

Body surface area and thermoregulation in giraffes

Graham Mitchell^{a,b}, Sybrand van Sittert^a, David Roberts^a, Duncan Mitchell^c.

a) Department of Zoology and Physiology, 1000E University Avenue, Laramie, WY 82071, USA.

b) Centre for Veterinary Wildlife Studies, Faculty of Veterinary Science, University of Pretoria, South Africa.

c) Department of Physiology, University of the Witwatersrand, York Road, Parktown, Johannesburg, South Africa.

Corresponding author: G Mitchell email: mitchg@uwyo.edu

Highlights

- The thermoregulatory advantages of the shape of giraffes are analyzed.
- They do not arise from a larger than expected surface area.
- They arise from enhanced convective and evaporative heat loss.
- Their shape reduces incident radiation.
- These have advantages in the hot arid environments that giraffes inhabit by preference.

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.

Key Words: Giraffe, body surface area, thermoregulation

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 (boissieri)* ~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 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 & 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 that would be wetted (which is not the total surface area) would be 17.7 m². If Stahl's (1967) allometric equation linking surface area to body mass in a standard mammal ($0.11 * M_b^{.65}$) is applied to a giraffe with a body mass of 1611 kg the resultant surface area is 13.3 m², that is, 22% 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:

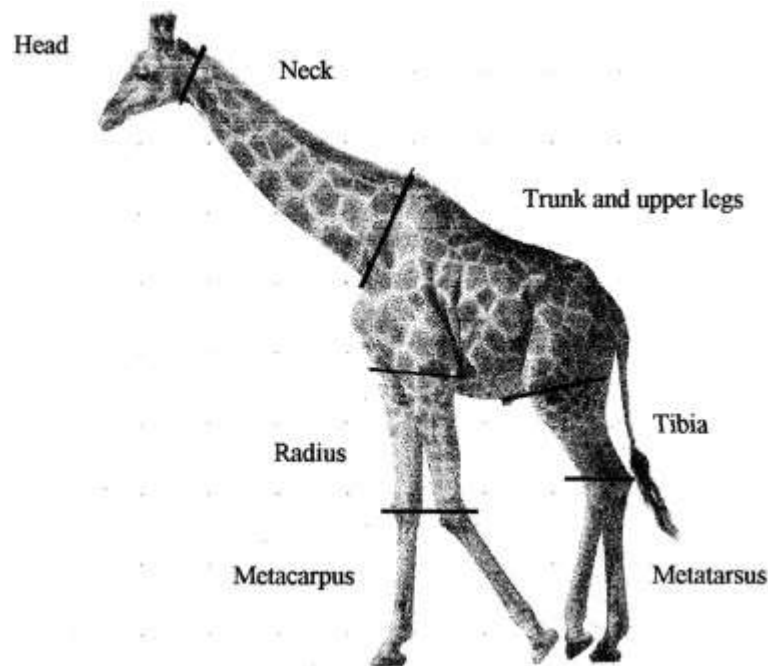


Fig. 1. The four areas into which the surface of a giraffe was divided.

2.1. *Body mass (kg)*

2.1.1. *Total body mass (M_b , 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 the atlanto-occipital articulation and the neck was separated from the trunk at the cervico-

thoracic articulation.

2.1.3. *Lower Leg mass (kg)* mainly depends on the mass of the lower leg bones. In giraffes as in all artiodactyls muscles occupy the upper legs and are continued as tendons into the lower legs. The mass of the radius, tibia, metacarpal, and metatarsal bones was measured directly. The masses of the carpus, tarsus and phalanges were not measured.

2.1.4. *Trunk and upper leg mass (kg)* was calculated by subtracting head, neck and lower leg mass from total body mass.

