The energetics of low browsing in sauropods

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It has recently been argued that the probable high cost of travel for sauropod dinosaurs would have made exploiting high forage energetically attractive, if this reduced the need to travel between food patches. This argument was supported by simple calculations. Here, we take a similar approach to evaluate the energetics of foraging close to the ground. We predict that small extensions of the neck beyond the minimum required for the mouth to reach the ground bring substantial energetic savings. Each increment of length brings a further saving, but the sizes of such benefits decrease with increasing neck length. However, the observed neck length of around 9 m for Brachiosaurus (for example) is predicted to reduce the overall cost of foraging by 80 per cent, compared with a minimally necked individual. We argue that the long neck of the sauropods may have been under positive selection for low foraging (instead of, or as well as, exploitation of high foraging), if this long neck allowed a greater area of food to be exploited from a given position and thus reduced the energetically expensive movement of the whole animal.

Keywords: sauropod; dinosaur; neck; feeding; energy expenditures; Brachiosaurus

1. INTRODUCTION

Sauropod dinosaurs are fascinating because of their generally very large size and their unusual body shape, featuring a small head at the end of a very long neck. Their diversity and geographical range suggest that sauropods may have been keystone species in many ecosystems during the Jurassic and Cretaceous [1,2]. It has previously been argued that foraging with the neck raised to access high vegetation would have been prohibitively energetically expensive for sauropods, compared with low grazing [3]. However, Christian [4] recently argued that the probable high cost of travel for such giant animals would have made exploiting high forage energetically attractive, if this reduced the need to travel between food patches. This argument was supported by simple calculations. Here, we take a similar and complementary approach to evaluate the energetics of foraging low to the ground. We argue that a long neck may have been subject to positive selection pressure for low foraging (instead of, or as well as, exploitation of high foraging), if this long neck allowed a greater swath of food to be exploited from a given position and thus reduced the energetically expensive movement of the whole animal.

We draw analogy here with the cylinder vacuum cleaners that were commonplace in households in industrialized countries from the 1950s through to the 1970s. Because the machinery required to create the suction was large and heavy, the main body of the vacuum cleaner was positioned by the user in a central location within a room, and the user then moved a light head-part at the end of a long tube across the surrounding carpet. Such machines were largely replaced for domestic use by upright vacuum cleaners, because weight reduction of the machinery made it more feasible for the human operator to push the whole cleaner across all parts of the carpet. By analogy with cylinder vacuum cleaners, the long neck of the sauropods might have been an adaptation to allow less movement of the exceptionally heavy body of these animals. Note that this argument does not in any way conflict with use of the neck to exploit high forage. It is possible that a given type of sauropod used both low and high foraging, and experienced selection for a long neck through both mechanisms; with the relative strengths of these two selective forces possibly varying between species. Thus, our aim here is not to argue against the possibility of high feeding by sauropods, but to argue that their very large body size may have created positive selection for a long neck to increase their reach when low foraging from a given position and thus reduce the movement of their large body.

2. THE MODEL

We are interested in estimating the energetic cost of foraging per unit area. Let us assume that the neck of the animal joins its body at a height \( H \) (m) above the forage, and the neck is held straight and is of a length \( L \) (m). Then (assuming the forage is of uniform height), by Pythagoras’s Theorem, the maximum distance from the body that the animal’s mouth can stretch to is \( R \) (m):

\[ R = \sqrt{L^2 - H^2}. \]

Assuming that the neck has lateral movement allowing it to turn 90° either side of straight ahead, then it can sweep an arc of chord length \( 2R \). Thus, as the animal moves through the environment at average speed, \( v \) (m s\(^{-1}\)), it accesses area of forage at a rate \( 2\pi R \left( m^2 s^{-1}\right) \).

Christian [4] assumed that for an animal of mass \( M \) (kg), the energy spent per unit time (J s\(^{-1}\)), when travelling at average speed \( v \), was given by \( 10.8eM^{0.68} \).

Combining these expressions gives the cost \( (E; J\, m^{-2}) \) of exploiting forage:

\[ E = \frac{10.8eM^{0.68}}{2\pi R} = \frac{10.8eM^{0.68}}{2\sqrt{L^2 - H^2}}. \]

From inspection of this equation, we can see that this cost increases with the animal’s mass and with the height of the connection of the neck to the body above the forage, but decreases with the length of the neck. In order to quantify this effect further, we need to postulate values for \( M, L \) and \( H \) for a representative sauropod. We choose Brachiosaurus, since it was...
considered by Christian [4], and is a conservative test case for our hypothesis (§3).

For Brachiosaurus, Christian [4] assumes $M = 26,000$ kg. From the diagram in Sander & Clauss [2], we estimate $H = 6$ m for forage at ground level and $L = 9$ m. For these values, the effects of different hypothetical lengths of neck are shown in figure 1. This shows that small extensions of the neck beyond the minimum required to reach the ground (6 m) bring substantial energetic savings. Each increment of length brings a further saving, but the sizes of such benefits decrease with increasing neck length. The observed neck length of around 9 m is predicted to be the minimum required to reach the ground (6 m) without support and control of a long structure—or breathing forage to a Brachiosaurus. Such forage raised a little off the ground would decrease the effective value of $H$ and thus accentuate the benefits of a longer neck. Our model assumed considerable lateral neck flexibility, with the ability to twist the neck so as to orient the mouth at right angles to the main body axis. It seems that sauropods may have varied in their neck flexibilities, and in at least some, the neutral pose would have allowed low foraging without muscular exertion [5]; however, our broad conclusions hold for more restricted movements provided that there is some ability to flex the neck laterally. The addition of extra cervical vertebrae associated with long necks is suggestive of considerable flexibility [7]. We assume that the neck is held straight except for pivoting at the neck joint to simplify our calculations, but again our general conclusions are robust to relaxation of this to allow for greater neck flexibility. Finally, average speed of movement $v$ will decline with increasing neck length $L$ because of the finite time taken to sweep the head through its foraging arc. However, since $v$ cancels out of our final equation, this biological complication should not affect our model predictions.

