Narrative 5: Relevance of body size: allometric scaling

The literature on evolution abounds with theories relating to potential constraints linked to body size. I participated in the generation of theories on constraints, resulting in an early, often-cited publication

Clauss et al. (**2003**) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. ***Oecologia*** 136: 14-27

that in my view still contains important information but that, in its core message, does not stand the test of time due to a wrong assumption on methanogene biology that was corrected in our 2020 methane review (see narrative 6 'Methane emissions in herbivores').

When dealing with so-called 'laws' linked to body mass scaling, also with respect to the 'Metabolic Theory of Ecology' which relies heavily on such laws, I realized that empirical data sometimes deviates widely from the claimed laws, which is reflected already in the titles of our publications

Clauss et al. (**2007**) A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. ***Comp Biochem Physiol A*** 148: 249-265

Clauss et al. (**2014**) Low scaling of a life history variable: analysing eutherian gestation periods with and without phylogeny-informed statistics. ***Mamm Biol*** 79: 9-16

Clauss et al. (**2021**) Camera trap data do not indicate scaling of diel activity and cathemerality with body mass in an East African mammal assemblage. ***Ecol Evol*** 11: 13846-13861

In a series of studies that produced new data, and included this in existing datasets, Jürgen Hummel and me showed that a classic, all-pervasive assumption of herbivore ecology, i.e. that larger animals can digest better, is not correct, and that differences in anatomy and physiology overrule presumptive effects of body mass. This topic was introduced early on:

Clauss, Hummel (**2005**) The digestive performance of mammalian herbivores: why big may not be *that* much better. ***Mamm Rev*** 35:174-187,

and brought to a conclusion by a set of three publications

Clauss et al. (**2013**) Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. ***PLoS One*** 8:e68714,

Müller, ..., **Clauss** (**2013**) Assessing the Jarman-Bell Principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. ***Comp Biochem Physiol A*** 164:129-140,

Steuer, ..., **Clauss**, Hummel (**2014**) Does body mass convey a digestive advantage for large herbivores? ***Funct Ecol*** 28:1127-1134.

These were summarized in an editorial that also called our approach *'elegant'*.

McArthur (**2014**) Do we ditch digestive physiology in explaining the classic relationship between herbivore body size diet and diet quality? ***Funct Ecol*** 28:1059-1060

We did not only address biological and mathematical errors in the traditional narrative. This work also opened a new perspective, stressing the relevance of *ecological opportunity* as a permissive factor in evolution (as in: 'small animals can afford to lose the ability for thorough digestion') as opposed to the traditionally more emphasized *physiological constraint* of body size (as in: 'small animals cannot digest efficiently due to their size').

These works led to the invitation as plenary speaker at the 2013 International Conference on Behaviour, Physiology and Genetics of Wildlife with a presentation titled *The art of allometry: relevance, functional logic and evolutionary history in comparative analyses*

The expertise also led to an invited lecture at an European Pet Food Industry (FEDIAF) meeting in Brussels, Belgium, 2015, on *Allometric principles and metabolic allometry*

In the course of this work we addressed one of the probably most prevailing fallacies in the evolutionary ecology: the rhetoric that large animals require relatively less energy. While elaborated in full in the 2013 PLos One paper cited above, I also summarized this in a single-page comment

Clauss (**2019**) No evidence for decreased metabolism in domestic mammals – reaction to Milla et al. (2018). ***Nature Ecology & Evolution*** 3: 322

In carnivores, body size effects differ distinctively between terrestrial and marine ecosystems (with small-prey feeding possible in large predators in the marine realm)

Carbone, ..., **Clauss** et al. (**2014**) Geometric factors influencing the diet of vertebrate predators in marine and terrestrial environments. ***Ecol Lett*** 17:1553-1559,

and for carnivores, large body size opens the possibility of intermittent feeding without the obligation for daily hunting, while a common 'law'-type of scaling of kill frequency does not match empirical data:

De Cuyper, **Clauss** et al. (**2019**) Predator size and prey size-gut capacity ratios determine kill frequency and carcass production in terrestrial carnivorous mammals. ***Oikos*** 128:13-22.

In my experience, the realm of allometric scaling continues to be the one that I am most sought for by peers, in terms of discussion and advice, which led to various collaborations – from fish

Argyriou, **Clauss** et al. (**2016**) Exceptional preservation reveals gastrointestinal anatomy and evolution in early actinopterygian fishes. ***Sci Rep*** 6: 18758

to recent work on the allometric scaling of sodium requirements

Duvall, ..., **Clauss**, et al. (**2023**) Allometry of sodium requirements and mineral lick use among herbivorous mammals. ***Oikos*** 2023:e10058

This topic is also the one where I keep astonishing audiences or individuals who have ingrained beliefs about scaling laws, by showing that empirical data does not match these laws. I myself keep being astonished at the variety of excuses brought forward to defend the laws, rather than letting empirical data judge the validity of a theory.