The long necks of sauropods did not evolve primarily through sexual selection

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Abstract

It has recently been argued that the elongate necks of sauropod dinosaurs evolved primarily through selection for their use as sexual and dominance signals, and not as an adaptation for accessing a large 'feeding envelope' as traditionally thought. Here we explore this idea and show that all six arguments that have been advanced in support of the sexual selection hypothesis are flawed: there is no evidence for sexual dimorphism in the necks of sauropods; neither is there any evidence that they were used in dominance displays; long necks provided significant survival benefits in allowing high browsing and energetically efficient grazing; their fitness cost was likely less than has been assumed; their positive allometry through ontogeny is uninformative given that ontogenetic allometry is common in animals; apparent lack of correlation between neck and leg length across phylogeny is illusory due to over-representation of mamenchisaurids in a previously analysed dataset, and in any case is not informative as the unique morphology of sauropod necks suggests they, rather than legs, may have been cheaper to elongate when evolving increased vertical reach. In no speciose, morphologically varied, long-lived tetrapod clade has sexual selection consistently acted on a single part of the body, and it is unlikely that Sauropoda is the exception to this. In summary, there is no convincing evidence that sexual selection was the primary force driving the evolution of sauropod necks. While a subsidiary role for sexual selection cannot be discounted, the traditional hypothesis that sauropod necks evolved primarily due to the feeding benefits that they conferred is, by comparison, far better supported.

Introduction

Sauropod dinosaurs are instantly recognizable thanks to their unique bauplan: a huge, robust torso borne on four columnar limbs, a long neck, a proportionally small head and a long tail. The long necks of sauropods have long fascinated palaeontologists. For much of the 20th century, sauropods were imagined to be amphibious or aquatic herbivores that used their long necks as snorkels (e.g. Wiman, 1929). However, Bakker (1971) and Coombs (1975) used diverse lines of evidence to show that sauropods were predominantly terrestrial herbivores that foraged on terrestrial vegetation, and subsequent discoveries and studies have endorsed this interpretation (Taylor, 2010). Within this terrestrial paradigm, the sauropod neck has most usually been imagined as an adaptation allowing access to a large 'feeding envelope': that is, a foraging area that extends from ground level to many metres up into tall plants (e.g. Bakker, 1971; Martin, 1987; Paul, 1998; Upchurch & Barrett, 2000; Wedel, Cifelli & Sanders, 2000).

The use of the long neck as a tool for foraging is intuitively appealing given that these very large herbivores would have required huge amounts of energy and would have benefited from access to the largest possible feeding envelope. Furthermore, an ability to reach food inaccessible to species belonging to the other great herbivorous dynasties of the Jurassic and Cretaceous (thyreophorans, ornithopods and marginocephalians) would be an obvious advantage. The different neck lengths of the various sauropod taxa (Fig. 1) would conceivably create ecological partitioning among contemporaneous sauropod species similar to that seen in modern African ungulates (Leuthold, 1978; Bakker, 1986). Such niche partitioning would go some way towards explaining the extraordinary level of sauropod diversity in the Late Jurassic: 19 genera were contemporaneous during the 3.4 million years of the Kimmeridgian Age alone (Taylor, 2006). Alternatives to a foraging role for the neck have rarely been proposed. However, Senter (2006) – inspired by a controversial hypothesis about giraffe neck
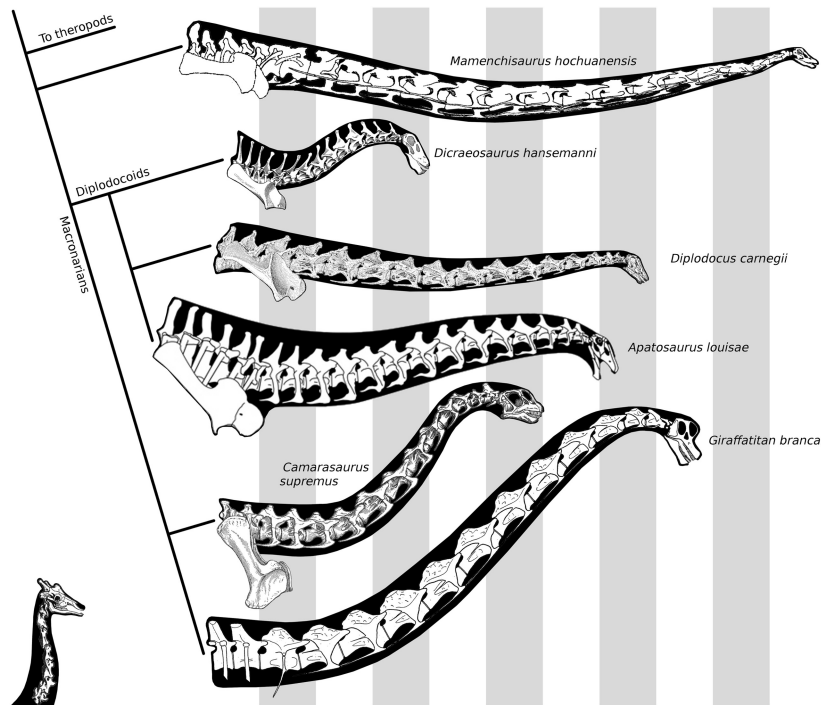
Figure 1 Sauropod necks, showing relationships for a selection of species, and the range of necks lengths and morphologies that they encompass. Phylogeny based on that of Upchurch *et al.* (2004: fig. 13.18). *Mamenchisaurus hochuanensis* (neck 9.5 m long) modified from Young & Zhao (1972: fig. 4); *Dicraeosaurus hansemanni* (2.7 m) modified from Janensch (1936: plate XVI); *Diplodocus carnegii* (6.5 m) modified from Hatcher (1903: plate VI); *Apatosaurus louisae* (6 m) modified from Lovelace, Hartman & Wahl (2008: fig. 7); *Camarasaurus supremus* (5.25 m) modified from Osborn & Mook (1921: plate 84); *Giraffatitan brancai* (8.75 m) modified from Janensch (1950: plate VIII); giraffe (1.8 m) modified from Lydekker (1894:332). Alternating grey and white vertical bars mark 1 m increments.

evolution – recently suggested that sauropod necks were sexually selected display ornaments.