2.2. *Body Surface areas (m²).*

2.2.1. *Neck surface area (NSA, m²).* Giraffe neck skin has the shape of a trapezium. We calculated its surface area as:

$$NSA = [(a+b)/2]*NL$$

where *a* was neck circumference at the apex, *b* the circumference at the base and neck length (NL) was measured as the mean of the distances from the occipital crest to the withers and from the angle of the jaw to the point of the shoulder (*tuberculum supraglenoidale*) (Fig 1).

2.2.2. *Trunk and upper leg surface area (TSA, m²).* We calculated the surface area of the trunk and upper legs of giraffes by assuming that together they have the shape of a cylinder, and using the equation for the surface area of a closed cylinder:

$$TSA (m^2) = 2\pi R * L + 2\pi R^2$$

where R is the radius derived from the girth of the thorax and L was body length. Girth was measured as the circumference of the thorax immediately caudal to the front legs and body length was measured as the distance between the base of the neck and the base of the tail.

2.2.3. *Lower leg surface area (LSA, m²)*. We considered that the lower legs of a giraffe consist of four cylinders (Fig 1; van Schalkwyk et al, 2004; van Sittert et al, 2015). The surface area of each cylinder was calculated from the length and diameter of each bone using the equation for the surface area of a closed cylinder. Ten (10) mm was added to the diameter in each case to account for the thickness of the skin covering the lower legs (Mitchell & Skinner, 2004; Sathar et al, 2010).

2.2.4. *Head surface area (HSA, m²)* could not be measured directly because of its fragmented shape, but following the method of Hogan & Skouby (1923) we estimated its surface area from the mass of its skin, as there is a strong correlation between skin thickness, its mass, and its surface area. The relationship between neck surface area and neck skin mass for our giraffes was $0.15 \pm 0.02 \text{ m}^2/\text{kg}$. Neck skin (average $5.7 \pm 0.1 \text{ mm}$, Mitchell & Skinner, 2004) is thicker than head skin (average = 4 mm , Sathar et al, 2010) so the proportional adjustment for the relationship between head skin mass and head skin surface area to $0.21 \text{ m}^2/\text{kg}$ ($5.7 \div 4 * 0.15$).

2.2.5. *Total Surface Area (m²)* was the sum of head, neck, trunk and upper legs, and lower leg surface areas.

2.2.6. *Surface area to mass ratio* was calculated from these data by division. Because mass is related to volume and therefore the cube of linear dimensions, and surface area to the square of linear dimensions, surface area should scale with mass to the power of 0.67 (i.e. 2/3). To determine if this relationship exists for each of the four body parts and for the whole animal we have derived allometric equations to describe it.

2.3. *Data analysis*

Surface area was calculated for each giraffe from components using actual values where possible. Missing values were determined by regression equations. The relationships between

body dimensions and organ dimensions/functions during growth can be described through power functions of the form $y = aM^b$, where a is the intercept, M body mass, and b the slope (Huxley, 1932). No gender differences between giraffes of equivalent body masses were found for any of the variables and the data were combined for further analyses. Allometric regression equations and correlation coefficients were determined using the two variable geometric regression calculator available at www.benchmarkcalculations.com. The standard error of the estimate of Y from X (STEYX) was calculated using EXCEL. Where appropriate, differences were evaluated by the two-tailed t-test assuming unequal variances. P values < 0.05 were regarded as significant.

3. Results

The data analyzed were obtained from young, middle-aged and old animals of both sexes. The body mass of males ranged from 177 to 1358kg, and in females from 141 to 1056kg, a range that allowed ontogenic allometric analysis of changes in surface area with growth. The other physical characteristics of the group are shown in Fig 2. In males average height was 4.4 ± 0.9 m and ranged from 2.61 to 5.47 m, and in females it was 4.0 ± 0.7 m and ranged from 2.44 to 4.79 m. In males average girth was 2.6 ± 0.6 m and ranged from 1.48 to 3.32 m and in females it was 2.4 ± 0.4 m and ranged from 1.28 to 2.92 m. On average body length was 1.1 ± 0.2 m in both males and females and ranged from 0.61 to 1.33 m in males and from 0.58 to 1.30 m in females. There were no significant differences between sexes for height ($P=0.0637$), girth ($P=0.1162$) or body length ($P= 0.1716$) for giraffes of equivalent body mass. The mass of each body part and the proportion contributed to total; body mass by each is shown in Tables 2 & 4. The proportions stay remarkably constant as size increases.

