



REPLY TO WEIHMANN:

# Fifty gazelles do not equal an elephant, and other ecological misunderstandings

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Weihmann's (1) comment on our recent paper (2) presents a misunderstanding of the principles of large herbivore ecology and the African fossil record. We welcome this opportunity to correct certain misunderstandings, focusing here on the two most important issues. Our previous work shows that the richness of megaherbivores (>1,000 kg) in eastern African fossil assemblages declined over the last ~4.5 My (2, 3). Drawing from the abundant research documenting the effects of megaherbivores on vegetation structure, fire regimes, and nutrient cycling, among other processes (4–7), we argue that the exceptional richness of megaherbivores in the past implies that ancient ecosystems functioned unlike any in Africa today (2).

Weihmann suggests otherwise, proposing that extant African elephants (*Loxodonta* spp.) simply replaced ecological roles vacated by extinction. His argument assumes functional equivalence across very different taxa, which is problematic considering the vast majority of extinct African megaherbivores—chalicotheres, hippos, rhinos, sivatheres, and even camels—were undeniably unlike past or present *Loxodonta*. Modern African elephants are primarily C<sub>3</sub> browsers (8), yet extinct megaherbivores include browsers, grazers, and mixed feeders occupying various terrestrial and aquatic habitats. These basic ecological contrasts imply very different herbivore–ecosystem interactions, as indicated by contemporary observations that megaherbivore impacts cannot be described as one size fits all (4–7). For example, browsing elephants topple trees and open up habitats, whereas grazing pressure from white rhinos (*Ceratotherium simum*) and hippos (*Hippopotamus amphibius*) maintains short grasslands, which suppresses fire and allows tree regeneration (7). It is therefore highly unlikely that modern African

elephants are the ecological equivalents of claw-footed chalicotheres, mixed-feeding sivatheres, or any other extinct taxon for which we have no comparison today. Indeed, even the hypergrazing Plio-Pleistocene elephants (8) would have had widely different impacts compared to their living relatives.

In a second misunderstanding, Weihmann suggests that a given biomass of small-bodied herbivores would have the same effects on vegetation as a comparable biomass of megaherbivores. Thus, in his view, the transition from megaherbivore-rich communities to those comprised of smaller-bodied species need not imply ecosystem change. We beg to differ—an elephant is not the ecological equivalent of 50 gazelles. Larger body size allows megaherbivores to subsist on low-quality forage that is inaccessible to smaller-bodied animals, meaning that a considerably greater proportion of vegetation is available for consumption (6, 7). Likewise, most megaherbivores are non-ruminants, whereas small herbivores and mesoherbivores are mostly ruminants. When scaled to body mass, non-ruminants have higher forage intake compared to ruminants (9), implying greater consumptive influence on vegetation. Finally, Weihmann's focus on metabolic scaling ignores the unique nonconsumptive effects of megaherbivores on vegetation. For example, their large body size allows them to topple trees and shrubs, thus opening impenetrable thickets (6, 7). The fact that we (and others) even use the term “megaherbivore” for animals >1,000 kg is a reflection of their unique impacts on ecosystems (4–7).

Taken together, there is little reason to believe that present-day African ecosystems are close approximations of those that existed much deeper in time—the past is indeed a foreign country.

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The authors declare no competing interest.

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First published February 4, 2020.

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- 1 T. Weihmann, Species richness and composition are not sufficient for determining the functionality of ancient ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 3368–3369 (2020).
  - 2 J. T. Faith, J. Rowan, A. Du, Early hominins evolved within non-analog ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 21478–21483 (2019).
  - 3 J. T. Faith, J. Rowan, A. Du, P. L. Koch, Plio-Pleistocene decline of African megaherbivores: No evidence for ancient hominin impacts. *Science* **362**, 938–941 (2018).
  - 4 W. J. Ripple et al., Collapse of the world’s largest herbivores. *Sci. Adv.* **1**, e1400103 (2015).
  - 5 Y. Malhi et al., Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 838–846 (2016).
  - 6 R. N. Owen-Smith, *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge University Press, Cambridge, 1988).
  - 7 N. Owen-Smith, “Megaherbivores” in *Encyclopedia of Biodiversity*, S. Levin, Ed. (Elsevier, 2013), vol. 5, pp. 223–239.
  - 8 T. E. Cerling, J. M. Harris, M. G. Leakey, Browsing and grazing in elephants: The isotope record of modern and fossil proboscideans. *Oecologia* **120**, 364–374 (1999).
  - 9 M. Clauss et al., Faecal particle size: Digestive physiology meets herbivore diversity. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **179**, 182–191 (2015).