Like sauropods, the long-necked giraffes of the genus *Giraffa* are long-necked herbivores with necks traditionally inferred to be advantageous in feeding (e.g. Cameron & du Toit, 2007) and their gross similarity has not gone unnoticed (as, e.g. in the name of the sauropod *Giraffatitan*). However, the long-held idea that giraffes gained a competitive ecological advantage from a long neck and great vertical reach was challenged by Simmons & Scheepers (1996), who advanced the alternative hypothesis that sexual selection is the primary factor driving the evolution of the neck. Building on the work of Simmons & Scheepers (1996), and using giraffes as an analogue, Senter (2006) proposed the novel hypothesis that the long sauropod neck also evolved through sexual selection rather than for any benefit related to feeding.

Senter (2006) surveyed the criteria by which sexually selected characters are recognized in extant taxa, constructed a series of six predictions relating to the contrasting hypotheses of feeding benefit versus sexual selection, and then tested both hypotheses against fossil evidence. He concluded that the sexual selection hypothesis is more consistent with predictions than the feeding benefit hypothesis. The six predictions which Senter considered should be fulfilled by taxa in which neck elongation was sexually selected are as follows:

1. Sexual dimorphism of the neck.
2. Use of the neck in dominance or courtship displays.
3. Intraspecific differences in neck length that do not facilitate vertical partitioning.
4. Neck elongation that incurred a survival cost.
5. Positive allometry in neck growth through ontogeny.
6. Positive allometry across phylogeny that is not correlated with limb length.

While conceding that the first two hypotheses could not be tested, Senter found support consistent with the other predictions and thus considered the elongation of the sauropod neck to be the result of sexual selection.

Senter's hypothesis is novel, his assumptions and evidence are clearly stated, and his conclusion is at odds with conventional interpretations. Despite this, his work has not attracted critical analysis. Instead, the conclusion that sexual selection played an important or even dominant role in the evolution of the sauropod neck appears to have been accepted at face value in the literature on both selection (Swallow *et al.*, 2009) and sauropod palaeobiology (Sander & Clauss, 2008; Siegwarth, Smith & Redman, 2010). Mateus, Maidment & Christiansen (2009) applied Senter's criteria to the long-necked stegosaur *Miragaia longicollum*, but with inconclusive results. However, recent work on both giraffes (Cameron & du Toit, 2007; Mitchell, van Sittert & Skinner, 2009) and sauropods (Christian & Dzemski, 2007; Taylor, Wedel & Naish, 2009) challenges Senter's (2006) analyses and the assumptions underlying them. Also of relevance is the recent resurgence in work on sexual selection in non-avian dinosaurs: this research has involved the reassessment and reanalysis of 'conventional' hypotheses in the light of new data and new techniques (e.g. Knell & Sampson, 2010; Padian & Horner, 2010 on mate recognition and sympatric separation) or modern theory. Note, however, that 'classic' traits such as horns and crests have received the bulk of the attention to date.

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In this paper we explore the implications of these and other studies for the sexual selection hypothesis of long necks in sauropods. We show that Senter's sexual selection hypothesis rests on a false dichotomy, demonstrate that most of his predictions deemed indicative of sexual selection are not fulfilled, and introduce additional arguments in favour of the traditional feeding-advantage hypothesis.

Sexual selection and survival selection are not mutually exclusive

A foundational problem with Senter's argument that sauropod necks were sexually selected is that it rests on the false assumption that sexual selection and survival selection are mutually exclusive. This assumption can be seen, for example, in Senter's prediction 2: '[The feeding hypothesis] predicts that sauropod necks are not used in dominance contests and courtship displays, whereas [the sexual selection hypothesis] predicts that they are'. This ignores the possibility that long necks were under selection pressure from both factors.

Morphological adaptations rarely have a single function. While structures may originally arise under selection from a single dominant factor, they are almost invariably co-opted for others. For example, the horns of various bovids provide a sexual signal by advertising fitness (Ezenwa & Jolles, 2008), function in intra- and interspecific combat (Caro *et al.*, 2003), provide some defence against predators, and have a minor thermoregulatory role (Hoefs, 2000). Similarly, the casques of cassowaries fulfil a number of functions, both sexual and non-sexual: they are used for display, to help detect infrasonic calls (Mack & Jones, 2003), and for manipulating foliage at shoulder height and leaf litter on the ground (Folch, 1992). Perhaps the most obvious example of co-option is the elephant trunk, which, among many other functions, is used for breathing, as a tactile organ, to gather food and water, and as a social signal; and while elephants' tusks are used for both inter- and intraspecific combat, their primary use is to help collect food (Barnes, 1995).

If sauropod necks were used for dominance signals *and* increased reach for feeding then any test could result in a double positive or double negative result and no informative inference could be made. Such a dual use of long necks is not without precedent in the world of modern reptiles: the proportionally long necks of saddlebacked Galápagos giant tortoises *Geochelone nigra* are used both to enable great vertical reach during foraging, and to determine dominance in intra- and intersubspecific conflicts (Fritts, 1984; Fig. 2).