Table 1. Allometry of the rate of change in the variables used to calculate surface area with body mass as the independent variable. N is the number of giraffes measured, missing data were calculated from the allometric equations shown, the mean value is for a giraffe of average body mass (775 kg) and the range is for all 60 giraffes in the study.

Variable	N	Mean (range)	Allometric Equation	STEYX ^O	R ²
Head skin mass (kg)	21	3.1 (0.9-4.9)	$0.024 * Mb^{0.74}$	0.2	.92
Neck skin mass (kg)	21	12.9 (2-27)	$0.0156 * Mb^{1.0}$	1.3	.95
Neck base circumference (cm)	60	152 (80-195)	$11.3 * Mb^{0.39}$	6	.94
Neck apex circumference (cm)	60	67 (41-81)	$9.5 * Mb^{0.29}$	2	.82
Neck length (cm)	60	167 (83-219)	$9.9 * Mb^{0.43}$	6	.95
Girth (cm)	60	253 (128-332)	$20.2 * Mb^{0.38}$	14	.98
Body length (cm)	60	109 (58-133)	$8.7 * Mb^{0.38}$	10	.87
Radius circumference* (cm)	16	19 (11-23)	$2.01 * Mb^{0.34}$	1	.98
Radius length* (cm)	16	70 (39-87)	$7.01 * Mb^{0.35}$	3	.97
Metacarpal circumference* (cm)	16	17 (10-20)	$2.28 * Mb^{0.30}$	1	.95
Metacarpal length* (cm)	39	66 (43-79)	$8.95 * Mb^{0.30}$	3	.91
Tibia circumference* (cm)	16	19 (11-23)	$2.40 * Mb^{0.31}$	1	.98
Tibia length* (cm)	16	58 (35-70)	$7.79 * Mb^{0.30}$	2	.96
Metatarsal circumference* (cm)	16	17 (10-20)	$22.5 * Mb^{0.30}$	1	.99
Metatarsal length* (cm)	37	65 (42-82)	$8.86 * Mb^{0.30}$	3	.90

*From van Sittert et al, 2015; O = Standard error of the estimate of Y from X.

Table 2. Mass of the four body components and the allometric regression equations with body mass (Mb) as the independent variable. Mean values are for a giraffe of average body mass (775kg) and the range is for all 60 giraffes.

Variable (kg)	Mean (range)	Allometric equation	STEYX	R ²
Head	22 (6-39)	$0.064 * Mb^{.88}$	3	.92
Neck	69 (14-138)	$0.064 * Mb^{1.06}$	6	.98
Trunk and upper legs	637 (116-1142)	$0.823 * Mb^{1.0}$	7	.99
Lower forelegs	12 (2-19)	$0.016 * Mb^{.98}$	0.9	.99
Lower hindlegs	10 (2-15)	$.023 * Mb^{.90}$	0.7	.99
Total lower legs	22 (4-34)	$.039 * Mb^{.94}$	1.6	.99

