Patterns in Amino Acid $\delta^{15}N$ Values Are Inconsistent with Aridity Driving Megafaunal Extinction in Southwestern Madagascar

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Problem:

Early human colonists of Madagascar encountered a diverse endemic fauna during the late Holocene that included elephant birds, pygmy hippos, and giant lemurs. All fauna >10 kg in mass went extinct in the past 1,000-2,000 years. Direct human predation and anthropogenic landscape change help explain aspects of the extinction pattern. Increasing aridity may have also played a role in some regions, but its contribution remains controversial.

Approach:

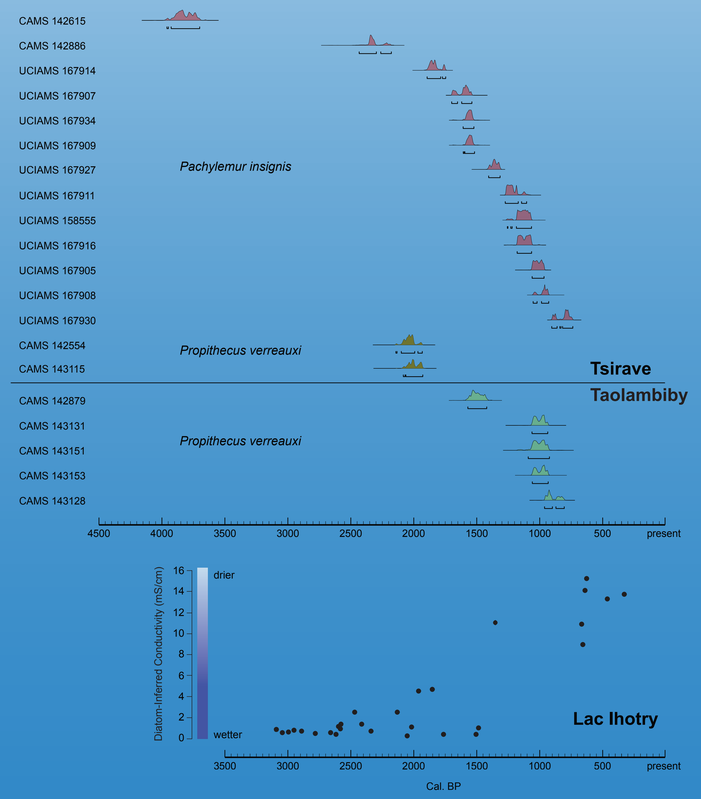
Stable nitrogen isotope ($\delta^{15}N$) values collected from the bones of terrestrial vertebrates reveal the aridity of the habitats in which these animals lived. Recently, Crowley et al. (2016) detected no directional change through time in $\delta^{15}N$ values from a sample (n = 238) of ancient bulk collagen from Malagasy vertebrates. However, other aspects of environment and the diet of an organism also affect $\delta^{15}N$ values in bulk collagen in poorly constrained ways and thus complicate the recognition of a signal related to aridity. Here, we use amino acid specific $\delta^{15}N$ values to strengthen the test of the hypothesis that populations of endemic lemurs lived in increasingly arid habitat during the past several thousand years. Support for this hypothesis leaves open the possibility that aridification and human activity acted synergistically to drive past megafaunal extinction.

Propithecus verreauxi

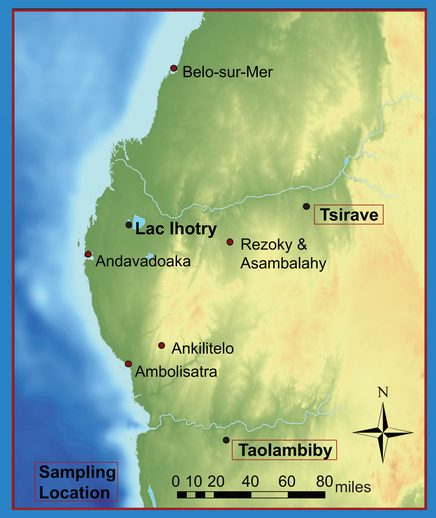
Pachylemur insignis

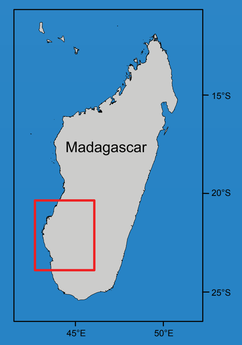
Study Species:

We analyzed 23 individuals that include the bones of two lemur species (*Pachylemur insignis* [n = 13] and *Propithecus verreauxi* [n = 10]) from two subfossil sites in SW Madagascar (Tsirave and Taolambiby). *Pachylemur* (the giant ruffed lemur) is an extinct member of the Lemuridae family, while *Propithecus verreauxi* (the Verreaux's sifaka) is an extant member of the Indriidae family. Tsirave includes remains of *Propithecus* and butchered remains of *Pachylemur*, and Taolambiby includes butchered remains of *Propithecus*.



