

# Does body mass convey a digestive advantage for large herbivores?

Patrick Steuer<sup>1</sup>, Karl-Heinz Südekum<sup>1</sup>, Thomas Tütken<sup>2,†</sup>, Dennis W. H. Müller<sup>3,4</sup>, Jacques Kaandorp<sup>5</sup>, Martin Bucher<sup>6</sup>, Marcus Clauss<sup>3</sup> and Jürgen Hummel<sup>\*,1,7</sup>

<sup>1</sup>Institute of Animal Science, University of Bonn, Bonn, Germany; <sup>2</sup>Steinmann Institute for Geology, Mineralogy and Palaeontology, University of Bonn, Bonn, Germany; <sup>3</sup>Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland; <sup>4</sup>National Park 'Bavarian Forest', Grafenau, Germany; <sup>5</sup>Safari Beekse Bergen, Hilvarenbeek, The Netherlands; <sup>6</sup>Zoo Zurich, Zurich, Switzerland; and <sup>7</sup>Department of Animal Sciences, Georg-August-University Göttingen, Göttingen, Germany

## Summary

1. A key concept of body mass (BM) in niche separation of large herbivores assumes that the decrease in diet quality inherent to increasing BM (due to less selective feeding behaviour) is balanced by a simultaneous increase in digestive ability (due to longer retention times), resulting in no or less-than-expected reduction in digestibility (as measured in the animal as a result of diet quality and digestive ability). However, the second part of this concept has been challenged recently due to theoretical problems and mismatch with empirical data.

2. A proxy for digestibility, such as metabolic faecal nitrogen (MFN), will comprise both information on diet quality and digestive ability in free-ranging animals. In captive animals, if diet is kept constant, such a proxy can exclusively indicate digestive ability. Comparing free-ranging and captive animals under such conditions, one would expect an increase in MFN with BM in captive animals and no relationship between these measures in free-ranging animals if BM was related to digestive ability.

3. We compared captive ungulates on a consistent grass hay diet (17 species; 30–4000 kg BM) to a sample of free-ranging East African ungulates (19 species; 12–4000 kg BM). MFN was used as the major proxy for digestibility.

4. In captive animals, there was no influence of BM on MFN ( $P = 0.466$ ); for free-ranging animals, a significant decreasing effect of body mass on MFN ( $P = 0.002$ ) and therefore diet quality was found at a scaling of  $BM^{-0.15}$ .

5. In conclusion, scenarios that assume a compensation of the evident decrease in diet quality with BM via an increased digestive ability are not supported by this study. This does not rule out other feeding-related factors in facilitating large BM, such as compensation by an increased diet intake.

**Key-words:** African ungulates, Diet quality, faecal nitrogen, feeding ecology, Jarman–Bell principle

## Introduction

Body size is an important biological characteristic that determines many anatomical, physiological, ecological and life-history characteristics of animals and hence represents an important feature in evolutionary scenarios (Case 1979; Clutton-Brock & Harvey 1983; Peters 1983; Schmidt-Nielsen 1984; Sibly, Brown & Kodric-Brown 2012). According to Cope's rule, an increase in body

mass (BM) is a typical feature in many lineages, implying a general advantage, which is likely to be composed of a variety of factors related directly to reproductive success or predation avoidance (Hone & Benton 2005). As a particularity of herbivores and especially ungulates, large BM has also been assumed to have an advantageous effect on the species-specific digestibility an animal can achieve on a given food source (digestive ability), influenced, for example, by food retention time (Demment & Van Soest 1985). The latter consideration is based on an influential concept of herbivore nutritional ecology, the Jarman–Bell principle (Bell 1970; Geist 1974; Jarman

\*Correspondence author. E-mail: jhummel@gwdg.de

†Present address. Institute for Geosciences, University of Mainz, Mainz, Germany.