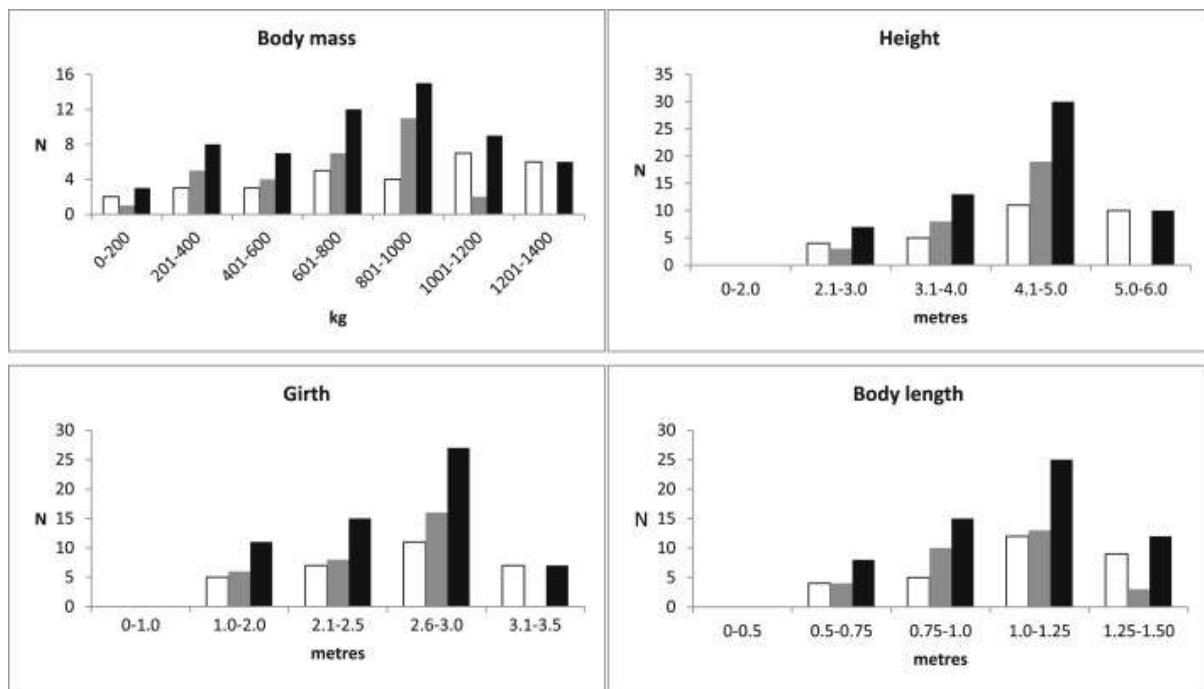


Fig. 2. The distribution of the physical characteristics of the giraffes in this study: male (□); female (■); both (■).

Table 3. Surface area of the four body components and the allometric regression equations with body mass (Mb) as the independent variable. Mean values are for a giraffe of average body mass (775kg) and the range is for all 60 giraffes.

Variable (m ²)	Mean (range) m ²	Allometric equation	STEYX	R ²
Head	0.7 (0.2-1.0)	$0.005 * Mb^{.74}$	0.1	.97
Neck	2.0 (0.5-3.0)	$0.011 * Mb^{.78}$	0.1	.99
Trunk and upper legs	4.0 (1.0-6.2)	$0.027 * Mb^{.75}$	0.4	.96
Lower legs	1.1 (0.4-1.6)	$0.027 * Mb^{.56}$	0.1	.98
Total	7.5 (2.1-11.8)	$0.071 * Mb^{.70}$	0.5	.98

Table 4. The relative (%) mass and surface area of the four body components. The range is for all 60 giraffes.

Body part	Mass (kg)	Mass (% of total body mass)	Surface Area (m ²)	Surface Area (% of total surface area)	Surface area: mass (m ² .kg ⁻¹)	Surface area : mass (range)
Head	6-39	2.9±0.5	0.2 - 1.0	8.9±0.7	0.033±0.005	0.052-0.022
Neck	14-138	9.0±0.8	0.5 - 3.0	24.4±1.3	0.15±0.02	0.21-0.10
Trunk & upper legs	117-1147	85.5±1.0	1.0 - 6.2	51.0±2.3	0.006±0.001	0.009-0.005
Lower legs	4-34	2.6±0.1	0.4 - 1.6	15.6±1.5	0.06±0.02	0.11-0.05
All	141-1358	100	2.1 - 11.8	100	0.009±0.002	0.014-0.007

The variables used to calculate surface area and the allometric equations describing their relationship with changes in body mass are shown in Table 1. The proportion of total surface area that each of the four components contribute is shown in Table 4, together with the surface area to mass ratio of each. The allometry of the prediction of surface area from the mass of each body part is shown in Table 5.

