

Scaling of plantar pressures in mammals

F. Michilsens^{1,2}, P. Aerts^{1,3}, R. Van Damme¹ & K. D'Août^{1,2}

¹ Laboratory for Functional Morphology, University of Antwerp, Wilrijk, Belgium

² Centre for Research and Conservation, Antwerp, Belgium

³ Department of Movement and Sport Sciences, Ghent University, Ghent, Belgium

Keywords

plantar pressure; pedobarography; mammals; scaling; foot use.

Correspondence

F. Michilsens, Laboratory for Functional Morphology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium.
Email: fana.michilsens@ua.ac.be

Editor: Nigel Bennett

Received 4 March 2009; revised 20 May 2009; accepted 11 June 2009

doi:10.1111/j.1469-7998.2009.00611.x

Abstract

The interaction of the limbs with the substrate can teach a lot about an animal's gait mechanics. Unlike ground-reaction forces, plantar pressure distributions are rarely studied in animals, but they may provide more detailed information about the loading patterns and locomotor function of specific anatomical structures. With this study, we aim to describe pressures for a large and diverse sample of mammalian species, focusing on scaling effects. We collected dynamic plantar pressure distributions during voluntary walking in 28 mammal species. A dynamic classification of foot use was made, which distinguished between plantiportal, digitiportal and ungulportal animals. Analysis focused on scaling effects of peak pressures, peak forces and foot contact areas. Peak pressure for the complete mammal sample was found to scale to $(\text{mass})^{1/2}$, higher than predicted assuming geometric similarity, and we found no difference between the different types of foot use. Only the scaling of peak force is dependent on the dynamic foot use. We conclude that plantar peak pressure rises faster with mass than expected, regardless of the type of foot use, and scales higher than in limb bones. These results might explain some anatomical and behavioural adaptations in graviportal animals.

Introduction

In order to move around, animals have to interact with their environment. Propulsive forces are exerted on the surroundings and the resulting substrate reaction forces act on the animal's body. In legged terrestrial locomotion, the latter forces are localized in time (during a limb's stance phase) and space (foot contact area), thus countering inertia and gravity only during the ground contact phases of the limbs. Consequently, stresses (force/area) on the supporting structures are typically high and transient.

The total ground reaction force (GRF) of all ground contacting limbs should be, on average, equal to the animal's weight (during level locomotion). Therefore, it can safely be assumed that GRF-related measures (such as vertical peak force) should be largely mass dependent, whereas the stress at the interface between the substrate and the limb will also depend on the contact area. This area is likely to be influenced by differences in limb posture (plantigrade, digitigrade and unguligrade; Chi & Roth, 2004), but also the dynamics of the roll-off of the contacting components of the foot during locomotion might instantaneously determine the size of the load-bearing surface.

To our knowledge, the only study that has attempted to correlate body mass, foot contact area and limb posture is that of Chi & Roth (2004). These authors found that contact areas as obtained from static footprints are (at any body mass) indeed larger in plantigrades than in digitigrades, which

in turn show a larger contact area than the unguligrades. The size of these areas increases more rapidly with body mass in unguligrades than in digitigrades and plantigrades (the latter showing the smallest body mass-specific exponent). Important, however, is that the exponent of the relationship between surface area and body mass is, in all groups, smaller than '1'. This suggests, when taking body weight (BW) as a measure for the forces involved, that the pressure (BW/contact area) at the body-ground interface becomes larger with body mass, but that it rises less fast than mass.

Yet, the unknown factor potentially influencing the precise nature of these relationships in the context of mechanical stress at the interface is the dynamics of the foot roll-off. Assessing the spatio-temporal pressure distribution at the interface during locomotion might reveal how load bearing changes over time and which parts of the foot are effectively loaded.

In this study, plantar pressure data are collected for 28 quadrupedal mammals during voluntary walking. First, the common postural classification (plantigrade, digitigrade and unguligrade) is functionally reconsidered on the basis of these pressure distributions. For instance, animals can posturally be plantigrade, but take the entire load only on the digits. Where appropriate, species are transferred to another class judging the pattern of experimentally measured load bearing. In order to avoid confusion with the terminology primarily based on posture, we introduce the

functional classes of plantiportal, digitiportal and unguliportal foot use.

