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Title	Size and shape of terrestrial animals
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Citation	The 9.5th International Symposium on Adaptive Motion of Animals and Machines (AMAM2021). 2021, p. 50
Version Type	VoR
URL	https://doi.org/10.18910/84890
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Size and shape of terrestrial animals

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1 Summary

Small insects sprawl and large animals are upright, suggesting a scaling of body shape with size in land animals. Physical factors that underlie the scaling remains debated and unresolved questions remain on the relative roles of ancestry versus selection and how the natural environment may have influenced body shape. Here we propose that the scaling of frontal shape is governed by lateral stability, and is driven by the size-dependence of unevenness of natural terrain. Measurements show that natural terrain is more uneven at smaller sizes than larger. This size-dependent unevenness may lead to a size-dependent frontal aspect ratio a of the width of the base of support to height of the center of mass in order to passively maintain lateral stability. Using the animal's mass m as a measure of its size and previously measured size-dependence of terrain unevenness, we derive the scaling law $a \propto m^{-n}$, where $n = 0.17$ for $a \ll 1$ and $n = 0.36$ for $a \gg 1$. Data from 369 species, spanning eight orders of magnitude in mass from 28 mg to 22,000 kg, follow the predicted scaling so that smaller animals have a wider aspect ratio. Furthermore, phylogenetic comparative analysis reveals that shared ancestry cannot explain the scaling. Thus, the need for stability on natural terrain likely drove the macroevolution of the overall body aspect ratio across terrestrial animals, despite vast differences in their body plans, morphological specializations of their limbs, and the use of neural control strategies for lateral stability.

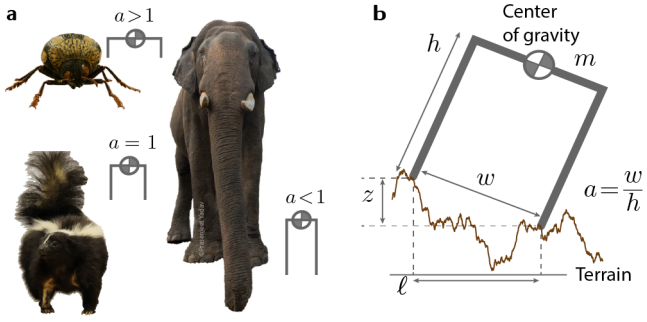


Figure 1: a. Small animals tend to sprawl and have a frontal aspect ratio $a > 1$, whereas large animals are upright with $a < 1$. **b.** The width of base of support dictates the degree of terrain height perturbations, but the aspect ratio dictates the tolerance to lateral tilting. We investigate whether the competition between the two underlies the frontal aspect ratio that is observed in nature.

2 Introduction

Lateral balance control is crucial for stable locomotion [1]. The typical standing posture of an animal sets a frontal aspect ratio of the width of the base of support to the center of mass height, which defines the passive lateral stability against tilting perturbations. The unevenness of natural terrain, the context in which evolutionary selection operates, is a ubiquitous source of tilting perturbations. It is well established that the unevenness of natural terrain is size-dependent, such that the variance of the vertical height difference between two points on the ground depends on the horizontal distance between them according to empirically estimated power laws [2]. We hypothesize that animals have evolved their frontal shape to remain passively stable against the random height perturbations of natural terrain. We test the stability hypothesis by translating natural terrain geomorphology into a probabilistic aspect ratio scaling law with mass as a proxy for animal size, and compare with measurements from legged terrestrial animals.

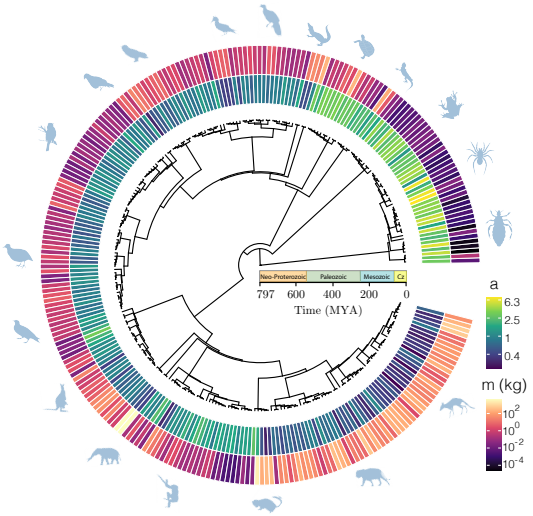


Figure 2: Phylogeny, aspect ratios, and masses of 264 extant species with available NCBI IDs, out of 369 that were used in this study.