Table 5. The allometry of prediction of surface area (m^2) from the mass (kg) of each body part.

Body part	Allometric equation	STEYX (m^2)	R ²	95% CI (exponent)
Head	$0.06 * M_{head}^{.78}$	0.08	.93	.73-.84
Neck	$0.08 * M_{neck}^{.73}$	0.12	.99	.71-.75
Trunk & upper legs	$0.03 * M_{trunk}^{.75}$	0.37	.96	.71-.79
Lower legs	$0.19 * M_{leg}^{.60}$	0.05	.99	.58-.62
All	$.07 * M_{body}^{.70}$	0.48	.98	.68-.73

The allometry of the absolute surface area of the components of total body surface area with body mass as the independent variable is shown in Table 3. The average surface area of giraffes calculated from the sum of trunk and upper legs, head, neck and lower legs was $7.3 \pm 2.5 m^2$ with a range of $2.1 m^2$ for a 141 kg female giraffe to $11.8 m^2$ for an adult male weighing 1358 kg. Fig 3A illustrates the change in total surface area in giraffes as their body mass increases compared to surface area predicted from Stahl's general mammal equation. The average total surface area of the giraffes with the body mass of those in our study as predicted by Stahl's equation is $7.9 \pm 2.5 m^2$ which is not significantly different to the surface area we have derived (Fig 3A; $P = 0.1843$). Relative surface area expressed as $cm^2 \cdot kg^{-1}$ declined as body mass increased with juvenile giraffes having a relative surface area approximately twice that of an adult (Fig 3B).

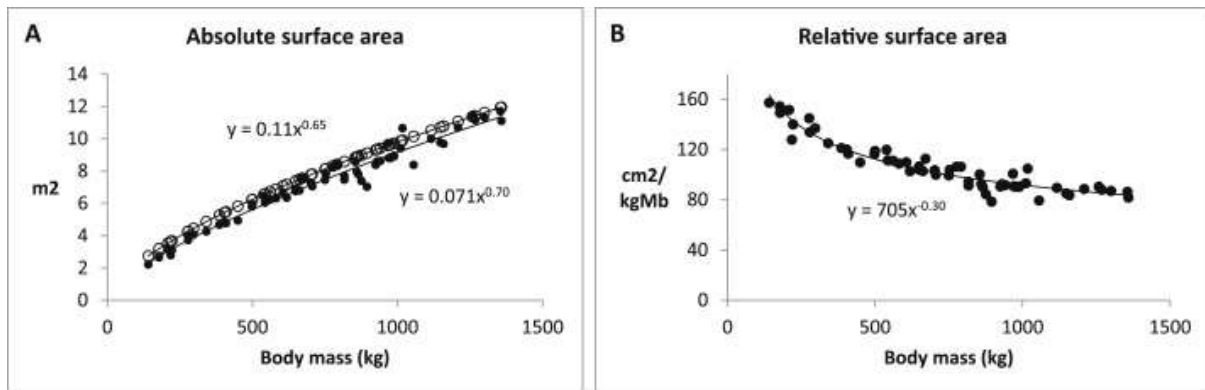


Fig. 3. A. The allometry of the increase in total surface area of giraffe (●) with increasing body mass and surface area (○) predicted from Stahl's general mammal equation. Stahl's equation is above, the giraffe equation below. **B.** The decrease in relative surface area with increases in body mass.