Next, peak pressures occurring during ground contact of a limb are related to body mass. Peak pressures are biologically more interesting than average pressures, because it is the maximum stress that can cause injuries to the feet (stress fractures: Neely, 1998 and Murphy, Connolly & Beynon, 2003). Therefore, we can expect a maximum peak pressure at which an animal can locomote without getting injured. Whereas the impulse of the GRFs during steady locomotion must be related to body mass (because impulse divided by time must equal BW during horizontal locomotion), the ratio of the peak force (or BW) over the total contact area does not necessarily reflect the peak stress at the interface with the ground, as the latter will also depend upon roll-off dynamics. Given the rather uniform material properties of load-bearing tissues in mammals (Close, 1972; Currey, 1981; Bennett *et al.*, 1986; Biewener, 1991) we could postulate that the dynamic peak pressures will be mass independent in each of the functional classes. However, it makes sense that the (peak) pressure will increase with body mass, because the volume of the body will increase with a different factor than the surface of the feet. If this is the case, we expect isometric similarity, with peak pressure scaling to $(\text{mass})^{1/3}$, like

Bennett (1999) found for plantar pressures in marsupials during hopping and Biewener (2005) in limb bones of mammals.

Materials and methods

Subjects

Animals to be analysed were selected from the collection of the RZSA (Royal Zoological Society of Antwerp, i.e. Antwerp Zoo and Wild Animal Park Planckendael). They were selected on several criteria: mass (minimum 3–4 kg), size of paws (they should at least cover four pressure sensors of 0.4 cm² each) and behaviour (very elusive, nervous or aggressive animals were omitted). In total, 28 mammal species were retained, of 18 families and eight orders, with an average mass of 279 kg and a range of mass from 4 to 3000 kg. Table 1 lists the mammals for which pressure measurements were successfully taken. This sample includes previous measurements of a bonobo *Pan paniscus* as an example of a typical plantigrade and plantiportal mammal (data from Vereecke *et al.*, 2003). Based on the general pressure pattern and skeletal background information, the animals were divided into three groups: plantiportals,

Table 1 Subject data, with foot posture (post: Pp=plantiportal; Dp=digitiportal and Up=unguliportal), the number of individuals (# ind), the number of analysed individual paws in total (# analysed paws) and the location where the measurements took place (location: P=animal park Planckendael; Z=Antwerp Zoo)

| English name | Latin name | Ordo | Family | Post | # ind | # analysed paws | Location |
|----------------------|----------------------------------|----------------|-----------------|------|-------|-----------------|----------|
| Cheetah | <i>Acinonyx jubatus</i> | Carnivora | Felidae | Dp | 2 | 8 | P |
| Snow leopard | <i>Panthera uncial</i> | Carnivora | Felidae | Dp | 1 | 4 | P |
| Raccoon | <i>Procyon lotor</i> | Carnivora | Procyonidae | Pp | 2 | 2 | P |
| S-American coati | <i>Nasua nasua</i> | Carnivora | Procyonidae | Pp | 1 | 8 | Z |
| Alpaca | <i>Lama guanicoe</i> | Artiodactyla | Camelidae | Dp | 3 | 17 | P |
| Camel | <i>Camelus bactrianus</i> | Artiodactyla | Camelidae | Dp | 1 | 3 | P |
| Scimitar-horned oryx | <i>Oryx dammah</i> | Artiodactyla | Bovidae | Up | 1 | 1 | P |
| Takin | <i>Budorcas taxicolor</i> | Artiodactyla | Bovidae | Up | 1 | 6 | Z |
| Goat | <i>Capra hircus</i> | Artiodactyla | Bovidae | Up | 6 | 11 | P |
| African buffalo | <i>Syncerus caffer</i> | Artiodactyla | Bovidae | Up | 1 | 2 | Z |
| Himalayan thar | <i>Hemitragus jemlahicus</i> | Artiodactyla | Bovidae | Up | 2 | 14 | Z |
| Wild boar | <i>Sus scrofa</i> | Artiodactyla | Suoidae | Up | 3 | 15 | P |
| Common warthog | <i>Phacochoerus africanus</i> | Artiodactyla | Suoidae | Up | 1 | 4 | Z |
| Babirusa | <i>Babirusa babirusa</i> | Artiodactyla | Suoidae | Up | 1 | 10 | Z |
| Moose | <i>Alces alces</i> | Artiodactyla | Cervidae | Up | 1 | 8 | P |
| Caribou | <i>Rangifer tarandus</i> | Artiodactyla | Cervidae | Up | 6 | 10 | Z |
| Giraffe | <i>Giraffa camelopardalis</i> | Artiodactyla | Giraffidae | Up | 2 | 2 | Z |
| Hippopotamus | <i>Hippopotamus amphibius</i> | Artiodactyla | Hippopotamidae | Dp | 2 | 4 | Z |
| Elephant (Indian) | <i>Elephas maximus</i> | Proboscidea | Elephantidae | Pp | 2 | 3 | Z |
| Aardvark | <i>Orycteropus afer</i> | Tubulidentata | Orycteropodidae | Pp | 2 | 6 | Z |
| Tamandua | <i>Tamandua tetradactyla</i> | Xenarthra | Myrmecophagidae | Pp | 1 | 8 | Z |
| Armadillo | <i>Dasypus novemcinctus</i> | Xenarthra | Dasypodidae | Pp | 1 | 19 | Z |
| N-American porcupine | <i>Erethizon dorsatum</i> | Rodentia | Erethizontidae | Pp | 3 | 33 | Z |
| Coyu | <i>Myocastor coypus</i> | Rodentia | Myocastoridae | Pp | 3 | 14 | Z |
| Capybara | <i>Hydrochoeris hydrochaeris</i> | Rodentia | Hydrochoeridae | Pp | 3 | 7 | P |
| Tapir | <i>Tapirus indicus</i> | Perissodactyla | Tapiridae | Dp | 1 | 1 | Z |
| Donkey | <i>Equus asinus</i> | Perissodactyla | Equidae | Up | 2 | 7 | P |
| Bonobo | <i>Pan paniscus</i> | Primates | Hominidae | Pp | 5 | 7 | P |