As noted above, Senter's hypothesis that sauropods used their necks as sexual signals was inspired by the hypothesis of Simmons & Scheepers (1996) that the length of the giraffe neck was driven by a role in sexual selection, and that its length offers no competitive benefit in foraging at height. This 'necks for sex' hypothesis is highly problematical and has not been supported by subsequent evaluation. Male and female giraffes have previously been shown to feed at different heights (Ginnett & Demment, 1997, 1999). Cameron & du Toit (2007) showed that elongate necks in giraffe do provide vertical stratification, and that giraffes gain an advantage by feeding above the reach of other herbivorous mammals. Importantly, Cameron & du Toit's (2007) study is based on experimental, rather than simple observational, evidence. More recent work (Simmons & Altwegg, 2010) has suggested that neck elongation in giraffes may indeed be linked to sexual selection, but concedes that the role of the neck as a browsing device cannot be ruled out and may well have been important. Finally, Van Sittert, Skinner & Mitchell (2010) argued that ontogenetic allometry of the neck does not differ between male and female giraffes. Therefore, in so far as Senter's argument rests on analogy with what had been asserted regarding sexual selection in giraffes, the argument is weakened by the subsequent challenges to Simmons & Scheepers' (1996) work.

In short, to assume that sexual selection can be considered both independent from, and exclusive of, a competitive ecological function is erroneous. It remains possible that the sauropod neck originally arose either as a sexually selected feature or to help gather food, but it cannot be demonstrated that the necks remained monofunctional throughout their evolution, or that they could not be co-opted for a secondary function.

Senter's predictions re-evaluated

We now consider in turn each of Senter's predictions for animals in which long necks are sexually selected rather than conferring an ecological advantage, and re-evaluate whether these predictions are fulfilled in sauropods.

Prediction 1: sexual dimorphism of the neck

Contrary to common perception (e.g. Padian & Horner, 2010), sexual dimorphism of a trait is not a prerequisite for any inference of sexual selection. While sexual dimorphism can of course be a strong indicator of sexual selection, the existence of mutual sexual selection complicates the issue. As originally noted by Huxley (1914), and more recently expanded upon by Hunt *et al.* (1999), Kraaijeveld *et al.* (2004) and others, sexually selected characters can appear in both males and females of a species: both sexes may be ornamented. Each may use ornaments to signal to the other; consequently a sexually selected trait may become exaggerated in both sexes. In the crested auklet *Aethia cristatella*, for example, both sexes bear feather plumes on their heads and both sexes prefer mates with longer crests (Jones & Hunter, 1993, 1999). Some sexual dimorphism may be evident in such cases, but it can be minor and far less dramatic than in 'classic' sexually selected traits like the tails of peacocks.

While a lack of dimorphism does not therefore provide a barrier to the possibility of sexual selection in sauropod necks (mutual sexual selection could be at play), it does cause serious issues for the way in which Senter (2006) tested sexual selection. For example, his prediction 1 that '[feeding advantage] predicts that sauropod neck dimensions are not greater in one sex than in the other, whereas [sexual
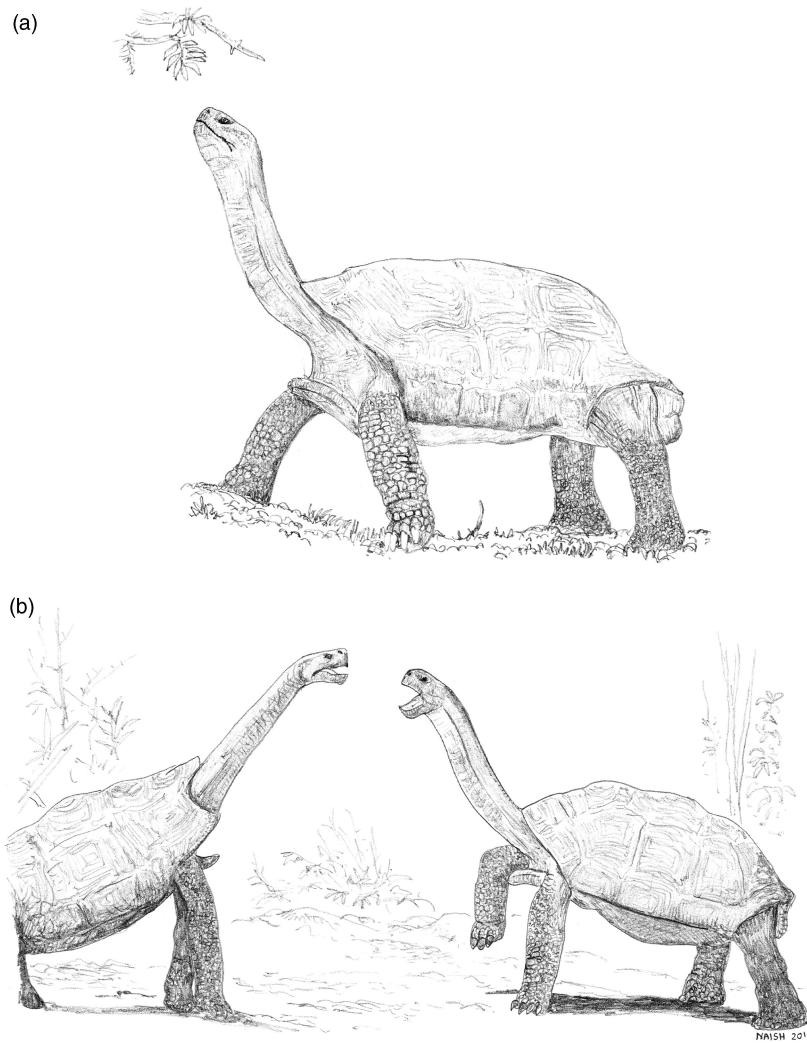
(a)

