## Reply to 'No evidence for different metabolism in domestic mammals'

To the Editor — Clauss¹ claims that one of the conclusions of our paper², "livestock species are relatively large mammals with low basal metabolic rates, which indicate moderate to slow life histories", is flawed. Clauss states that the appropriate metric to compare metabolism among mammals is metabolic rate per unit metabolic body mass (kJ d⁻¹ kg⁻⁰.75; Fig. 1c in Clauss¹) rather than metabolic rate per unit body mass (BMR, kJ d⁻¹ kg⁻¹; Fig. 3a in Milla et al.²).

Our research question was whether scores for key functional traits of domesticates constitute either a subsection or an extension of the phenotypic spaces of their wild relatives. For both animals and plants, we selected traits indicative of metabolism, ability to compete for resources, and survival. Within these three functions, we searched for patterns that were comparable among plants and mammals. We used leaf nitrogen content (mg N mg<sup>-1</sup>) for plant metabolism and BMR (kJ d-1 kg-1) for animal metabolism. Thus, for both the plant and animal metabolic traits that we analysed, we used the International System of Units (SI) rather than allometric units.

The key issue here is which reference system, allometric or SI, addresses the research question better. In this context, the statements "domesticates have low BMRm" (Fig. 4 in Milla et al.2) and "relative metabolic rates of wild and domesticated species do not change with body mass" (Fig. 1c in Clauss<sup>1</sup>) are two different propositions. For the purposes of our paper, the first statement, but not the second, is the one that addresses the issue under scrutiny. Investigating phenotypic profiles (addressed by the first statement) or deviations from bivariate allometries (addressed by the second statement) are two approaches that yield different results and are commonly

used at different stages of development of a research topic. For example, the discovery of trait co-variation patterns in plants, which was made using SI<sup>3</sup>, promoted later research on shifts in the slopes and elevations of those patterns (for example, ref. <sup>4</sup>), demonstrating the benefits of the two complementary steps.

We are well aware that plant and animal whole-organism metabolism tends to allometrically scale with size (but note the independence of leaf nitrogen content and size<sup>5</sup>). For animals, basal metabolism usually scales with body mass (BM)0.75, but the value of the exponent is debated<sup>6</sup>. Moreover, isometric approaches to comparative analyses that include mammals are also common (for example, ref. 7). Therefore, using allometric scaling exponents would have been troublesome for comparative purposes across kingdoms. An additional problem with the allometric approach is that each metric used should be scaled to the units of other traits with which the metric shows co-variation patterns. Seed and plant size or neonate body mass and adult body mass also co-vary to different degrees. Standardizing seed or neonate sizes relative to allometric units of body mass would yield results that are meaningless to the question at hand. Finally, the consequences of the use of different reference systems are exaggerated in Clauss' critique1. This is because arithmetic means are computed before log-scaling (an inadequate statistic for a sample distributed uniformly on a log-scale, as in Fig. 1b in Clauss1), which artificially inflates BMR-m differences among groups in Fig. 1b in Clauss1 and takes BMR-m means above the fit line.

Overall, the problem raised by Clauss is a relevant one, but it is part of a bigger discussion on the appropriate reference system for biological metrics. On one

hand, SI has great benefits in terms of standardization, comparability, long-term stability and dialog with other sciences. On the other hand, biological metrics might need reference systems that expand or compress SI units (allometric scaling, thermal times, or growing degrees). A wide synthesis on this topic, including guidelines on appropriate reference for addressing different types of questions, is called for.

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Published online: 18 February 2019 https://doi.org/10.1038/s41559-019-0827-0

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## Competing interests

The authors declare no competing interests.