digitiportals and unguliportals, referring to the part of the foot that carries the BW during walking (analogous to plantigrade, digitigrade and unguligrade as a static division of leg postures).

Set-up and data analysis

A pressure plate (RSscan International, Olen, Belgium) providing data at a high spatial and temporal resolution (pressure resolution: 2.53 sensors cm^{-2} and 300 samples s^{-1}) was connected to a laptop with specialized software (Footscan USB 7.0 Scientific). In this way, the pressure distribution and the centre of pressure movements could be studied during walking. Wooden plates mimicking the pressure plate were placed in the cages before measurements to let the animals get accustomed to the foreign object. The exact set-up was different every time because the animals had to stay in their usual enclosures. Typically, the plate was placed in between two cages, so that the animal had to walk over the plate if it was lured from the one to the other cage. The animals were manipulated as little as possible to avoid interruption of their normal gait pattern. All animals were thus free to walk over the pressure plate at their desired speed, which is (at least in humans) very close to the 'optimal' speed (e.g. Ralston, 1958; Saibene & Minetti, 2003).

A total of 227 measurements of individual paws were analysed. For every animal, the variables sex, age, mass (mass was estimated if direct measurements were impossible) and paw (left, right, hind and front) were registered. These data were used to create a general overview of the sampling set, but only mass was used for statistical analysis. Footscan software (7.8.07 and in-house developed LabView software) was used to extract the necessary parameters: peak pressure (N cm^{-2}), peak force (N) and contact area (cm^2).

Statistical analysis

Owing to the large mass range, the data were log₁₀ transformed. Averages per species were taken, because this paper focuses on inter-species variation and not on intra-species variation.

Several regression models [ordinary least square (OLS), reduced major axes (RMA), phylogenetic generalized least squares (PGLS) with real and constant branch lengths and Felsenstein-independent contrasts with real and constant branch lengths and using Pagel's, Grafen's and Nee's method] were run, of which the latter two accounted for phylogenetic relationships (which were taken from Bininda-Emonds *et al.*, 2007). SPSS v13.0 was used for the non-phylogenetic analysis and COMPARE v4.6 (Martins, 2004) and PDAP v6.0 (Garland *et al.*, 1993) for the phylogenetic analyses. Allometries between mass and contact area were evaluated, as well as between mass and peak force and between mass and peak pressure. For these analyses, each species was attributed to one of the three 'foot use' groups: plantiportals, digitiportals or unguliportals. If there was an effect of foot use, an ANCOVA was done with mass as

covariate and foot use as factor to know which groups differed from each other.