(b)

Figure 2 Long necks often serve multiple functions, as demonstrated here by Galápagos giant tortoises *Geochelone nigra*. (a) Use of the long neck for high browsing is commonly practiced by terrestrial testudines. Based on a photograph in Moll (1986:74–75). (b) Use of the long neck in establishing dominance. The two tortoises shown in the illustration were photographed on Santa Cruz Island: the dome-shelled animal on the right belongs to the native form *G. n. porteri* while the saddlebacked animal at left represents the Española form *G. n. hoodensis*. Based on a photograph in Fritts (1984: Fig. 2).

selection] predicts that they are' would test negatively for mutual sexual selection under this definition, even if in fact sexual selection were the sole driving force of neck length.

Nevertheless, if we are to follow the hypotheses as stated by Senter, strong sexual dimorphism in neck length is a requirement. As Senter himself recognized, available samples of sauropod taxa are unfortunately not large enough to demonstrate bimodal distribution of morphological features within any sauropod species. While Senter (2006, p. 46) tentatively suggested that the contemporaneous Late Jurassic diplodocids *Barosaurus* and *Diplodocus* of the USA's western interior might have been sexual dimorphs of a single taxon, he rightly concluded that 'it would be premature to synonymize the two taxa without a rigorous analysis with a large sample size'. In fact, these genera have different numbers of cervical vertebrae (McIntosh, 2005; M. J. Wedel, pers. obs.), and so cannot be sexual dimorphs of a single species. Furthermore, sexual dimorphism has not been persuasively demonstrated for any non-avian dinosaur species (Padian & Horner, 2010).

While it is not possible to statistically demonstrate dimorphism, qualitative comparisons can nevertheless be made. Robust and gracile 'morphs' have been identified in several dinosaur taxa – for example, *Coelophysis* (= 'Syntarsus') *rhodesiensis* (Raath, 1990) and *Tyrannosaurus rex* (Larson, 2008), so we may consider whether there is similarly any evidence for different neck lengths within a single sauropod species. To our knowledge, there is no such evidence in the fossil record. If anything, the uniformity of cervical morphology within sauropod species suggests that their necks were not sexually dimorphic. In general, isolated cervical vertebrae are diagnostic at least to the genus level (McIntosh, 1990). Upchurch, Tomida & Barrett (2005) identified differences in cervical neural spine height among species of *Apatosaurus*, but not differences in neck length. So not only is sexual dimorphism in sauropod neck length not amenable to statistical analysis, there is not even any anecdotal evidence to suggest its presence.

In conclusion, we simply do not have the data to determine whether sauropods were sexually dimorphic or not,

and dimorphism is in any case not a prerequisite for sexual selection. Therefore, prediction 1 contributes no information and can be discarded.

Prediction 2: use of the neck in dominance or courtship displays

As noted by Senter (2006, p. 46), this prediction 'cannot be tested for sauropods because the behaviour of extinct animals cannot be observed'. While this is generally true, some forms of agonistic behaviour, such as the 'necking' of male giraffes, are correlated with osteological features such as progressive thickening of skull bones through ontogeny (Simmons & Scheepers, 1996: p. 780) and signs of trauma. We would expect to see evidence of similar development in sauropods if their behaviour was similar; but again as noted by Senter, such features have not been observed in any sauropod.

Prediction 2, therefore, also contributes little information, and if anything weighs weakly against the sexual selection hypothesis.

Prediction 3: intraspecific differences in neck length that do not facilitate vertical partitioning

In formulating this prediction and arguing for its falsification, Senter relied on a sequence of assumptions. The indication of sexual selection from the literature, as originally stated (Senter 2006, p. 45) is that 'The character provides no immediate survival benefit – in contrast to characters driven by other kinds of selection, which are fixed in a population because of some survival benefit (Darwin, 1871; Simmons & Scheepers, 1996)'. From this, Senter derived the prediction that if sauropod necks were not sexually selected then 'interspecific differences in sauropod neck lengths provided vertical stratification of foraging among sauropod species and between sauropods and other species'. This is a very specific restatement of the original, general, prediction and makes the following assumptions: (A) that interspecific competition is the only kind that occurs or matters, (B) that the only way longer necks could have benefited sauropods was by an increase in vertical reach and (C) that the only value of increased vertical reach is niche partitioning due to stratification. In falsifying this revised prediction, Senter further assumed (D) that such niche partitioning is not possible due to overlapping juvenile and adult heights and (E) that the necks of sauropods could not be raised much above the horizontal. Every single link in this chain of reasoning is flawed.

(A) Senter implicitly assumed that increases in neck length due to survival benefits were driven only by interspecific competition; but one of the tenets of natural selection is that an organism competes most intensely with the organisms to which it is most similar, that is, the other members of its own population (Darwin, 1859). So even members of a single sauropod species with no close competing taxa – for example, *Sauroposeidon proteles* in the fauna of the Antlers Formation (Wedel *et al.*, 2000) – would still benefit from neck elongation due to intraspecific competition.

