Dietary isotopes of Madagascar’s extinct megafauna reveal Holocene browsing and grazing guilds

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Megafauna play a disproportionate role in developing and maintaining their biomes, by regulating plant dispersal, community structure and nutrient cycling. Understanding the ecological roles of extinct megafaunal communities, for example through dietary reconstruction using isotope analysis, is necessary to determine pre-human states and set evidence-based restoration goals. We use δ13C and δ15N isotopic analyses to reconstruct Holocene feeding guilds in Madagascar’s extinct megaherbivores, which included elephant birds, hippopotami and giant tortoises that occurred across multiple habitats and elevations. We compare isotopic data from seven taxa and two elephant bird eggshell morphotypes against contemporary regional floral baselines to infer dietary subsistence strategies. Most taxa show high consumption of C3 and/or CAM plants, providing evidence of widespread browsing ecology. However, Aepyornis hildebrandti, an elephant bird restricted to the central highlands region, has isotope values with much higher δ13C values than other taxa. This species is interpreted as having obtained up to 48% of its diet from C4 grasses. These findings provide new evidence for distinct browsing and grazing guilds in Madagascar’s Holocene megaherbivore fauna, with implications for past regional distribution of ecosystems dominated by endemic C4 grasses.

1. Introduction

Late Quaternary and older terrestrial ecosystems were typically dominated by megaherbivores, which shaped their environments through top–down interactions with plant communities and vegetation structure [1,2]. Megaherbivores impact diversity and structure of ecosystems by suppressing plant growth through physical disturbance and herbivory, influencing nutrient cycling within and between landscapes, and dispersing plant propagules [3,4]. However, megafauna have been disproportionately vulnerable to human-caused extinction, and many ecosystems now lack these keystone species [5]. Reconstructing the ecology of now-extinct megaherbivore guilds is essential to identify disrupted ecological processes and guide environmental management and restoration [1,6].

Late Quaternary Madagascar supported a diverse megafauna, including elephant birds, hippopotamuses and giant tortoises. Madagascar’s megaherbivores became extinct in the late Holocene during a period of intensive anthropogenic forest clearance and conversion to open habitats around 1100–1000 BP [7–9]. Today 80% of Madagascar is covered by grassland [10,11], but the pre-disturbance distribution and extent of native grasslands remain uncertain [12,13]. Madagascar contains native grass lineages dating from the Miocene, and 40%...
of its grass species are unique; it contains among the world’s highest grass diversity and endemism, with particularly diverse assemblages in the island’s central highlands ecogeographical region [10,11]. However, there is limited evidence for regional existence of a late Quaternary vertebrate grazing guild, suggesting that endemic grasses may have been limited to small, low-density clearings [13–16].

Most trees, shrubs and herbs use a C3 (Calvin) metabolic pathway for carbon fixation during photosynthesis, whereas most tropical grasses use a C4 (Hatch-Slack) pathway [17]. Stable carbon isotope ($\delta^{13}C$) values in bones of animals that consumed these plants can indicate likely former presence of forests or grasslands, and isotope analysis is widely used for late Quaternary palaeoecological reconstruction [14]. Animals with pure C3 diets have $\delta^{13}C$ values below $-21.5 \permil$ and pure C4 diets above $-9 \permil$. Reported $\delta^{13}C$ values for Madagascar megaherbivores are interpreted as indicating forest environments [18–20]. However, wetland C4 plants (rushes, sedges) also occur in Madagascar, so comparison of $\delta^{13}N$ values between co-occurring taxa can also be included in dietary assessments using $\delta^{13}C$ data; plants in arid environments have higher $\delta^{13}N$ values [24], enabling differentiation between wetland and dryland C4 plants.

Research into Madagascar’s extinct vertebrate ecology has mainly focused on giant lemurs, with studies of megaherbivores hindered by poorly resolved taxonomy [25]. However, recent taxonomic reassessments have clarified species diversity in elephant birds [26] and hippopotami [27], enabling the investigation of species-specific niches and landscape ecology. Here we investigate new and published dietary isotope data for all Madagascar hippopotamus and elephant bird species and for the regionally extinct giant tortoise Aldabrachelys across three distinct ecogeographical zones, to determine megaherbivore dietary niches and presence of natural open grassland habitats (e.g. savannahs, open wooded habitats) in Madagascar’s late Quaternary ecosystems [25].