Results

Dynamic foot use

Although most animals have a dynamic foot posture (e.g. plantiportal) that corresponds to the classical division based on static foot postures (e.g. plantigrade), some animals shift from category. The classical division is based on the near contact between foot bones and the ground during a static posture. Plantigrades stand on their entire foot, while digitigrades only stand on the phalanges and metacarpals and unguligrades only on the phalanges. During walking (dynamic posture), however, it is possible that some skeletal parts of the foot do carry load, although the foot posture suggests otherwise. Alternatively, the pressure recordings may show that only a small part of the foot sole carries the load. The hippopotamus and tapir are typically categorized as unguligrades. However, based on dynamic pressure measurements, we classify them as digitiportal, because it is clear that not only their phalanges carry the weight, but also the carpals (Fig. 1). Likewise, the elephant shifts from the digitigrade category to the plantiportals because of the fat tissue on which the heel bone rests (Benz, 2005; Weissen-gruber *et al.*, 2006; Miller *et al.*, 2008) and which likely causes the whole foot skeleton to be weight bearing (Fig. 2).

Effect of mass and dynamic foot posture on contact area, peak force and pressure during walking

All different regression models gave similar results. Therefore, we chose to present only the results of two models, namely RMA and PGLS (with real branch lengths), respectively excluding and including phylogenetic relationships. A strong overall correlation was found between mass ($\log M$) and peak force ($\log F$) (Table 2). All analyses resulted in a similar relationship with an exponent close to one ($P < 0.001$), showing that peak force can be regarded as proportional to body mass, thus confirming the hypothesized isometric conditions for this parameter. However, the foot use (unguliportal, digitiportal and plantiportal) has a significant effect on peak force (Table 3; $P = 0.021$). More specifically, the effect of mass on peak force in plantiportals, which have the biggest slope (0.889), differed significantly from that in unguliportals (slope = 0.668; $F = 6.79$; d.f. = 19; $P = 0.017$) and almost significantly from that in digitiportals (slope = 0.785; $F = 3.98$; d.f. = 13; $P = 0.067$). Between unguliportals and digitiportals no difference was found for peak force ($F = 0.59$; d.f. = 15; $P = 0.45$). This indicates that in the different groups the effect of mass on peak force cannot always be regarded as isometric. In Fig. 3a, the different effects of mass on peak force for the different types of foot use are visualized.

A significant relationship with an exponent of $c. 0.5$ (Table 2, $P < 0.001$) was found between $\log M$ and the

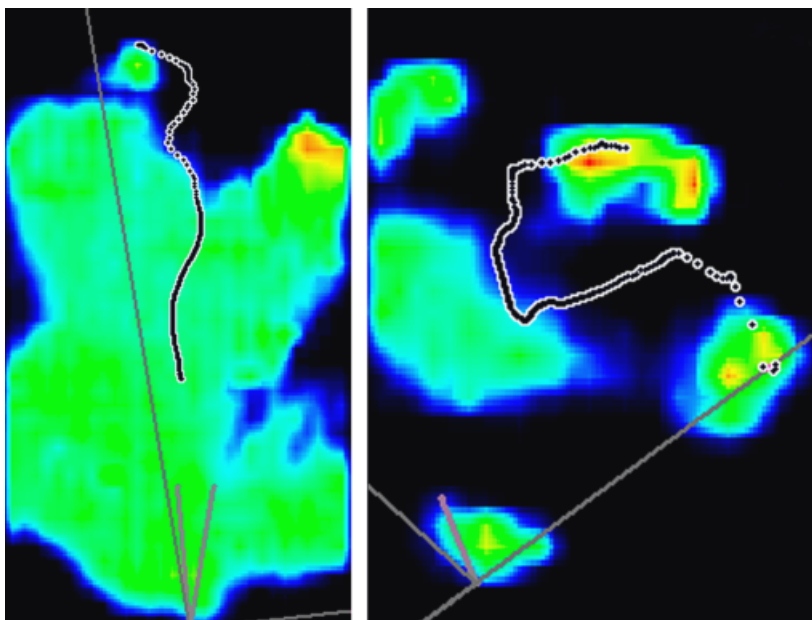


Figure 1 Pressure distribution during walking of hippopotamus (left) and tapir (right). Notice that also the carpals bear pressure, indicating these animals belong to the digitiportal animals. (Note: the black, bended line shows the course of the centre of pressure; the grey, straight line should be ignored for our purposes).