(B) The second assumption is that the only survival benefit of the long neck would be from improved vertical reach. However, it has repeatedly been argued that even if sauropod necks could not be raised high, their owners would nevertheless benefit from a larger feeding envelope at ground level – see, for example Martin (1987) on *Cetiosaurus*, Stevens & Parrish (1999) on *Diplodocus* and *Apatosaurus*, Sereno *et al.* (2007) on *Nigersaurus* and Ruxton & Wilkinson (2011) on *Giraffatitan* (= '*Brachiosaurus*' of their usage). Extant geese (e.g. *Branta canadensis*) provide a useful analogue: although they use their long necks to 'grub' for aquatic vegetation (thus improving their vertical reach, albeit downward), they also graze on low-lying terrestrial plants, and such 'green browse' makes up most of their diet (Owen, 1980). Grazing geese sweep their heads and necks from side to side during grazing, exactly as has been proposed for low-necked sauropods.

(C) The assumption is made that niche partitioning is the only putative benefit of increased feeding height. This is a very complex ecological scenario that explores only one of several possible survival benefits. Sauropods would also benefit from access to better quality food, and from the ability to reach the only available food during times of unusually intense competition.

The analogy with giraffes is instructive here: while giraffes do feed at low heights where food plants are shorter (Young & Isbell, 1991), the most important factor is what is consumed. Giraffes prefer to feed at higher levels, both because there is less competition from other browsers, and because higher foliage (in acacia trees) tends to have more protein and less tannin than foliage lower down. Feeding higher up is more productive and thus faster, meaning that giraffes need spend less time than when feeding at lower levels (Woolnough & Du Toit, 2001; Cameron & du Toit, 2007). High level browsing by giraffes can be intensive on some plants, and indeed the famous 'bell' shape of *Balanites* trees is formed by this habit (Foster, 1966).

Even if it were true that giraffes habitually browsed with their necks horizontal whenever possible, it would remain the case that the long necks, enabling higher browsing when necessary, would provide access to scarce food during times of environmental stress. Therefore, other things being equal, animals able to browse at higher levels are at an evolutionary advantage in terms of their ability to survive prolonged drought even if they do not use high browsing at other times. In conclusion, giraffes use their necks to maximize their exploitation of available browse, and there is no reason to doubt that analogous high browsing in sauropods would share the same evolutionary benefits.

The significance of this sequence of assumptions (A)–(C) is that even if it were demonstrated that sauropods were not niche-partitioned by feeding height, this would by no means exhaust the many other survival benefits they might have enjoyed thanks to their long necks. Shorn of these unwarranted assumptions, the prediction should be much more

general: that longer necks provided some kind of immediate survival benefit. However, the vertical feeding stratification hypothesis is not in fact disproven, as we will now show.

(D) Senter used the inevitable overlap among taxa in browsing height as evidence against the stratification hypothesis: 'vertical stratification due to neck length would have existed only for adult sauropods'. The vertical foraging ranges of juveniles of all species overlapped each other' (Senter, 2006: p. 46). But this criterion would make it impossible for any organisms that change size over ontogeny to pass the test; it is equivalent to arguing that canopy trees in rain forests do not compete for open spaces because juvenile trees of different species overlap in height. In any case, extant ecosystems show that there is marked overlap in browsing heights and competition between taxa where stratification is possible. For example, in African savannahs, vertical stratification can be seen between various taxa, yet they still overlap with dominant herbivores (Leuthold, 1978). Various species of giraffe, elephant, rhinoceros, zebra, suid, buffalo and antelope feed in overlapping environments (Sinclair, 1985; McNaughton & Georgiadis, 1986; Woolnough & Du Toit, 2001), yet each manages to occupy a separate ecological niche. Stratification is therefore by no means the only way to eliminate or reduce competition. Feeding guilds of taxa are likely to be influenced in their distribution by more than just one aspect of food acquisition (Sinclair, 1985).

(E) Senter's claim that sauropods could not derive a survival benefit from their long necks also rests on the assumption that they could not raise their necks in order to reach high branches. Senter (2006: p. 47) stated that 'The ability to lift the head above the level of the back was limited or absent in sauropods [. . .] Obviously, if a neck is held horizontally, its length does not influence vertical reach'. This concept of restricted vertical reach is based on the work of Martin (1987) and Stevens & Parrish (1999, 2005): based on inferences made about the neck's 'neutral posture' and the range of vertical movement allowed by the dry bones in the neck skeleton, these authors suggested that sauropods were mostly restricted to near-horizontal neck postures, and that their vertical reach was limited.

However, the neck posture and range of motion estimates of Martin (1987) and Stevens & Parrish (1999, 2005) are hypotheses rather than established facts, and have not been validated by subsequent studies. In particular, the underlying osteological data is too poor to support the reported precision of the estimates (Upchurch, 2000); assumptions about the mobility of intervertebral joints are probably incorrect (Taylor, 2009; Taylor *et al.*, 2009); and verification of the methods using extant animals has not been demonstrated. Indeed, most extant tetrapods habitually hold their necks maximally extended at the base (Vidal, Graf & Berthoz, 1986), and achieve this posture by extending the cervico-dorsal joint farther than osteology alone would suggest is possible (Taylor *et al.*, 2009). Until convincing evidence to the contrary is presented, habitual elevated neck posture should be the null hypothesis for sauropods (Taylor *et al.*, 2009).

Furthermore, even if sauropod necks were not habitually held in the elevated posture common to extant tetrapods, recent work by Stevens & Parrish (2005) themselves suggested that the necks of some sauropod taxa sloped gently upward even in 'neutral posture'. Note the substantial difference between having a limited ability to raise the neck and being completely unable to raise the neck; a neck need only be elevated at 30° to achieve half of the vertical reach of a neck elevated at 90°.