4. Discussion

The most widely accepted explanation for the evolution of tallness in giraffes is that it confers a feeding advantage, and many studies have confirmed that tallness does give giraffes access to browse free of competition from smaller browsers (e.g. Cameron & du Toit, 2007). Brownlee (1963) argued that this explanation applied best to large adult males and an advantage for them is unlikely to be an advantage for the species generally. Thus he proposed that if their shape conferred a more general advantage like better thermoregulation, and in particular better heat loss, giraffes of all sizes and ages would benefit, not just the tallest, and it would exert greater selective pressure than does better access to browse. Although he did not quantify or in any way describe how a dolichomorphic shape could aid heat loss Brownlee was extrapolating from a study that concluded that men who lived in desert or tropical surroundings had a high surface area: body mass ratio (Schreider, 1950), which itself is an extension of Allen's Rule: endotherms living in hot climates should be long and thin and should have a high surface area to body mass ratio (Allen, 1877). The implication for giraffes is that their elongated legs and neck and slender form increase the surface area: mass ratio

and thus provide the anatomical substrate for heat loss by convection and evaporation, in the same way that they do in dolichomorphic humans.

Giraffes have a mean body temperature of 38.5 °C and use a wide range of thermoregulatory mechanisms to regulate it (Mitchell and Skinner, 2004), but whether their shape contributes to their thermoregulatory competence has not been analyzed. In assessing this possibility we set out to measure surface area and mass in *G.c. giraffa* extant in Zimbabwe. Contrary to the one previous estimate of the surface area of a ~1600 kg giraffe (17.7 m²; Henderson and Naish, 2010), our calculations show that the surface area of a giraffe of that body mass would be about 12.4 m². Furthermore we have found that the total body surface area of giraffes is not significantly different to the surface area predicted from equations for standard mammals (Fig. 3; Stahl, 1967). That conclusion is contrary to expectations and requires an explanation. An explanation for it is that the length of a giraffe's body measured from the base of the neck to the base of the tail (Fig. 1) is significantly shorter than that of a standard “cylindrical” mammal of similar mass, and, for example, is significantly shorter than it is in cattle of the same mass. We fitted allometric equations to the data of (Hogan and Skouby 1923) for cattle ranging in body mass from 55 kg to 883 kg. Our equations predicted that body length (cm) in cattle would be given by $20.0 * Mb^{0.32}$ ($R^2 = 0.87$; STEYX = 13 cm; N = 37), and girth (cm) by $16.1 * Mb^{0.41}$ ($R^2 = 0.98$; STEYX = 14 cm; N = 37). For an ox weighing 775 kg, the equations predict a length of 168 cm, which is 54% more than the body length, and a girth of 246 cm, which is 8% less than the girth, of a 775 kg giraffe (Table 1). From these data SA (m²) of the trunk of an ox is $= 0.14 * Mb^{.58}$ ($R^2 = 0.97$; STEYX = 0.41 m²), and based on cylindrical geometry, the surface area of the trunk and upper legs of a 775 kg ox would be 6.64 m². The equation that describes the SA of a giraffe's trunk and upper legs is $0.03 * M_{trunk}^{.75}$ (Table 5) and the SA of a 775 kg giraffe is then 4.4 m², or two-thirds that of a

775 kg ox. In giraffes the trunk and upper legs provide less (51%) and their long necks and lower legs more (40%) of surface area. The combination produces a surface area that is not significantly different to that of an ox and a surface area to mass ratio similar to any other mammal that conforms to Stahl's equation. Thus we have concluded that the dolichomorphic shape of a giraffe does not result in either a larger surface area or a surface area larger than would be expected from its mass. If Brownlee was correct in concluding that “*dolichomorphism is an aid in achieving heat loss*”, it is not because giraffe have a high surface area to mass ratio. In general the ratio of SA to mass for the whole body meets the expectation that it should scale with mass to the power of 0.67 (Table 5). The mean exponent for the ratio of leg SA: mass of 0.60 shows that leg surface area increases slower than expected, which is offset by a faster rate of increase in head, neck and trunk SA (mean exponent = 0.75).