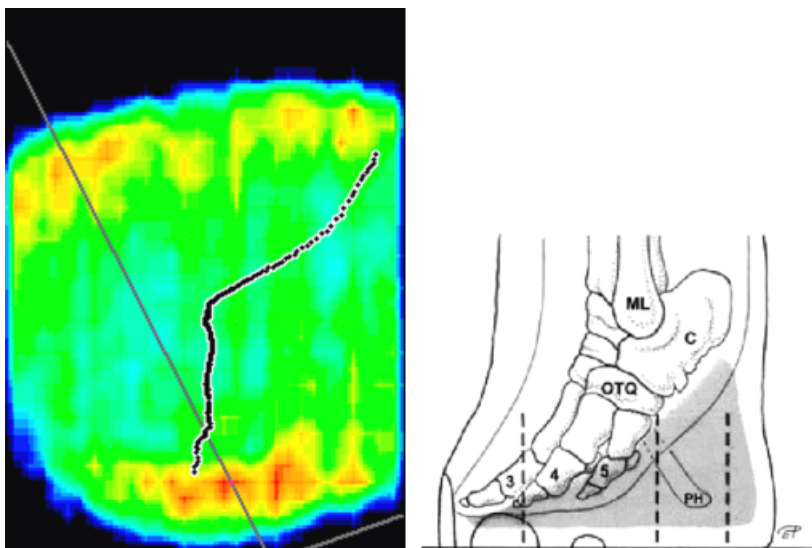


Figure 2 Left: pressure distribution during walking of elephant. Although it is not very clear from this picture that the entire foot bears pressure, the right picture shows clearly that the calcaneus rests on the cushion (picture taken from Weissengruber *et al.*, 2006) indicating that the entire foot will carry the loading during walking and thus elephants belong to the plantiportal animals (Note: the black, bended line shows the course of the centre of pressure; the grey, straight line should be ignored for our purposes).

measured peak pressures ($\log P$). This means that peak pressure can be regarded as proportional to $(\text{body mass})^{1/2}$. There is no significant effect of foot use (Table 3; $P = 0.14$), however, there seems to be a trend that unguliportals have higher peak pressures that rise less fast with body mass than the pressures in plantiportals (Fig. 3b). Note that the

regression line for the digitiportal animals is not significant ($P = 0.231$).

For the contact surface of the paw, all analyses show a relationship of around 0.63 between $\log M$ and the logarithmic value of the measured contact surface ($\log S$) (Table 2, $P < 0.001$). As a consequence, the measured contact surface

Table 2 Effect of mass on peak force, peak pressure and contact area during walking according to two statistical models (with and without phylogenetic relations)

| X | Y | Regression model | r^2 | Intercept | Slope | se | 95% CI | |
|--------------|--------------|--|-------|-----------|-------|-------|--------|-------|
| Log <i>M</i> | Log <i>F</i> | RMA | | 0.847 | 0.922 | 0.052 | 0.815 | 1.029 |
| | | PGLS ($\alpha = 2.50$) real branch lengths | 0.92 | | 0.870 | 0.100 | 0.770 | 0.970 |
| Log <i>M</i> | Log <i>P</i> | RMA | | 0.719 | 0.647 | 0.068 | 0.507 | 0.787 |
| | | PGLS ($\alpha = 15.5$) real branch lengths | 0.68 | | 0.530 | 0.140 | 0.390 | 0.670 |
| Log <i>M</i> | Log <i>S</i> | RMA | | 0.318 | 0.666 | 0.036 | 0.592 | 0.740 |
| | | PGLS ($\alpha = 15.5$) real branch lengths | 0.89 | | 0.630 | 0.08 | 0.55 | 0.71 |

PGLS, phylogenetic generalized least squares; RMA, reduced major axes

Table 3 Effect of foot use on regression models

| Covariate | Dependent variable | Factor | Regression model | Covariate \times factor effect | | Factor effect | |
|--------------|--------------------|----------|------------------|----------------------------------|----------|-----------------|----------|
| | | | | <i>F</i> (2,22) | <i>P</i> | <i>F</i> (2,24) | <i>P</i> |
| Log <i>M</i> | Log <i>F</i> | Foot use | OLS (U, D, P) | 1,76 | 0.19 | 4,53 | 0.021 |
| Log <i>M</i> | Log <i>S</i> | Foot use | OLS (U, D, P) | 0,10 | 0.9 | 0,28 | 0.75 |
| Log <i>M</i> | Log <i>P</i> | Foot use | OLS (U, D, P) | 0,64 | 0.54 | 2,15 | 0.14 |