It has also been suggested that sauropods were limited in their ability to raise their necks due to the difficulty of circulating blood to the head (e.g. Seymour, 2009). Some of the calculations supporting this argument are flawed, and two of us (Taylor & Wedel) are working on a refutation.

As Senter's prediction 3 is a very specific case of the much broader originally proposed indication of survival selection, and as even that subset cannot be supported by evidence, this prediction does not provide evidence in favour of sexual selection. In fact, the numerous ways in which the long necks of sauropods might have provided survival benefits mean that, contra Senter, this prediction provides support for the competing hypothesis that the long necks of sauropods were indeed selected for their benefits in ecological competition.

Prediction 4: neck elongation that incurred a survival cost

This prediction is misstated in Senter's argument. It is given as 'The character incurs a survival cost – in contrast to characters driven by other kinds of selection, which are fixed in a population only if they incur minimal or no survival cost'. In fact, things are never this simple: in general, each evolutionary innovation has both a cost and a benefit: the question is whether the former outweighs the latter. For example, the large brains of humans – like the long necks of sauropods – impose a significant metabolic cost; but their benefits outweigh the cost and so the trait survives. Accordingly, while we wholeheartedly agree that the long necks of sauropods imposed real costs on their owners, this fact in itself does not constitute evidence of sexual selection.

Besides this, the costs of long necks seem to have been overstated. The only example given by Senter (2006, p. 47) was his claim that a horizontal sauropod neck would leave the animal vulnerable to attack from large predatory theropods, as 'a single bite that severed carotid arteries, jugular veins or vagus nerves would have been sufficient to dispatch a sauropod'. However, this assertion is problematic. Extant predators rarely attack adult animals (especially those many times larger than themselves) when juvenile prey is much more vulnerable, and there is evidence from the size distribution of bones in the fossil record that this was also true of Mesozoic theropods (Hone & Rauhut, 2009). Injuring or killing a sauropod with a single bite to the neck would be more difficult than the phrase 'a single bite that severed carotid arteries' suggests. The neck was not simply a mass of external blood vessels and nerves, but was constructed from tough elements including the often robust cervical ribs, bony

laminae, ligaments and tendons. A theropod could hardly dispatch a moving apatosaur with one swift bite, and a raised neck would further reduce vulnerability. (Other costs associated with sauropod anatomy, such as the need to acquire large amounts of food, are related to size in general rather than neck length in particular.)

The assumption that long necks impose a significant survival cost in giraffes is also flawed. Senter (2006) suggested that, as male giraffes more frequently fall victim to predation than females do (Simmons & Scheepers, 1996), the long neck of a sauropod imposes a substantial survival penalty by analogy. However, male African ungulates as a whole are typically more vulnerable to predation then females due to their behaviour, including solitary lifestyles and intraspecific combat (Owen-Smith, 2007). In giraffes specifically, males are primarily solitary (Dagg, 1971) while females tend to associate in herds. Males are thus more vulnerable through social factors, rather than necessarily as a consequence of their longer necks (Leuthold, 1979; van der Jeugd & Prins, 2000). Thus there is no evidence that the vulnerability of male giraffe to predators is in any way due to their neck length, and no reason to infer by analogy that male sauropods were similarly vulnerable.

As it cannot be shown that the cost of the long necks of sauropods outweighed their benefits, and as analogy with giraffes suggests that these costs were in any case lower than suggested by Senter, prediction 4 has little value in determining the function of sauropod necks.

Prediction 5: positive allometry in neck growth through ontogeny

Senter (2006, p. 47) correctly noted that positive allometry through ontogeny is known in the neck of *Camarasaurus*: this has been briefly noted by both Britt & Naylor (1994, p. 261) and Ikejiri, Tidwell & Trexler (2005, p. 173). Furthermore, Wedel *et al.* (2000, p. 368) showed that the cervical vertebrae of adult *Apatosaurus* individuals were proportionally 35–65% longer than those of juveniles, indicating that the neck elongated over ontogeny. (Given the very small sample of available cervical series for sauropod taxa, it is not possible to meaningfully calculate the allometric slope for any taxon.)

However, Senter's claim that positive allometry necessarily indicates sexual selection is flawed, resting as it does on publications from the 1980s and very early 1990s. In the last two decades, research in this area has progressed rapidly, and there is now an extensive literature on the relationship between allometric growth and sexual selection. Reviews such as that of Bonduriansky (2007) show that the picture is more complicated than previously recognized. While sexually selected features are often positively allometric, they may be isometric and even negatively allometric: in 10 of the 12 studies reviewed by Bonduriansky (2007, p. 843), isometry or negative allometry was reported for some or all of the sexually selected traits analysed, and Hosken, Minder & Ward (2005, p. 510) noted that 'male genitalia appear to show negative allometry in most invertebrates studied'.

Furthermore, non-sexual features may be positively allometric: for example, Lammers & German (2002) showed that in all four mammals that they analysed (chinchilla, rabbit, rat and opossum), femur length and tibia length are strongly positively allometric with respect to body mass. Similarly, Farlow & Pianka (2000) demonstrated ontogenetic allometry in the limb bones of several species of monitor lizard, and Simmons & Tomkins (1996) found that the non-sexually selected elytra of earwigs were positively allometric (though not so strongly as the sexually selected forceps).

As both positive and negative allometry occurs for both sexually selected and other body parts in extant animals, its presence in the necks of sauropods cannot be construed as compelling evidence for sexual selection, especially in the absence of quantification of the degree of allometry. Therefore, prediction 5 contributes little or no information to the question of whether sauropod necks were sexually selected.

