period [1]. If so, the facilitation of visual plasticity after binocular deprivation [8] may be due to the removal of mutual inhibitions between the two eyes. Moreover, the improvement in performance with an amblyopic eye as a result of occluding the fellow eye [5] might be at least partially accounted for by this boosting effect, although the combination of training with an amblyopic eye and deprivation of the fellow eye may be more effective [5,7].

Supplemental Information

Supplemental Information includes one figure and supplemental experimental procedures and can be found with this article online at doi: 10.1016/j.cub.2012.03.010.

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Could methane produced by sauropod dinosaurs have helped drive Mesozoic climate warmth?

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Mesozoic sauropods, like many modern herbivores, are likely to have hosted microbial methanogenic symbionts for the fermentative digestion of their plant food [1]. Today methane from livestock is a significant component of the global methane budget [2]. Sauropod methane emission would probably also have been considerable. Here, we use a simple quantitative approach to estimate the magnitude of such methane production and show that the production of the ‘greenhouse’ gas methane by sauropods could have been an important factor in warm Mesozoic climates.

Sauropod dinosaurs include the largest terrestrial animals known and exhibit a distinctive body shape, featuring a small head at the end of a very long neck. Their diversity and geographic range suggest that sauropods may have been keystone species in many ecosystems during the Jurassic and Cretaceous [1]. Based in part on data from the Late Jurassic Morrison Formation (Western USA), Farlow *et al.* [3] estimated population densities for sauropods ranging from a few large adult animals to a few tens of individuals per km^2. Specifically, they estimate that if dinosaurs had an endothermic, mammalian-style metabolism, then the total abundance of these megaherbivores would have been 11–15 animals/km^2 with a total biomass density of around 42,000 kg/km^2. It is, however, very unlikely that large-bodied sauropods had metabolisms as high as predicted by the assumption of mammalian metabolism [1]. If instead a reptilian metabolism in assumed, then Farlow *et al.* [3] calculate a predicted biomass density of 377,000 kg/km^2. The palaeoenvironment of the Morrison Formation was, at least in part, semi-arid — probably not optimal megaherbivore habitat. For our calculation, we conservatively assume sauropod biomass density, averaged over the global vegetated land area, to be around 200,000 kg/km^2. Other recent estimates of the biomass density of herbivorous dinosaurs are 80,000–90,000 kg/km^2 [4] and 7–24 times the biomass of extant large-bodied herbivorous mammals [5], which taking a value of 28,000 kg/km^2 for mammals (Table 7 of [3]) gives a range between 186,000–672,000 kg/km^2. These studies all predict a higher herbivore biomass in the Mesozoic than seen in modern systems with large herbivorous mammals — such as African savannah. Three potential underlying mechanisms are conceivable: first, Mesozoic primary production per km^2 would reflect higher temperatures and CO_2 concentrations [6]. Second, large herbivorous dinosaurs would have had lower mass-specific metabolic rates than endothermic mammals of the same size [1]. Third, herbivorous dinosaurs featured a very large individual body size, and — as metabolism scales less than linearly — a larger individual body size allows a given primary production to support a greater herbivore biomass.

To estimate methane production we follow the relationship derived by Franz *et al.* [7] for modern non-ruminant herbivores, where Methane (litres per day) = 0.18 (body mass in kg)$^{0.97}$. The exponent (0.97) is not statistically different from one [8], indicating that to calculate total sauropod methane emissions, we need only estimate the total biomass density, since methane emissions will be insensitive to body size distribution of the constituent animals. As an illustrative example, we consider the sauropod biomass density of 200,000 kg/km^2 to consist of ten 20,000 kg sauropods; this is a conservative estimate of the adult mass of the medium sized sauropod *Apatosaurus louise*, colloquially known as ‘Brontosaurus’. For this, the allometric relation gives methane emission of 2675 litres per day for one animal, equivalent to about 1.9 kg per day under the standard temperature and pressure conditions assumed in [7]. For a density of ten adults per km^2, assuming, for comparability,

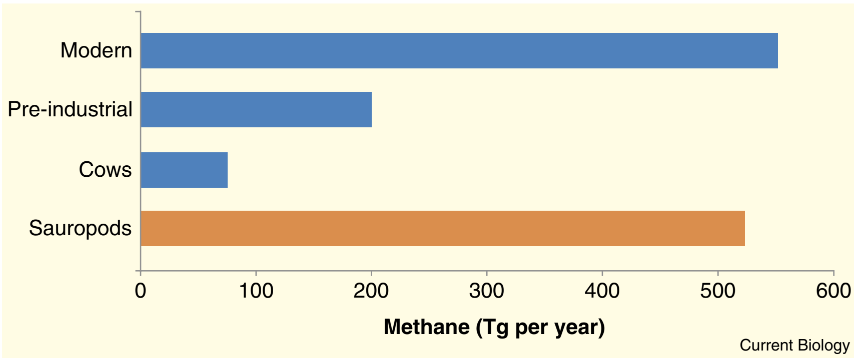

Figure 1. Estimated emissions.
Estimated sauropod methane production compared to total modern (both natural and anthropogenic), global pre-industrial and estimated modern methane production from ruminants. Even reducing our estimate by half still predicts a major role for sauropod methane in the Mesozoic.

modern day and year lengths (the Mesozoic day was slightly shorter), we get 6.9 tonnes/km^2 of methane per year methane emissions. Scaling up, assuming a global vegetated area of 75 x 10^6 km^2 (equivalent to half the total land area), gives global methane production from sauropods of 520 Tg (520 million tonnes). This is comparable to the total modern-day methane emission (Figure 1) [2]. For comparison, total pre-industrial Holocene global methane emission was roughly 200 Tg per year, capable of sustaining an atmospheric methane mixing ratio of about 0.7 ppm, and the modern mixing ratio of about 1.8 ppm is supported by roughly 500–600 Tg of global emission.

Unlike most modern browsers which are restricted to low growing vegetation, sauropods could access high tree foliage. This ability to access high as well as low browse because of their large body mass may partly explain why we infer sauropod methane emissions to have been much greater than those of modern-day ruminants which produce ~50–100 Tg per year. However, the dominant reason is the much greater global primary productivity available for exploitation. First, the land area able to support large herbivores was larger than currently: the Mesozoic climate was warm, moist and without permanent polar ice cover. Second, primary production is likely to have been higher on land per unit area, given the elevated atmospheric CO_2 concentration [9].

Take together, our calculations suggest that sauropod dinosaurs could potentially have played a significant role in influencing climate through their methane emissions. Even if our 520 Tg estimate is overstated by a factor of 2, it suggests that global methane emission from Mesozoic sauropods alone was capable of sustaining an atmospheric methane mixing ratio of 1 to 2 ppm [2,9]. Equally, our estimate may be understated by a similar factor, (i.e. possibly supporting 4 ppm methane). In the warm wet Mesozoic world, wetlands, forest fires, and leaking gasfields may have added around another 4 ppm methane to the air [9]. Thus, a Mesozoic methane mixing ratio of 6–8 ppm seems very plausible.

The Mesozoic trend to sauropod gigantism led to the evolution of immense microbial vats unequalled in modern land animals. Methane was probably important in Mesozoic greenhouse warming [9]. Our simple proof-of-concept model suggests greenhouse warming by sauropod megaherbivores could have been significant in sustaining warm climates. Although dinosaurs are unique in the large body sizes they achieved, there may have been other occasions in the past where animal-produced methane contributed substantially to global environmental gas composition: for example, it has been speculated that the extinction of megafauna coincident with human colonisation of the Americas may be related to a reduction of atmospheric methane levels [10].

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