### Table 1. Mean isotope values and dietary proportion estimates for Madagascar’s megaherbivores, inclusive of bone/eggshell correction and Suess correction.

| taxon                  | no. specimens | $\delta^{13}C$ (mean) | s.d. | est. diet proportion (mean) | C3 plants | est. diet proportion (mean) | CAM plants | s.e. |
|------------------------|---------------|-----------------------|------|-----------------------------|-----------|-----------------------------|------------|------|
| 1. Arid spiny bush     |               |                       |      |                             |           |                             |            |      |
| Aepyornis maximus      | 2             | -28.42                | 0.71 | 0.93                        | 0.07      |                             | 0.04       |      |
| Mullerornis modestus   | 7             | -26.44                | 0.81 | 0.79                        | 0.21      |                             | 0.02       |      |
| Mullerornis modestus   | 9             | -25.58                | 0.48 | 0.73                        | 0.27      |                             | 0.01       |      |
| thick eggshell         | 93            | -26.35                | 0.92 | 0.79                        | 0.21      |                             | 0.01       |      |
| Hippopotamus lamerlei | 10            | -21.87                | 2.49 | 0.48                        | 0.52      |                             | 0.06       |      |
| Hippopotamus sp.       | 18            | -22.99                | 2.33 | 0.55                        | 0.45      |                             | 0.04       |      |
| Aldabrachelys sp.      | 18            | -25.18                | 2.75 | 0.71                        | 0.29      |                             | 0.05       |      |
| 2. Succulent woodland  |               |                       |      |                             |           |                             |            |      |
| Aepyornis maximus      | 1             | -28.02                | 0.71 | a                           | 0.9       |                             | 0.1        | 0.05 |
| Vorombe titan          | 11            | -29.26                | 0.72 | 0.99                        | 0.01      |                             | 0.02       |      |
| Hippopotamus lamerlei | 4             | -28.13                | 0.73 | 0.91                        | 0.09      |                             | 0.03       |      |
| Hippopotamus           | 3             | -20.17                | 1.56 | 0.36                        | 0.64      |                             | 0.06       |      |
| madagascariensis       |               |                       |      |                             |           |                             |            |      |
| Hippopotamus sp.       | 15            | -26.07                | 3.71 | 0.77                        | 0.23      |                             | 0.07       |      |
| Aldabrachelys sp.      | 1             | -33.52                | 2.75 | 1                           | 0         |                             | 0.19       |      |
| 3. Central highlands   |               |                       |      |                             |           |                             |            |      |
| Aepyornis hildebrandti | 8             | -21.12                | 1.42 | 0.52                        | 0.48      |                             | 0.03       |      |
| Mullerornis modestus   | 1             | -28.22                | 0.81 | 0.98                        | 0.02      |                             | 0.06       |      |
| madagascariensis       | 3             | -28.27                | 3.25 | 0.99                        | 0.01      |                             | 0.12       |      |
| Hippopotamus sp.       | 13            | -27.83                | 4.29 | 0.96                        | 0.04      |                             | 0.08       |      |

*a* s.d. not available and arid spiny bush value used.
3. Results

In arid spiny bush, elephant birds and giant tortoises show low $\delta^{13}C$ values (species means: $-25.18 \pm -28.42\%$), with dietary fractionation indicating these taxa all consumed mainly $C_3$ plants and only limited amounts of CAM plants (mean estimated proportions of CAM consumption: 0.07–0.27). $M. modestus$ (bone and thin eggshell) shows highest estimated CAM consumption (sample means: 0.21–0.27).

Hippopotamai ($H. lemerlei$ and samples unidentified to species) show higher $\delta^{13}C$ values (sample means: $-21.87 \pm -22.99\%$) and correspondingly much higher estimated proportions of CAM consumption, with $C_3$ and CAM plants both comprising about half of their diet (mean estimated proportions, $C_3$: 0.48–0.55, CAM: 0.45–0.52) (table 1 and figure 2; electronic supplementary material, file S1).

