

## Body surface area and thermoregulation in giraffes



Graham Mitchell <sup>a, b, \*</sup>, Sybrand van Sittert <sup>b</sup>, David Roberts <sup>b</sup>, Duncan Mitchell <sup>c, d</sup>

<sup>a</sup> Department of Zoology and Physiology, 1000E University Avenue, Laramie, WY 82071, USA

<sup>b</sup> Centre for Veterinary Wildlife Studies, Faculty of Veterinary Science, University of Pretoria, South Africa

<sup>c</sup> Brain Function Research Group, Faculty of Health Sciences, School of Physiology, University of the Witwatersrand, York Road, Parktown, Johannesburg, South Africa

<sup>d</sup> School of Human Sciences, University of Western Australia, Perth, Australia

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### ABSTRACT

One of several hypotheses for the evolution of the shape of giraffes is that it evolved to maximize heat loss via a high surface area to mass ratio. We calculated the surface area (SA) of the head, neck, trunk and upper legs, and the lower legs in 60 giraffes of both sexes and a body mass range of 141–1358 kg. No sex differences were found for giraffes of equivalent body mass. Relative surface area ( $\text{cm}^2 \text{kg}^{-1}$  body mass) declined from 145 in juvenile giraffes to 90 in adults. Average total body SA was  $7.3 \pm 2.5 \text{ m}^2$  (range 2.2–11.7), which is not significantly different to that of mammals of equivalent mass. The extra area of the neck and legs was offset by smaller trunk area. However, the narrow diameters of the neck and lower legs enhance the rate of convective and evaporative heat loss and reduce the incident solar radiant heat load when giraffe face the sun, a behaviour supplemented by seeking shade if it is available. We have concluded that giraffes do not have an unusually large SA for their mass, but their shape confers other thermoregulatory benefits that have advantages for survival in the arid habitat they prefer.

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## 1. Introduction

Extant giraffes (*Giraffa camelopardalis*) appeared ~1 million years ago (Mya) having evolved over a period of ~15 My via *Canthumeryx*, *Giraffokeryx*, *Paleotragus* sp., *Samotherium* sp. and *Bohlinia* (Churcher, 1978; Hamilton, 1978; Geraads, 1986; Mitchell and Skinner, 2003). The neck length of *Canthumeryx* was ~550 mm *Palaeotragus germaini* and *Samotherium (boisseri)* ~850 mm (Badlangana et al., 2009), *Bohlinia* ~1500 mm and in extant giraffes up to 2200 mm long (Mitchell et al., 2009). Similarly, leg length increased from 800 mm in *Canthumeryx* to 1560 mm in *Paleotragus* sp to 1740 mm in *Samotherium* sp and 2100 mm in adult extant giraffes (Colbert, 1938; Mitchell et al., 2009; van Sittert et al., 2015). Thus, during their evolution natural selection favoured progressive leg elongation of ~3 fold and a neck ~4-fold longer than it was in *Canthumeryx* to produce their familiar tall, slender, dolichomorphic shape.

There have been at least six explanations for the evolution of their shape. Lamarck (1914) suggested that as giraffes were obliged

to browse from trees, and had to make constant efforts to reach them, the legs and necks of giraffes elongated. Wallace (in Darwin and Wallace, 1858) refuted Lamarck's idea and wrote “the giraffe did not acquire its long neck by –constantly stretching its neck –, but with a longer neck than usual at once secured a fresh range of pasture. Darwin entrenched this explanation in a famous passage in the sixth edition of Origin of Species (Darwin, 1872): “The giraffe, by its lofty stature, much elongated neck, forelegs, head and tongue, has its whole frame beautifully adapted for browsing on the higher branches of trees. It can thus obtain food beyond the reach of other Ungulata or hoofed animals inhabiting the same country; and this must be a great advantage to it during dearths”. Pincher (1949) rejected the Wallace–Darwin story. He concluded that a life punctuated by Darwinian “dearths” severe and long-lasting enough for evolution to operate, would place less tall members of the species at a permanent disadvantage and extinction would be inevitable. His alternative explanation, following an idea announced by Colbert (1938), was that there had to be concomitant elongation of the neck as a response to increasing limb length if a giraffe was to reach the ground to drink water. However, throughout giraffid evolution leg lengths were almost twice as long as neck length, until the evolution of *Giraffa* as a species, when, for the first time, neck length exceeded leg length. Clearly, ancestral giraffids were not

\* Corresponding author. Department of Zoology and Physiology, University of Wyoming, 1000E University Avenue, Laramie, WY 82071, USA.

E-mail address: [mitchg@uwyo.edu](mailto:mitchg@uwyo.edu) (G. Mitchell).

compromised and thus Pincher's hypothesis can be dismissed. Another hypothesis is that there has been sexual selection for a long neck and heavy heads in males for use in contests to obtain access to females with the best endowed males winning (Simmons and Scheepers, 1996). However, females show no preference for any specific male (Bercovitch et al., 2006) and there is no sexual jealousy between males when they are testing to see if a female is in oestrus (Innis, 1958). Moreover, sexual selection implies sexual dimorphism and higher mortality (Darwin, 1874), but long necks are not associated with higher mortality and there is no sexual dimorphism in neck mass or length or head mass (Mitchell et al., 2009, 2013a).