OLS, ordinary least square.

can be roughly regarded as proportional to (body mass)^{2/3} (a predicted slope of 0.67 lying within the confidence interval). Most remarkable is that there is no significant effect of foot use (Table 3; $P = 0.75$), indicating that plantiportals, digitiportals and plantiportals of the same body mass, have similar contact surfaces during walking (Fig. 3c).

Discussion

Based on the rather uniform material properties of load-bearing tissues in mammals (Close, 1972; Currey, 1981; Bennett *et al.*, 1986; Biewener, 1991) it would seem sensible if every animal had the same absolute plantar peak pressure (and thus, tissue loading) regardless of body mass. Larger animals would then be expected to have larger contact areas, to adjust their locomotion behaviour (e.g. by using a cautious gait) or to have 'cushioning' materials underneath the foot sole to reduce the peak pressure on the foot bones. If no measures are taken (i.e. constant contact area) peak plantar pressures will increase as body mass and thus peak force increase. However, in the hypothetical case of isometry we expect that plantar peak pressure will rise with (body mass)^{1/3}, because pressure equals force divided by area and force will be proportional to body mass while contact area will be proportional to (body mass)^{2/3} (Table 4). Isometry is found valid during hopping in marsupials (Bennett, 1999) and for pressures in mammalian limb bones during walking (Biewener, 2005) and indicates that although more heavy animals will have larger absolute pressures, the pressure will increase slower than body mass. Again, larger animals are expected to have certain adaptations to cope with these larger plantar pressures.

Our dataset, however, indicates a relation of peak pressure to (body mass)^{1/2}, meaning not only that larger animals do not succeed in lowering their plantar pressures to be

equal with those of smaller animals, but they do not even maintain isometric similarity (Table 4). On the contrary, plantar peak pressures increase even faster with body mass than expected under isometry, namely with (body mass)^{1/2} instead of with (body mass)^{1/3} (Table 4). How can this high scaling effect of peak pressure with body mass be explained? Firstly, although we found a scaling effect between body mass and contact area that is not significantly different from the isometric hypothesis (factor of 0.67), it is consistently lower for all regression models (average of 0.63, Table 2). If this difference is biomechanically meaningful and combined with the fact that peak force does scale (nearly) isometrically (not significantly different from 1, Table 2), this can partly explain why peak pressure scales higher than under isometric circumstances. Secondly, although we measured the contact area during walking, this is still a generalized image of the foot use. The instantaneous contact area at which the peak pressure arises can be smaller than the measured contact area during the entire roll-off. If, for example, larger animals tend to use smaller parts of their feet during some part of the contact phase, then this can also partly explain the high scaling effect. Thirdly, it is also possible that the scaling effect found is some sort of compromise between isometric scaling and some other effects, biomechanical or developmental.

Now we know that large animals have high (and higher than expected) peak pressures during quiet walking, we predict that these animals will have adaptations to cope with these large stresses, especially during faster locomotion. In the limb bones, the pressure scales isometrically (Biewener, 2005) and heavy animals tend to walk with straighter legs (morphological and behavioural adaptations, e.g. elephant). If their peak pressures would increase, the safety threshold could be overrun and the bone would break. However in the foot, it is not only the bone that carries the