Prediction 6: positive allometry across phylogeny that is not correlated with limb length

The characteristic sauropod body shape was established in the earliest sauropods (e.g. the Late Triassic *Antetonitrus*; Yates & Kitching, 2003) and remained in place until the very end of the Mesozoic. The major sauropod clades modified the body plan in various ways with differences in the proportions of the neck and the limbs being relevant here. Brachiosaurids had longer forelimbs than hindlimbs, for example, whereas diplodocoids had apomorphically short forelimbs, some only 65% the length of the hindlimbs (Upchurch, Barrett & Dodson, 2004).

Almost all sauropods were long-necked in comparison with non-sauropods, both proportionally and absolutely; but proportional variation within Sauropoda was nevertheless pronounced. Relatively short-necked sauropods include dicraeosaurids (e.g. *Brachytrachelopan mesai*, Rauhut *et al.*, 2005) and the titanosaur *Isisaurus* (= '*Titanosaurus*') *colberti* (Jain & Bandyopadhyay, 1997). In all other sauropods, the neck was much longer than necessary to reach the ground, and could be exceptionally long: in the diplodocid *Supersaurus vivianae*, for example, the neck has an estimated length of 13–16 m (Wedel, 2007, p. 195–197) compared with a shoulder height of < 4 m. Necks on the order of 10 m in length evolved independently in mamenchisaurids (Russell & Zheng, 1993), brachiosaurids (Wedel *et al.*, 2000) and diplodocids (Wedel, 2007), and possibly in giant titanosaurs (e.g. *Puertasaurus reuili*; Novas *et al.*, 2005).

One of Senter's (2006, p. 46) key arguments is that if the long sauropod neck evolved for use in feeding, then '[when] selection pressure is towards increasing the vertical reach of the head, the limbs – the lengths of which also influence head height – increase in relative length along with the neck across phylogeny'. His analysis showed no correlation between limb length and neck length in sauropods, which he interpreted as evidence that neck elongation was not

selected for vertical reach. On the face of it, this result seems reasonable, given the diversity of sizes and shapes among sauropods (Fig. 1). However, there are two problems with Senter's (2006, p. 47) analysis. First, the sample size is too small for the results to be statistically significant; and second, the taxon selection is poor, containing an over-representation of the small clade Mamenchisauridae and not a single representative of the great clade Titanosauria, which encompasses more than a third of all sauropod genera (Taylor, 2006). Mamenchisaurids are notable among sauropods in having the proportionally longest necks, and the inclusion of three (*Mamenchisaurus hochuanensis*, *Mamenchisaurus youngi* and *Omeisaurus junghsiensis*) in the sample of 11 sauropods biases the results away from recognizing a neck-length/limb-length correlation. When we replicated Senter's correlation analysis, using the data in his table 1 and reducing the mamenchisaurid sampling to only *O. junghsiensis*, the forelimb-neck correlation improved from 0.3484 to 0.4129, though this is also not statistically significant. A more comprehensive sampling, which lies beyond the scope of this study, will be required to determine whether significant correlation exists.

A hidden assumption in Senter's (2006) prediction 6 is that a long neck can contribute to feeding performance only by increasing vertical reach (as is the case in giraffes). However, most sauropods differed from giraffes in that their necks were much longer than they needed to be to reach the ground. In addition to improving vertical reach, such 'excessively' long necks could have improved feeding performance by allowing energetically efficient access to resources broadly distributed on the ground (Stevens & Parrish, 1999; Ruxton & Wilkinson, 2011) or in a three-dimensional feeding envelope (Martin, 1987; Wedel *et al.*, 2000). In light of this, it is perfectly reasonable to conclude that sauropods might have evolved long necks for feeding purposes without also evolving correspondingly long legs.

Even in committed high-browsers, vertical reach can be extended by evolving either a longer neck or longer limbs. But these two paths are not subject to equal constraints, especially in the case of sauropods. The cervical vertebrae of most sauropods were highly pneumatic (Wedel, 2005) and much less dense than the limb bones, which had very thick cortices and small (or absent) medullary cavities (Stein *et al.*, 2010). Sauropods were able to offset the mass penalty imposed by a longer neck by reducing the bone-to-air ratio of their cervical vertebrae, as seen for example in the clade Brachiosauridae, in which the very long-necked *S. proteles* has much more pneumatic vertebrae than its less elongate relative *Giraffatitan brancai* (Wedel & Cifelli, 2005: fig. 13). The tendency for longer necks to correlate with greater cervical pneumaticity is also seen in Sauropoda as a whole (Wedel, 2007: p. 219). Because at least part of neck elongation in sauropods came 'for free' (though not all; longer necks still required longer muscles, tracheae, and blood vessels and greater transport costs), it may have been more advantageous for sauropods to extend their vertical reach by adding or elongating cervical vertebrae instead of changing the length of the limbs; the latter would be free to evolve in

other ways based on the demands of body support and locomotion. This is not a trivial consideration: most sauropods were an order of magnitude more massive than giraffes, and locomotory stresses would have been completely different from those affecting smaller animals. Their four dense, columnar limbs had to be accelerated twice in each step cycle (from stance, to swing, back to stance), while their single comparatively lightweight, pneumatic necks did not. Energetics alone may have been sufficient to prevent sauropods from evolving a body form similar to that of giraffes and camelids, with necks and limbs of comparable lengths.

In summary, even if Senter's statistical analysis is taken at face value as showing that sauropod neck length is not strongly correlated with leg length, this does not necessarily mean that neck elongation did not contribute to feeding. Consequently, prediction 6 contributes no information.