Brownlee (1963) suggested two other hypotheses. Like Pincher, he disputed the Wallace-Darwin explanation on the grounds that tallness only favours the biggest giraffes. Smaller females and young giraffes would have to compete for food with other browsers, are not therefore at an advantage, and in a drought would succumb. Instead he proposed that as “*In certain human races living in hot climates, dolichomorphism is an aid in achieving heat loss. So also to the giraffes, living as they do in hot climates, their dolichomorphic structure will serve a similar purpose to young and old, male or female continuously and not merely in times of drought, while at the same time enabling them to achieve that size and tallness which confers greater ability to evade, or defend against, predators and to reach a source of food otherwise unavailable to them.*”

Brownlee's suggestion of improved vigilance as an advantageous consequence of their height has been supported by analysis of eye anatomy and its allometry (Schiviz et al., 2008; Mitchell et al., 2013b; Coimbra et al., 2013). Confirmation or rebuttal of Brownlee's thermoregulation hypothesis depends on adequate measurements of the factors affecting heat transfer. This paper seeks to address the most basic of those factors, the surface area to mass ratio of giraffes, and its consequences for thermoregulation. Mass can be measured directly. Direct measurement of surface area in large animals rarely is attempted because it is difficult. Methods used (reviewed in Ruggieri and Rocca, 2010) are “coating” in which the body is covered by an inelastic material that can be removed and its surface area measured, “integration” by which surface area is measured by a planimeter, and “triangulation” in which all surfaces are marked with triangles of known dimensions. In a measurement of cattle surface area Hogan and Skouby (1923) used gummed paper as the “coating” and deduced surface area from the paper's weight. In another study of cattle surface area Elting (1926) used a purpose built planimeter, and in two cases confirmed its accuracy by measuring the area of hides. More recently photogrammetry, previously used in humans (Li et al., 2011), has become the gold standard technique for measuring body dimensions in animals (Postma et al., 2015) but has not been applied to giraffes. It has been used to measure surface area in swamp buffalo (Buranakari et al., 2012), but in that case the surface area measured was not reported so its accuracy in a large herbivore could not be assessed.

Rather than being measured, surface area of mammals usually is predicted from mass, or from mass and height. Several predictive equations have been reported for humans, originally by Du Bois and du Bois (1916), but since by others (Mitchell et al., 1971; Vu, 2002), and for other mammals (e.g. Hogan and Skouby, 1923; Elting, 1926; Stahl, 1967). All those equations assume that the animals involved differ in size but not in shape. The usual analogy for the shape of the body of a mammal is a cylinder (Jessen, 2001) and consequently measurements of girth and length have been shown to give very accurate estimates of body mass in short-necked artiodactyls such as wildebeest and cattle (McCulloch and Talbot, 1965) and mountain goats (Rideout and Worthen, 1975) and in perissodactyls such as rhinoceroses (Freeman and King, 1969) and thus of surface area. Checking whether girth and length accurately predict mass is

relatively easy because mass can be measured independently. Checking whether girth and length predict surface area is not easy, however, because it requires an independent measure of surface area. Giraffe, in any case, have an unusual shape that defies characterization as a single cylinder, so, for them measurements of girth and length are unlikely to indicate surface area.

So far there has only been one attempt to quantify giraffe surface area (Henderson and Naish, 2010) and this was in the context of determining buoyancy and potential swimming ability not thermoregulation. Henderson & Naish used a computerized digital slicing method based on illustrations and calculated that in a theoretical giraffe weighing 1611 kg the surface area of the skin would be 17.7 m<sup>2</sup>. If Stahl's (1967) allometric equation linking surface area to body mass in a standard mammal ( $0.11 \cdot Mb^{.65}$ ) is applied to a giraffe with a body mass of 1611 kg the resultant surface area is 13.3 m<sup>2</sup>, that is, 25% less. Giraffe therefore seem to have a body surface area much bigger than a standard mammal of the same mass. If so, how much bigger and why is it bigger? To answer those questions we report here an analysis of surface area of giraffes based on measurements obtained from 60 giraffes ranging in body mass from 141 kg to 1358 kg.

## 2. Method

We subdivided the surface of giraffes into four components - the head, neck, trunk and upper legs, and lower legs (Fig. 1). To determine the relationships between the component surface areas and their mass and with body mass, we obtained data from 30 male and 30 female giraffes culled in south eastern Zimbabwe. In each animal the following measurements were made within an hour of being culled:

### 2.1. Body mass (kg)

#### 2.1.1. Total body mass (Mb, kg)

Was determined by piecemeal weighing of all parts to the nearest kg using a Salter suspended spring balance with a capacity of 200 kg.

#### 2.1.2. Head and neck mass (kg)

Were measured after the head was separated from the neck at

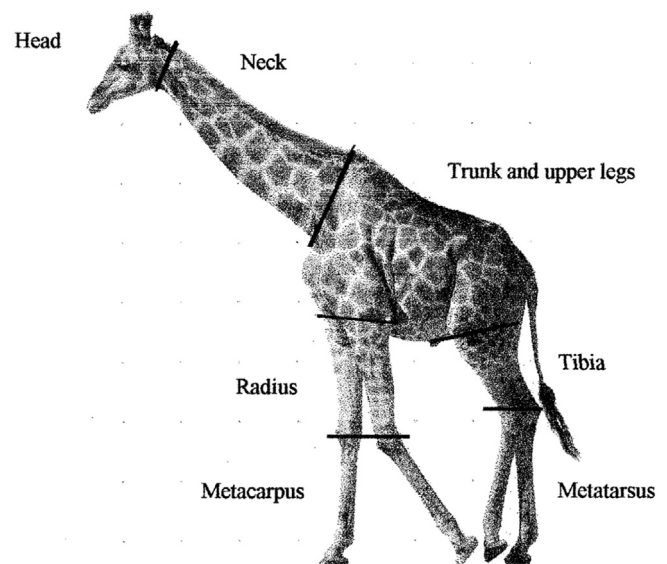


Fig. 1. The four areas into which the surface of a giraffe was divided.

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