauropod with its head in the trees would therefore have to increase its

Figure 1. A model of the energy cost of the circulatory systems of sauropod dinosaurs in relation to the metabolic cost of maintaining the body alone. The assumptions of the model are that total basal metabolic rate in an animal is equivalent to $\text{watts} = 3.6 \text{ mass}^{0.71}$, an allometric relationship derived from mammals (White *et al.* in press). The heart consumes 10%, and the body 90%, of the total metabolic rate, if the blood pressure is 100 mm Hg. A blood pressure of 750 mm Hg causes the circulatory cost to equal approximately that of the rest of the body. Because circulatory work is a constant proportion of metabolic rate at a given blood pressure, assuming a lower metabolic rate of an ectotherm or a higher rate of an active animal in the field has no effect other than to change the scale of the y-axis.

Figure 2. Model of the effects of raising the neck on the arterial blood pressure at the heart and the potential volume of food available to a stationary sauropod. Blood pressure is assumed to be regulated at 100 mm Hg when the neck is horizontal or lowered. Raising the head above horizontal increases central blood pressure according to the density of blood and the vertical distance above the chest region. The feeding volume increments are the volumes of the 'spherical segments', i.e. stacked slices of the sphere enclosed by horizontal planes arbitrarily set 1 m apart. The radius of the sphere is assumed to be 9 m (the distance from the heart to the head), and the heart is placed 3 m above the ground. The graph is illustrative of the diminishing returns from lifting the head; it is not assumed that the entire volume of each segment is available for feeding, but only an arbitrary fraction of it.

metabolic rate to 175 per cent, and, at this level, expend 49 per cent of its total energy requirements just to circulate the blood. These percentages are independent of the amount of blood sent to the head,

because the single ventricle must perfuse the entire body at the high pressure determined by the neck. They are also independent of the metabolic rate, because the blood flow rate, the second component

of cardiac work rate, is proportional to the metabolic rate. So the relative increases would be the same, whether the animals were active or resting, or whether they had inherently high metabolic rates characteristic of 'warm-blooded' endotherms or 'cold-blooded' ectotherms.

Would the increased availability of food be worth the added cost of the circulation?

This seems doubtful. The cost of the heart increases in proportion to the height of the head, but the volume of the feeding sphere around the stationary animal decreases with height (figure 2). Simple geometry shows that, as the animal lifts its head, the greatest increases in blood pressure occur at low neck angles. By the time the neck reaches 70° upwards, the vertical component of the blood column is nearly maximal, and increases to 90° have little effect. Lifting or lowering the neck from horizontal makes available the largest volume of space per unit height, but when the neck is raised above approximately 30°, the increment diminishes substantially. It would probably make more energetic sense for the animal to feed with its neck close to horizontal. In this position, the long neck would have allowed access to the greatest volume of the feeding sphere, rising from ground level to perhaps 6 m high, or approximately 3 m above the heart, without getting into serious cardiovascular problems. (By comparison, an adult giraffe is 4.5 m high. The long front legs of *Brachiosaurus* may be an adaptation for raising the heart, much as the long legs of the giraffe.) The neck might also swing in a 9 m radius laterally, permitting feeding without the energy cost of moving the bulk of the body (Stevens & Parrish 1999). Taking a pace of 1 m horizontally would potentially make more food available than raising the head 1 m.

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Roger S. Seymour*

*Ecology and Evolutionary Biology, University of Adelaide,
Adelaide, South Australia 5005, Australia*

*roger.seymour@adelaide.edu.au

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