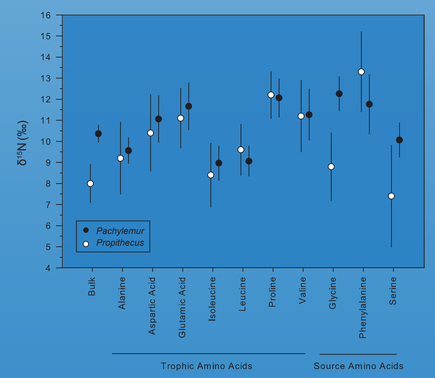
Radiocarbon dates (above) of individuals used in this study from sampling locations (below). The record of the salinization of Lac Ihotry is modified from Vallett-Coulomb et al. (2006): "Hydrological modeling of tropical closed Lake Ihotry (SW Madagascar): Sensitivity analysis and implications for paleohydrological reconstructions over the past 4000 years." Additional locations below are archaeological and paleoecological sites.

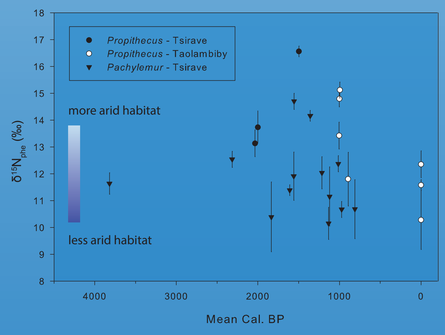




Trophic and Source Amino Acids:

For each radiocarbon-dated individual, we measured $\delta^{15}N$ values from ten amino acids by using gas chromatography combustion isotope ratio mass spectrometry (genus averages below left). The trophic level of an organism strongly influences the $\delta^{15}N$ values of "trophic" amino acids and only weakly influences the $\delta^{15}N$ values of "source" amino acids. Consequently, $\delta^{15}N$ values from source amino acids serve as a proxy for baseline $\delta^{15}N$ values in an ecosystem. Baseline $\delta^{15}N$ values increase with aridity.





Trends through Time:

There does not exist a significant monotonic relationship between time and $\delta^{15}N$ values in phenylalanine ($\delta^{15}N_{phe}$) in the Tsirave sample (see above right). However, there is a significant monotonic *decrease* in $\delta^{15}N_{phe}$ values through time at Taolambiby. These data suggest that lemurs living at Tsirave and Taolambiby did not live in increasingly arid habitat during the past several thousand years. If anything, *Propithecus* at Taolambiby came to live in increasingly mesic habitat, which may represent a case of ecological retreat in the face of colonizing humans and introduced species (Crowley et al. 2012).

Future Work:

The existing amino acid specific $\delta^{15}N$ data make aridification an unlikely primary driver of past lemur extinctions. However, the ecology and geomorphology of Madagascar are diverse, and additional amino acid specific $\delta^{15}N$ values with samples from other regions may reveal different patterns. A more refined understanding of past climate change in Madagascar could clarify expectations for when and where humans and endemic species faced water scarcity in the past. The details of anthropogenic disturbance that contributed to ecological retreat among *Propithecus* and the extinction of other genera are largely unknown. Landscape burning, the introduction of bovids and dogs, and occasional hunting in the region during the past two thousand years are factors worth considering in future research.

Background References

Crowley, B. E., Godfrey, L. R., Bankoff, R. J., Perry, G. H., Culleton, B. J., Kennett, D. J., ... & Burney, D. A. (2016). Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar. Ecography.

Crowley, B. E., Godfrey, L. R., Guilderson, T. P., Zermeño, P., Koch, P. L., & Dominy, N. J. (2012). Extinction and ecological retreat in a community of primates. Proceedings of the Royal Society of London B: Biological Sciences, 279(1742), 3597-3605.