In succulent woodland, elephant birds ($A. maximus$, $V. tititan$), giant tortoises and $H. lemerlei$ show low $\delta^{13}C$ values (species means: $-26.46 \pm -33.52\%$) and very low estimated proportions of CAM consumption (0.01–0.09). By contrast, $H. madagascariensis$ shows high $\delta^{13}C$ values (species mean: $-20.16\%$) and much higher mean estimated CAM consumption (0.64).

In the central highlands, $M. modestus$ and hippopotamai ($H. madagascariensis$ and samples unidentified to species) show high $\delta^{13}C$ values (sample means: $-28.22 \pm -28.83\%$), and are estimated to have consumed almost entirely $C_3$ plants and minimal $C_4$ grasses (mean estimated proportions of $C_3$ consumption: 0.02–0.04). Conversely, $A. hildebrandti$ shows high $\delta^{13}C$ values (sample mean: $-21.12\%$) and much higher mean estimated $C_4$ consumption (0.48).

For hippopotamai, $H. madagascariensis$ had $\delta^{13}C$ values of 3.0–5.2\%, and $H. lemerlei$ of 7.0–13.3\%. The lowest hippopotamai $\delta^{13}C$ value was from Antsirabe, central highlands (13.3\%) and the highest was from Beloha, arid spiny bush (13.3\%). For elephant birds, $A. hildebrandti$ had $\delta^{13}C$ values of 5.0–7.8\%, $A. maximus$ of 11.8–15.3\%, $M. modestus$ of 6.4–16.0\%, $V. tititan$ of 5.5–13.7\% and ‘thick eggshell’ of 8.7–17.6\%. $Aldabrachelys$ in arid spiny bush had values of 8.4–13.3\%. Across ecoregions, non-overlapping $\delta^{15}N$ ranges were observed for single measurements in $A. maximus$ (dry deciduous forest, 11.8\%; arid spiny bush, 12.7–15.3\%) and $M. modestus$ (central highlands, 6.4\%; arid spiny bush, 6.5–15.8\%).

4. Discussion

We present the first species-level dietary niche reconstruction for Madagascar’s megaherbivores, revealing a range of $\delta^{13}C$ and $\delta^{15}N$ values and the dietary fractionation for each species.
...and δ15N values and trophic ecologies across taxa and ecoregions. Our findings indicate the former existence of multiple herbivore guilds across Madagascar. These data support previous identification of a widespread browsing guild and provide the first direct evidence for a megaherbivore grazing guild in Madagascar’s central highlands.

δ13C values in hippopotamus samples indicate broad trophic niches for both species, suggesting both browsing and grazing behaviours. This contrasts with the mainland African hippopotamus (H. amphibius), which is predominantly a terrestrial grazer [37]. Madagascar hippopotami were trophically closer to Africa’s extinct pygmy hippopotamus (Choeropsis liberiensis), which is comparable in size to Madagascar’s extinct species, and browse on forest plants [38]. Interestingly, δ15N ratios indicate more aquatic feeding in H. madagascariensis than H. lemerlei. Aquatic habitats were available for H. madagascariensis in the central highlands [25]. This result contrasts with aquatic adaptations inferred from cranial morphology in H. lemerlei [39], but is consistent with behavioural ecology (emergence onto land for feeding) in the otherwise aquatic H. amphibius, suggesting a similar lifestyle for H. lemerlei. Aldabrachelys isotopes from arid spiny bush show a comparable δ13C/δ15N signal to H. lemerlei, indicating a similar browsing niche in this ecoregion.

