REPLY TO SITTERS AND OLDE VENTERINK:

Untangling the relative importance of processes that influence fecal nutrient stoichiometry

Elizabeth le Roux[a,1], Graham I. H. Kerley[b], and Joris P. G. M. Cromsigt[b,c,d]

Sitters and Olde Venterink (1) question the generality of the positive relationship that we show between herbivore body size and fecal N:P stoichiometry (2). Their data show different and at times opposite patterns. They highlight dietary composition and metabolic requirement as two additional size-related mechanisms determining fecal nutrient ratios and argue that the increased skeletal phosphorus requirements of larger animals that we suggest may not be the primary determinant of fecal P concentrations.

We fully agree that dietary nutrients strongly determine fecal nutrients, and the latter often serves as a proxy for the former (3, 4). This is particularly clear when comparing grazers and browsers. However, in our study, the size-related differences in herbivore diets were minimized through our experimental design. First, we collected fecal samples during the wet season, when a high-quality diet is achievable even for large herbivores. Second, we included mostly grazers that predominately feed on grazing lawns during this season [a high-quality food resource, often consisting of the same grass species and fed from by impala-sized to white rhino-sized grazers (2, 5)]. Moreover, stems of stoloniferous lawn grasses grow close to the ground, and thus even large bites contain little stem material. Therefore, dietary quality was likely more similar among our vastly different-sized herbivores than it may be in other systems/seasons in which this variability is less standardized. The diet similarity is supported by the weak correlation between body size and fecal N shown in our figure 2A (2). This may be why our data show patterns that differ from those of Sitters and Olde Venterink, that differ either by season, the proportions of grazers included, or ecoregion.

Regardless, this dialogue raises a crucial issue: Multiple mechanisms shape fecal nutrients, which likely explains why the patterns described by Sitters and Olde Venterink differ not only from ours (2) but also among the ecoregions, functional herbivore types, and seasons within ref. 1. Empirical field studies cannot capture all the contributing variables, particularly when confronted with severely depauperate herbivore communities, often missing the largest size classes. As is often true in ecology, "pesky biological detail matters a lot" (6). To unravel the relative importance of these different drivers, we are now in the process of combining our datasets with those of other researchers (including Sitters and Olde Venterink) to model and identify the role of these individual factors using more comprehensive species sets. A greater variety of species will allow for better stratification of functional types, diet types, and seasons.

In ref. 2, we argue that higher N:P fecal fertilization led to higher grass N:P content. It is also possible, as Sitters and Olde Venterink suggest, that larger animals had higher fecal N:P because they ate grass from grazing lawns with higher N:P ratios. However, this does not explain why these grazing lawns had higher N:P ratios to begin with. We provided a possible mechanism supported by empirical data, although we entirely agree that P investment in bone will not be the only mechanism, and there is clearly much more to be learned.

Acknowledgments

E.l.R. is funded by Royal Society Newton International Fellowship NIF\R1\192618.

[a]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, United Kingdom; [b]Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela University, Port Elizabeth 6031, South Africa; [c]Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden; and [d]Copernicus Institute of Sustainable Development, Utrecht University, 3584 CB Utrecht, The Netherlands

Author contributions: E.l.R., G.I.H.K., and J.P.G.M.C. wrote the paper.

The authors declare no competing interest.

[1]To whom correspondence may be addressed. Email: elizabeth.liza.le.roux@gmail.com.

Published February 1, 2021.

1 J. Sitters, H. Olde Venterink, Body size–fecal nutrient patterns of mammalian herbivores. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.2020137118 (2021).
2 E. le Roux, L. S. van Veenhuisen, G. I. H. Kerley, J. P. G. M. Cromsigt, Animal body size distribution influences the ratios of nutrients supplied to plants. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 22256–22263 (2020).
3 C. C. Grant, H. H. Meissner, W. A. Schultheiss, The nutritive value of veld as indicated by faecal phosphorus and nitrogen and its relation to the condition and movement of prominent ruminants during the 1992-1993 drought in the Kruger National Park. *Koedoe* **38**, 17–31 (1995).
4 C. C. Grant, M. J. S. Peel, J. B. J. van Ryssen, Nitrogen and phosphorus concentration in faeces: An indicator of range quality as a practical adjunct to existing range evaluation methods. *Afr. J. Range Forage Sci.* **17**, 81–92 (2000).
5 R. Arsenault, N. Owen-Smith, Competition and coexistence among short-grass grazers in the Hluhluwe-iMfolozi Park, South Africa. *Can. J. Zool.* **89**, 900–907 (2011).
6 R. P. McIntosh, Pluralism in ecology. *Annu. Rev. Ecol. Syst.* **18**, 321–341 (1987).