Heat exchange is not simply a function of surface area but also of heat transfer coefficients. For animals of the size of giraffes, for a given difference in temperature between body surface and surrounding air, the rate of convective heat transfer from the surface of the body is inversely proportional to the square root of the diameter of the body element from which heat is being lost (Mitchell, 1974). The necks (mean diameter=68±13cm; range 39-88 cm) of giraffes have average diameters far lower than the average diameter of the thorax (= 80±16 cm; range 41-106 cm) so the rate of convective heat transfer from the neck will be 9% higher, per unit of surface area, than it is from the trunk. Moreover, the lower legs have a diameter 13 times narrower (mean diameter=53±8 mm; range 33-65 mm) than the mean diameter of the neck so the legs contribute far more to convective heat transfer than does the neck. The contribution of the legs and neck is amplified when a giraffe moves because convective heat transfer is also proportional to the square root of the wind speed over them, and leg

movement creates a higher wind speed over the legs than over the trunk. In addition, long legs elevate the giraffe above the boundary layer of intense heat and low wind speed close to the earth's surface (Wheeler, 1991a) into cooler a layer, which increases convective cooling.

High convective heat transfer coefficients in the neck and legs help giraffe dissipate heat only if air temperature is below skin temperature. As soon as air temperature exceeds skin temperature, heat will transfer from the environment to the animal by convection. Then the enhanced convective heat transfer bestowed by a dolichomorphic shape and leg movement becomes a major disadvantage. That disadvantage would have been amplified if the giraffe had an unusually high surface area to mass ratio. But other consequences of a dolichomorphic shape benefit thermoregulation even at ambient temperatures higher than skin temperature. The first of these relates to radiant heat exchange. In Etosha National Park in Namibia, as ambient temperature increased progressively from 20 to 37 °C, the proportion of 290 giraffes studied facing the sun, rather than standing perpendicular to incident solar radiation, increased from 35% to 60% (Kuntzsch and Nel, 1990). By having a dolichomorphic shape and pointing their heads towards the sun, giraffes can reduce the proportion of body surface intercepting incident solar radiation to well below the proportion in a "cylindrical" animal. That advantage accrues to other taxa, including ants (Sommer and Wehner, 2012) and snakes (Robinson and Hughes, 1978) active in the Namib Desert sun, in wildebeest (Maloney et al., 2005), and has been considered an advantage of hominin bipedalism allowing invasion of open plains (Wheeler, 1991b).

Where large enough refuges are available, giraffe can reduce radiant heat loads better by seeking shade, as they do in Etosha National Park (Kuntzsch and Nel, 1990). Provided that temperature in the shade is below skin temperature the advantage of their dolichomorphic shape is restored. Body size has a significant effect on behaviour (Kuntzsch and Nel, 1990). When ambient temperatures were greater than 30 °C and solar radiation was high, more than 80% of adult males, which typically have an body mass >1000 kg, faced the sun, as did 60%

of adult females ($Mb > 800$ kg) and 20% of calves ($Mb < 300$ kg) but 70% of calves selected shade, as did 32% of females and 13% of males. This behaviour is consistent with the idea that smaller animals exposed to intense solar radiation gain heat at a higher rate per unit of body mass than do larger ones because they have a larger relative surface area, an argument that applies as much to species of different size as it does to small and large individuals of the same species (Jessen, 2001). Giraffe calves have a surface area: mass ratio 1.6 times more than that of an adult (145 vs 91 $\text{cm}^2 \text{kg}^{-1} Mb$; Fig. 3B).