No single feature is sexually selected across any speciose tetrapod clade

In evaluating any palaeobiological or palaeoecological hypothesis, analogy with extant animals and ecosystems is always instructive. One important question to ask about the sexual selection hypothesis of sauropod neck elongation is whether there is any large extant tetrapod clade in which the members all show a uniform maladaptive feature analogous to the long sauropod neck. Sauropoda was a diverse and disparate group, encompassing many genera, great morphological variation, a range of habitat preferences (Mannion & Upchurch, 2010) and huge ecological significance: it is reasonable to compare it in these terms with modern tetrapod clades such as Artiodactyla or even Passeriformes. If the long necks of sauropods had negative survival value, their retention across the whole clade is analogous to a hypothetical situation where the maladaptively long tails of birds-of-paradise are found throughout Passeriformes, or where the enormous antlers of the Irish Elk *Megaloceros* are ubiquitous in Artiodactyla. Instead, we see long-term progressive evolution of characters that have survival benefit, while sexually selected characteristics are subject to evolutionary 'fashion' and tend to be much more labile.

As well as being diverse, Sauropoda also had a long evolutionary history, originating about 210 million years ago in the Carnian or Norian Age of the Late Triassic, and persisting until the end-Cretaceous extinction of all non-avian dinosaurs about 65 millions years ago. Thus the 'necks-for-sex' hypothesis requires that this clade continued to sexually select for exaggeration of the same organ for nearly 150 million years, a scenario without precedent in tetrapod evolutionary history.

Furthermore, neck elongation was a long-term evolutionary trend not just within Sauropoda, but also along the entire archosaurian lineage leading to this clade. The clades Ornithodira, Saurischia, Sauropodomorpha and Sauropoda are all characterized by having longer necks than their immediate outgroups (Gauthier, 1986; Sereno, 1991; Wilson & Sereno, 1998). The evolution of even longer necks in

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various sauropod lineages must be understood within the framework of this evolutionary history, which extends even farther back into the Triassic than that of sauropods alone, and which encompasses many more species. The notion of sexually selected neck elongation persisting throughout this sequence of clades is yet further removed from anything that has been observed in other groups, and as an outlier its credibility is further undermined.

Although there is no long-lived or speciose tetrapod clade that has consistently sexually selected for a single feature, there are a few such invertebrate clades. For example, among insects, sexual dimorphism in Diopsidae (stalk-eyed flies) has been described from Eocene Baltic amber (Kotrba 2004), and the pincer-like cerci of Dermaptera (earwigs) evolved in the Early Jurassic (Grimaldi & Engel 2005: fig. 7.50). It is not clear why this disparity in the persistence of single sexually-selected features exists between insects and tetrapods. It might be connected with the vast differences in biomechanics and life history between the two clades, or with the persistence of certain body forms in the clades themselves – hardly any tetrapods have persisted essentially unchanged since the Early Jurassic, as have earwigs. Nevertheless, the absence of such long-term (i.e. 150+ million years) sexual selection in tetrapods casts doubt on the hypothesis of sexual selection as the primary driver of neck elongation in sauropods, which retained essentially the same body form from the Late Triassic through the Late Cretaceous, a span of almost 150 million years.

Conclusion

The assumption that sexual selection and feeding benefit are mutually exclusive mechanisms in accounting for the evolution of the long necks of sauropods is mistaken. The inspiration for the sexual selection hypothesis – the proposal that the length of the giraffe neck predominantly resulted from sexual selection pressure (Simmons & Scheepers, 1996) – is at best controversial, and further study has shown it likely that giraffe's necks evolved under the pressure of ecological competition.

Revisiting the six predictions used to evaluate whether sauropod necks were sexually selected, we find that:
1. There is no statistical evidence for sexual dimorphism in the necks of sauropods, but what anecdotal evidence we do have indicates that it was absent.
2. It is impossible to determine whether sauropod necks were used in dominance or courtship displays, but what little evidence there is (e.g. absence of skull thickening) suggests that they were not.
3. The long necks of sauropods provided significant survival benefit, both in access to higher browse and in energetically efficient feeding at ground level.
4. The survival cost imposed by the long necks of sauropods was probably less than has been proposed, and was likely outweighed by the survival benefits.
5. Although there is evidence that sauropod necks were positively allometric through ontogeny, this observation has little predictive power as allometric growth is very common in animals whether or not sexual selection is at work.
6. The finding that sauropod neck length does not correlate strongly with leg length is skewed by the over-representation of the bizarrely long-necked and morphologically uniform mamenchisaurids, and there are anatomical reasons why sauropods might have favoured lengthening necks rather than legs in order to increase vertical reach.

The proposal that the necks of sauropods – a speciose, morphologically varied clade spanning 150 million years – evolved due to the persistent action of sexual selection on a single part of the body is not paralleled by sexual selection in any tetrapod clade that is remotely comparable in diversity, disparity or longevity.

The idea that sauropod necks were the result, fully or in part, of sexual selection is novel and should not be dismissed out of hand. However, evidence that might support this hypothesis is lacking and we find no compelling support for the idea. Further research and improved tests may yet reveal the nature of selection acting on the sauropod neck, but at the moment there is no convincing evidence supporting the hypothesis that long necks in sauropods were sexually selected, and several reasons to accept the traditional hypothesis that their necks evolved primarily due to the feeding benefits that they conferred. The traditional model fits well with the fossil evidence, so far as that is informative, and it is supported by behaviour observed in extant analogues. In the absence of credible alternatives, it must remain the null hypothesis for the evolution of long necks in sauropods.

Acknowledgements

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