3 Model and Methods

Natural terrain are well-approximated by a fractional Brownian process, namely a random process with fractional Gaussian increments [2]. The variance of the height difference z between two points that are horizontally separated by

a distance ℓ is given by $E[z^2] \propto \ell^{2H}$, where $0 < H < 1$ is the fractional Hurst exponent estimated from measurements of different natural terrains over varying length scales [3]. For an animal with center of mass height h, width w of the base of support, and fore-aft length d, the mass $m \propto dwh$. The fore-aft length is empirically known to scale as $d \propto m^{1/3}$ [4], yielding a relationship between mass and frontal plane dimensions. Wider is not always better, because muscle stress and energy consumption increase with wider postures [5]. So to be stable, but only marginally, the critical angle of lateral tipping for a frontal aspect ratio $a = w/h$ should equal the tilt induced by the terrain z/ℓ (Figure 1). The competition between width-dependent tilting due to terrain unevenness and aspect-ratio dependent critical tilting angle results in the scaling law $a \propto m^{-n}$ for a critically stable animal, where $n = 0.17$ for $a \ll 1$ and $n = 0.36$ for $a \gg 1$.

The deterministic scaling law ignores the stochastic nature of natural terrain. So we extend our analysis to derive a probability density landscape of a and m for critically stable animals. The risk of falling is laterally symmetric. So only the absolute terrain height difference impacts stability, which is modelled as a half-normal distribution with density function $p_Z(z;\ell)$ that parametrically depends on the horizontal distance ℓ. Under the critical animal hypothesis, the one-parameter family of density functions $p_Z(z;\ell)$ maps to a one-parameter family of density functions in the $(\log a, \log m)$ space. Thus, by varying ℓ, we produce a 2-D probability density plot in the $(\log a, \log m)$ space that describes the probability of a critically stable animal for terrain with empirically measured size-dependent random unevenness. There is one fitting parameter corresponding to the horizontal shift of the map, which is equivalent to a mass-scale associated with the model. The locus of the modes of the univariate distributions in the $(\log a, \log m)$ space recovers the deterministic scaling between aspect ratio and size, and additionally predicts a distribution of animals that would be found if natural selection of frontal aspect ratio was influenced by lateral stability.

We collected data on 369 animals using live specimens, museum specimens, private collections, published studies, photographs, and handbooks. Photographs of the front profiles were analyzed to calculate the aspect ratio using Fiji (Version 1.0), and we either measured or used published values of animal masses.

To find the effect of size on aspect ratio with a control for phylogeny, we performed phylogenetic comparative analysis [6] on 264 unique extant species from our data (Figure 2). NCBI taxonomy was used to generate the phylogenetic tree, and Grafen's method [6], which is based on the tree topology, was used to compute the branch lengths.

4 Results

Data show systematic scaling of the aspect ratio with animal mass across over eight orders of magnitude such that small animals sprawl and larger animals are upright. The predicted scaling law and the probability densities agree with the trend and spread in the data (Figure 3). Phylogenetic comparative analysis shows that $\log a$ depends on $\log m$ with slope -0.07 ($p < 1e-3$, $R^2 = 0.12$), revealing that shared ancestry does not explain the aspect ratio scaling. Together, the results suggest that adaptation for stability on uneven natural terrain is the likely explanation for the scaling of frontal aspect ratio with size.

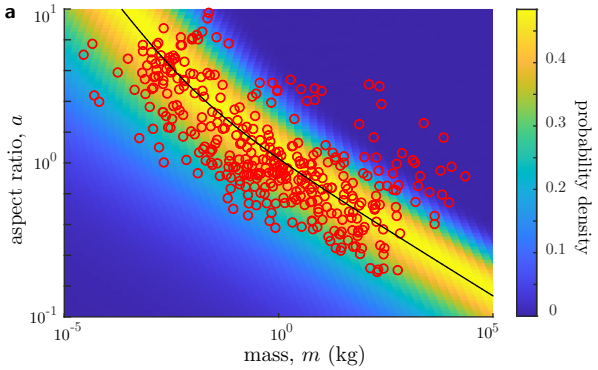


Figure 3: Data from 369 animals (red dots) follow the predicted deterministic scaling (black curve) and probability densities (heatmap) of aspect ratio and mass.

5 Conclusions

The frontal profile of diverse taxa, spanning a large range of body masses and habitats, show systematic variation with mass that agrees with the scaling law derived using terrain unevenness statistics alone. A varying H captures the degrees of unevenness [3] and partially explains the spread in data. The scaling may not apply to microarthropods that move against gravity or to fossorial species that solely live underground. However, our result may still apply to animals with adhesive pads because adhesion does not work on all substrates, and to arboreal species because vegetation is also fractal [7]. Our results provide a baseline scaling of the overall body shape, and further work is needed to understand how environmental, developmental, and genetic factors determine additional modulation of aspect ratio and further details in body plans. Our results may guide the overall shape design of legged robots used on uneven natural terrain.

6 Acknowledgements

L. Gall, M. Dickman, Yale Peabody Museum, Chicago Field Museum, J. Sartore, P. Yadav for specimens.

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