A second potential benefit of a dolichomorphic shape relates to evaporative cooling, and it is the only benefit that applies at ambient temperatures such that radiation and convection are imposing a heat load on the body. It derives from the Lewis Relationship (Mitchell, 1976) which holds that the physical factors that determine evaporative heat transfer coefficient are identical to those that determine the convective heat transfer coefficient. So narrow diameter of body elements (and increasing wind speed) increase evaporative heat transfer by exactly the same amount as they increase convective heat transfer, and thus the dolichomorphic shape of giraffes enhances the rate of evaporative cooling. Evaporative loss takes place down a water vapour pressure gradient, and giraffe are unlikely ever to be in an environment in which the ambient water vapour pressure is higher than that on their skins, so they always will be able to invoke evaporative cooling, no matter how hot the environment. Evaporative cooling requires that giraffe can evaporate water off their skins, which, for most large mammals, would require an ability to sweat. Giraffe have active sweat glands (Dimond & Montagna, 1976) concentrated in the patched areas of the skin on the legs, neck, and trunk (Mitchell & Skinner, 2004). However sweat rate has not so far been measured in giraffes. Large mammals do not have to be able to sweat to invoke evaporative cooling. Without sweat glands, elephants regulate rates of water diffusion through their skin to produce effective

cooling (Dunkin et al, 2013).

When Brownlee contended that it was facilitation of heat loss that underpinned the evolution of the giraffe's dolichomorphic body shape, he offered no explanation of how it would do so. We have addressed four possible mechanisms based on data from 60 *G.c. giraffa*. Whether our data can be applied to other regional variants will depend on their dimensions. *G.c. giraffa* extant in South Africa has identical dimensions to those in Zimbabwe, but *G.c. capensis* in Namibia may be smaller (Mitchell et al., 2013b). No comparative data on dimensions of other variants are known but if they are different thermoregulatory mechanisms may differ in magnitude but not in their effect, and we know now, as a result of our estimates of surface area and mass in 60 giraffe, that, surprisingly, the heat loss mechanisms are not related to a high surface area to mass ratio. Both the benefits of enhanced convective heat loss and the benefits of a high ratio of surface area to body mass, had there been a high ratio, would have manifested only in environments in which air temperature was below skin temperature. In environments in which air temperature exceeded skin temperature, those presumed benefits would transform to disadvantages.

In what thermal environments did giraffe evolve their dolichomorphic shape? Their morphology would have been shaped by the conditions that existed before or at the time of appearance of *Bohlinia* the first genus with a giraffe-like shape and reinforced by the conditions that existed at the time of the radiation of *Giraffa*. *Bohlinia* lived in the last part of the Miocene between 9 and 7 Mya (Geraads, 1986) and the radiation of *Giraffa* occurred 5-3 Mya. This latter period was a time of substantial climate change brought about by the second phase of the Himalaya uplift and the retreat of the paratethys sea (Ramstein et al., 1997; Zhiseng et al., 2001), changes that caused tropical vegetation to give way to an arid, open

woodland savannah (Janis, 1993), which is the preferred current habitat of giraffes. There is no doubt that in that habitat an increase in height would have given them access to browse unavailable to smaller browsers. Temperatures then were warmer than they are today (Knorr et al., 2011), but, on average, still well below giraffe skin temperature. Occupation of open woodland then, as it does now, would have exposed the giraffe's ancestral lineage to high solar radiation, and evolution of a dolichomorphic shape would have reduced its impact by reducing the area of interception. Finally, the giraffe's narrow body elements, and their long necks and legs offer benefits for convective as well as evaporative heat loss, even if they moved into an environment of ambient temperatures above skin temperature and even if their long necks and legs were not used to reach high level browse. So Brownlee's contention is feasible. It is, of course, quite impossible to gauge the relative contributions that the many anatomical, physiological, biochemical and behavioural adaptations in giraffes have made to the evolution of their shape. However, our analysis here suggests that the thermoregulatory advantages that flow from an elongated, dolichomorphic shape are significant and in our view may have supplemented, or been a component of, the selection pressures that resulted in the shape of giraffes. As Brownlee noted “*dolichomorphism is an aid in achieving heat loss—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*”. We agree.

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