If we argue that long necks are selected (at least in part) to reduce transport costs during foraging, then we must address why this selection pressure was important for sauropods more than for other herbivorous vertebrates. The dominant feature of sauropods was their massive size. This size is intrinsically linked to their small, light head and long neck [2]. From the elementary theory of levers [8], the cost of supporting the head increases with neck length, and thus a small, light head is a necessary consequence of a long neck. This light head means that sauropods lacked the massive dental batteries of elephants for example, and thus could do little processing of forage prior to ingestion. This in turn requires a massive body in order to achieve long digestion times and good digestive efficiency. However, the key to our argument is that the cost of moving the head and neck of such an animal would have been much less than that of minimizing energy expenditure of exploiting 2 m$^2$ of foraging area for a notional Brachiosaurus with different lengths of neck. The observed length is 9 m, and 6 m is the minimum length required to allow the head to reach ground level (required, for example, for drinking).

\[ E = \frac{1}{2} g \frac{L^2}{H} \]

Figure 1. The cost (in J m$^{-2}$) of low foraging for a notional Brachiosaurus with different lengths of neck. The observed length is 9 m, and 6 m is the minimum length required to allow the head to reach ground level (required, for example, for drinking).

where other factors (perhaps mechanical aspects of the support and control of a long structure—or breathing considerations) prevent evolution of further neck extension.

Our calculations involve many simplifying assumptions. However, we expect the qualitative conclusions drawn from our calculations to hold quite broadly. For example, although sauropods varied considerably in mass, the mass exponents of basal metabolism and cost of transport assumed in our calculations are very similar, so we would expect our conclusions to hold across all sizes of sauropods. The Brachiosaurus was unusual in that its front legs were substantially bigger than its hind legs, whereas normally the reverse was true [1]. This means that the height of the neck attachment is unusually high on Brachiosaurus, increasing the value of $H$. For most other sauropods, we would expect $H$ to be proportionately smaller; and this will have the effect of accentuating our predicted benefit from neck elongation. We were similarly conservative in assuming that the low-growing forage was at ground level. However, forage up to 3 m off the ground might still reasonably be considered as providing low-growing forage to a Brachiosaurus. Such forage raised a little off the ground would decrease the effective value of $H$ and thus accentuate the benefits of a longer neck. Our model assumed considerable lateral neck flexibility, with the ability to twist the neck so as to orient the mouth at right angles to the main body axis. It seems that sauropods may have varied in their neck flexibilities, and in at least some, the neutral pose would have allowed low foraging without muscular exertion [5]; however, our broad conclusions hold for more restricted movements provided that there is some ability to flex the neck laterally. The addition of extra cervical vertebrae associated with long necks is suggestive of considerable flexibility [7]. We assume that the neck is held straight except for pivoting at the neck joint to simplify our calculations, but again our general conclusions are robust to relaxation of this to allow for greater neck flexibility. Finally, average speed of movement $v$ will decline with increasing neck length $L$ because of the finite time taken to sweep the head through its foraging arc. However, since $v$ cancels out of our final equation, this biological complication should not affect our model predictions.

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moving the whole animal; thus, if this neck movement (because of the long neck) allowed a greater envelope of feeding from a stationary position, then considerable energetic saving could be had. Our model implicitly assumes that forage is available as a uniform carpet through which the animal moves. However, our argument also holds if the animal experiences a mosaic of different quality forages within which it must select the choicest patches, provided the variation in forage quality occurs on scales smaller than the length of the animal. Here, the saving comes because the animal can save costs of moving its whole body by small increments as it moves from one small micropatch to the next, by instead swinging its neck.

It is reasonable to ask why sauropod-style long necks have not evolved in the large mammalian herbivores that arose after the K-T extinction of the dinosaurs. First, it should be noted that none of these mammals have ever reached the huge size of the largest dinosaurs: perhaps because a mammalian high metabolism combined with a mammalian respiratory system (that is less efficient than an avian one—which sauropods might have shared [9]) would have made overheating difficult to avoid for such giants [10]. However, again analogy with domestic vacuum cleaners may be instructive. Cylinder vacuum cleaners were largely replaced by upright ones, only because improvements in materials and technology allowed reduction in size and weight: allowing the user to easily manoeuvre the whole machine. One of the defining features of the mammals is their more complex dentition than previous groups; it may have been the preprocessing of forage by the dental batteries characteristic of large herbivorous mammals that allowed more efficient processing of forage and thus removed the need for exceptionally large body size.

We believe that we have made a strong case here for low browsing causing a substantial positive selection pressure for sauropods to evolve long necks. However, we do not see this as an argument against the potential benefits that a long-necked individual could obtain from high browsing. It is entirely plausible that a given sauropod experienced both these selection pressures, and that these two pressures would then have interacted. It seems very probable that there is no one answer to the question of why sauropods had long necks. Different species would probably have experienced these two different selection pressures to varying degrees (along with other functions, such as potentially reaching otherwise inaccessible aquatic plants). For some species, high browsing may have been very important; however, an important inference from our work is that long necks might have been selected even in groups that devoted themselves entirely to low browsing.

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