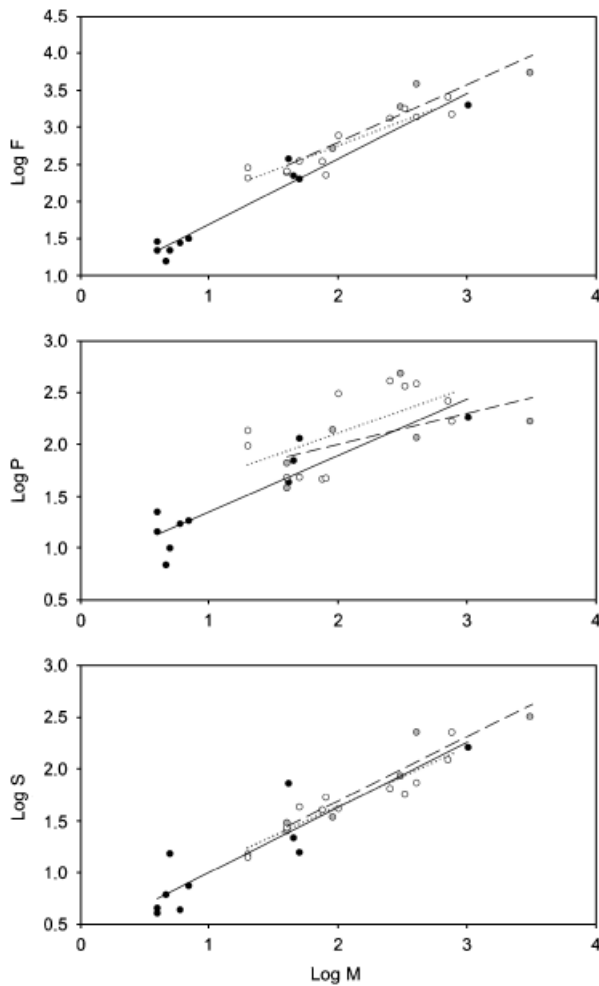


Figure 3 For the three different types of dynamic foot use (—, plantiportals; ---, digitiportals;, unguliportals), the relationship, during walking, is shown between (log) body mass and (a) (log) peak force [the overall relationship is isometrically (relative to mass), but there is a significant effect of foot use, with plantiportals showing a steeper slope than digitiportals and unguliportals]; (b) (log) peak pressure [an overall relationship of peak pressure to (mass)^{1/2} is found and there is no significant difference between the groups; notice however, that the trend line of the digitiportals is not significant] and (c) (log) contact area [a near isometrically relationship is found between contact area and body mass (exponent of 2/3)].

Table 4 Summary of scaling relationships

| | Peak force (<i>F</i>) | Contact area (<i>A</i>) | Peak pressure (<i>P</i>) |
|------------------------------------|-------------------------|---------------------------|----------------------------|
| Isometry | M^1 | $M^{2/3}$ | $M^{1/3}$ |
| Example: M^{*2} | F^{*2} | $A^{*1.587}$ | $P^{*1.260}$ |
| Found dynamic plantar measurements | M^1 | $M^{0.63} = M^{2/3}$ | $M^{1/2}$ |
| Example: M^{*2} | F^{*2} | $A^{*1.587}$ | $P^{*1.414}$ |
| Effect of foot use? | Yes | No | No |

M, mass.

weight and the peak pressure. It is exactly in very large animals, like elephant, rhinoceros and hippopotamus, that we find a specialized foot anatomy with large cushions of connective tissue (Benz, 2005; Weissengruber *et al.*, 2006; Miller *et al.*, 2008). These kinds of adaptations provide a spreading of pressure and could decrease the pressure that is transferred to the bone. This would explain why it is possible to have high plantar peak pressures without breaking the foot bones and thus remove the constraint of a high scaling factor.

Interesting to notice is that the reasoning above is valid regardless of the foot use (plantiportal, digitiportal or unguliportal). Although we expected that animals of the same body mass with a different foot use would show a difference in contact area (Chi & Roth, 2004), this is not the case in our large dataset. Plantiportals, digitiportals and unguliportals of the same body mass have consequently feet with a similar contact area during walking (Fig. 3c). The foot use did, however, have an effect on the scaling of peak force (Fig. 3a and Table 3). The plantar peak force of unguliportals scales lower than that of plantiportals, although the absolute values are higher. Consequently, animals with a low body mass will have smaller peak forces when plantiportal than when unguliportal; but for larger animals the scaling lines come together and differences in foot use disappears. It should be noted that the measured peak force can be influenced by walking speed, for which we did not control. Although all animals walked (duty factor > 0.5) at preferred speed, we cannot exclude the effect of different relative speeds between the animals. This might explain partly the found difference in scaling of peak force for the different types of foot use.

To conclude, we have shown that in a large sample of mammal species, peak pressure increases faster with body mass than predicted from (hypothesized) isometry. Surprisingly, animals with different functional foot use are remarkably similar in this respect, the most prominent difference being unguliportals having relatively high forces in small animals and relatively low forces in large animals.