CAM plants comprised a substantial proportion of the diets of one or both hippopotamus species in arid spiny bush and succulent woodland, but δ13C values are lower in the central highlands, suggesting higher reliance upon C3 plants. CAM plants are relatively scarce in this region; however, they occur across numerous biomes and elevations in Madagascar, with a range of δ13C values (e.g. Kalanchoë, −11.4 to −27.3‰) [23]. CAM plant CO2 is fixed by the C3 pathway in humid environments such as the central highlands, producing δ13C values below −22‰ [23] and thus consistent with CAM consumption in this region as well. Hippopotami therefore probably consumed C3 and CAM plants across Madagascar, matching the varying δ13C pattern in the CAM-specialist Hadropterus across different ecoregions [14].

Elephant bird δ13C values from arid spiny bush and succulent woodland fall outside the range for C4 consumption (open-habitat dryland grasses or wetland sedges and rushes). In arid spiny bush, δ13C values indicate that all elephant birds had predominantly C3 diets, with some CAM consumption by M. modestus; higher δ15N values compared to sympatric hippopotami indicate that these plants were less likely to be from wetlands. Differences between sympatric elephant birds may indicate further species-specific dietary differences; for example, higher δ13C values (e.g. in A. maximus) are associated with frugivory or omnivory (including invertebrate or small vertebrate consumption) [32], which comprise extant ratite dietary strategies [40]. Eggshell and bone values also differ in M. modestus, possibly indicating seasonal reliance upon dietary resources during oogenesis, or that eggshell and bone fractionation rates may need separate assessment.

Our most striking result is that δ13C data for A. hildebrandtii provide the first evidence for grazing ecology in elephant birds. Although unique within Madagascar’s ratites, grazing is also the primary dietary strategy in greater rhea (Rhea americana) [41], and other large flightless birds (e.g. geese) also have important regulatory effects on island grasslands [42]. Our results thus identify A. hildebrandtii as a likely top–down regulator of native grassland ecosystems in the central highlands [13,15,16]. δ13C values for this species indicate a mixed diet containing large quantities of C4 plants (c. 48%), whereas co-occurring hippopotami consumed only tiny amounts of C4 plants (1–4%). Although A. hildebrandtii had higher mean δ15N values compared to sympatric hippopotami, this disparity is much lower than between species in other ecoregions. Indeed, lower δ13C values in CAM plants within mesic conditions [23] suggest that A. hildebrandtii might not have consumed any forest plants and was exclusively an open-habitat forager, consuming a mixture of C4...
and CAM plants. High variability in CAM plant δ13C values complicates interpretation of results, but the likelihood of A. hildebrandti exhibiting grazing behaviour is supported by the non-matching regional δ13C signature of the CAM specialist Hadropterus (mean: −24.2 13C‰) [14]. This hypothesis is consistent with the small olfactory bulb in skulls assigned to A. hildebrandti, comparable to the neuroanatomy of extant open-habitat palaecognaths [43]. However, the taxonomic identity of these crania is uncertain; they are not associated with diagnostic postcranial or locality data, and two separate skull morphotypes have been referred to A. hildebrandti [44–46].

δ13C data from skeletal collagen provide a comprehensive new understanding of Madagascar megaherbivore dietary ecology. Most available subfossils originate from southern Madagascar, and further research should investigate data across wider areas. For example, giant tortoises from the central highlands remain isotopically unstudied; these animals might also have been grazers, but their shell shape (associated with biomechanical advantage for grazing or browsing in extant species [47]) is poorly understood, making ecological inference difficult. However, whereas most modern-day open habitats on Madagascar are anthropogenic in origin, our results provide important evidence for former existence of native ecosystems dominated by endemic C4 grasses. It is clear that Madagascar supported multiple megaherbivore trophic guilds with differing relationships to native vegetation, which must have played important roles in regulating diverse natural landscapes. Madagascar’s ecosystems are now highly degraded, and protection and sustainable management of landscapes and ecosystem services represents a global priority for biodiversity conservation and human well-being [48,49]. Hypotheses of what constitutes a ‘natural’ Madagascar ecosystem must therefore consider the ecologies and regulatory roles of the island’s now-extinct megafauna, to support evidence-based restoration of this ecologically complex island.

Data accessibility. All data are available in electronic supplementary material, file S1 [50].

Authors’ contributions. J.P.H.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; S.T.T.: Funding acquisition, investigation, supervision, visualization, writing—review and editing.

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