This study has demonstrated the importance of using dynamic data in order to address functional tissue loading. Future studies should extend this approach by incorporating full dynamic data of the entire stance phase and, if possible, include a wider range of locomotor modes and speeds.

Acknowledgements

We would like to thank the RZSA and the cooperation of all animal keepers for the opportunity to measure all the animals from their collection.

References

Bennett, M.B. (1999). Foot areas, ground reaction forces and pressures beneath the feet of kangaroos, wallabies and rat-kangaroos (Marsupialia: Macropodoidea). *J. Zool. (Lond.)* **247**, 365–369.

- Bennett, M.B., Ker, R.F., Dimery, N.J. & Alexander, R.McN. (1986). Mechanical properties of various mammalian tendons. *J. Zool. (Lond.)* **209**, 537–548.
- Benz, A. (2005) *The elephant's hoof: macroscopic and microscopic morphology of defined locations under consideration of pathological changes*. PhD thesis, University of Zürich, RoNexus Services AG, Basel.
- Biewener, A.A. (1991). Musculoskeletal design in relation to body-size. *J. Biomech.* **24** (Suppl. 1), 19–29. (Online DOI: 10.1016/0021-9290(91)90374-V).
- Biewener, A.A. (2005). Biomechanical consequences of scaling. *J. Exp. Biol.* **208**, 1665–1676. (Online DOI: 10.1242/jeb.01520).
- Bininda-Emonds, R.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007). The delayed rise of the present-day mammals. *Nature* **446**, 507–512.
- Chi, K.J. & Roth, V.L. (2004). Scaling of foot contact area and its mechanical implications for mammals of different foot postures. *Integr. Comp. Biol.* **44**, 535–535.
- Close, R.I. (1972). Dynamic properties of mammalian skeletal fibers. *Physiol. Rev.* **52**, 129–197.
- Currey, J.D. (1981). What is bone for? Property–function relationships in bone. In *Mechanical properties of bone: presented at the joint ASME ± ASCE applied mechanics, fluids engineering and bioengineering conference*: 13–26. Cowin, S.C. (Ed.). Boulder, CO: The American Society of Mechanical Engineers.
- Garland, T. Jr. Dickerman, A.W., Janis, C.M. & Jones, J.A. (1993). Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**, 265–292.
- Martins, E.P. (2004). *COMPARE, version 4.6b. Computer programs for the statistical analysis of comparative data*. Bloomington, IN: Distributed by the Author, Department of Biology, Indiana University. Available at <http://compare.bio.indiana.edu/> (accessed on January 2009).
- Miller, C.E., Basu, C., Fritsch, G., Hildebrandt, T. & Hutchinson, J.R. (2008). Ontogenetic scaling of foot musculoskeletal anatomy in elephants. *J. Roy. Soc. Interface* **5**, 465–475. (Online DOI: 10.1098/rsif.2007.1220).
- Murphy, D.F., Connolly, D.A.J. & Beynonn, B.D. (2003). Risk factors for lower extremity injury: a review of the literature. *J. Sports Med.* **37**, 13–29. (Online DOI: 10.1136/bjism.37.1.13).
- Neely, F.G. (1998). Intrinsic risk factors for exercise-related lower limb injuries. *J. Sports Med.* **26**, 253–263. (Online DOI: 10.2165/00007256-199826040-00004).
- Ralston, H.J. (1958). Energy-speed relation and optimal speed during level walking. *Eur. J. Appl. Physiol.* **17**, 277–283.
- Saibene, F. & Minetti, A.E. (2003). Biomechanical and physiological aspects of legged locomotion in humans. *Eur. J. Appl. Physiol.* **88**, 297–316.
- Vereecke, E., D'Août, K., De Clercq, D., Van Elsacker, L. & Aerts, P. (2003). Dynamic plantar pressure distribution during terrestrial locomotion of bonobos (*Pan paniscus*). *Am. J. Phys. Anthropol.* **120**, 373–383. (Online DOI: 10.1002/ajpa.10163).
- Weissenruber, G.E., Egger, G.F., Hutchinson, J.R., Gorenewald, H.B., Famini, D. & Forstenpointner, G. (2006). The structure of the cushions in the feet of African elephants (*Loxodonta africana*). *J. Anat.* **209**, 781–792.