Late Holocene Changes in Madagascar's Large Vertebrates

Recent cave findings offer insights into what caused the extinction of some megafauna.

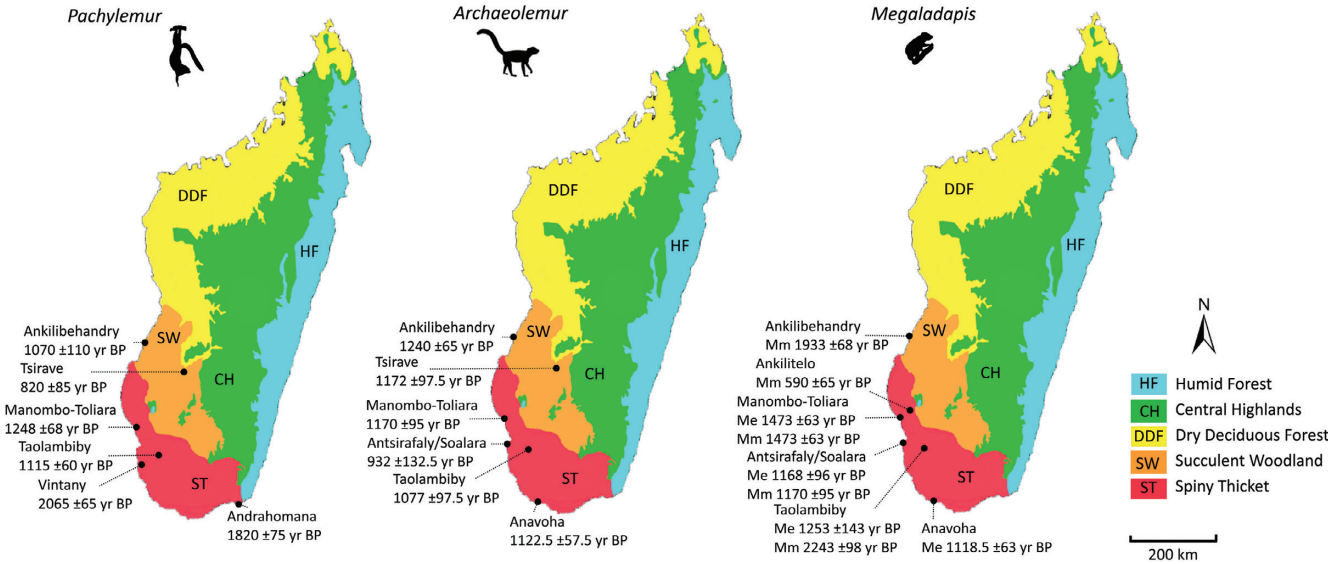
Madagascar experienced a major faunal turnover near the end of the first millennium CE that particularly affected terrestrial, large-bodied vertebrate species. As my colleagues and I reported in the September 2021 issue of *Frontiers in Ecology and Evolution*—from which this article is adapted—the literature on what triggered this turnover has grown enormously over the past few years, but no consensus has emerged. Was it human activity or a climate shift? There are cultural sites where humans have been present over extended periods of time with little impact on megafauna. Likewise, climate fluctuations in the Late Quaternary have been documented from northern to southern Madagascar with little apparent impact on the fauna. The notion that neither climate nor humans alone, but the combination of the two, was responsible for the megafaunal crash of the Late Holocene has gained broad acceptance in recent years, but no single hypothesis appears to apply across the island.

PHILLIP LEHMAN, MCDA

Diving site at Mitoho Cave in southwest Madagascar where divers collected fossils of extinct species and stalagmites

To address the question requires a focus on regional records with good chronological control that document coeval changes in rainfall, faunal composition, and human activities. We obtained new paleontological and paleoclimatological data from southwestern Madagascar, the driest part of the island today. We collected over 1,500 subfossil bones from lacustrine deposits at a coastal site called Antsirafaly and from both flooded and dry cave deposits at Tsimanampesotse National Park (TNP). We built a chronology of Late Holocene changes in faunal assemblages based on sixty-five radiocarbon-dated vertebrate specimens and subfossil associations. We also collected and analyzed stalagmites from TNP and two other locations in southern Madagascar to provide histories of past changes in rainfall, droughts, and pluvials over the past 120,000 years.

Prior research has supported a primary role for drought (rather than humans) in triggering faunal turnover at Tsimanampesotse. This theory is based on four forms of evidence: a large freshwater ecosystem west of what is now the hypersaline Lake Tsimanampesotse, which once supported freshwater mollusks and waterfowl; abundant now-extinct terrestrial vertebrates; regional decline or disappearance of certain tree species; and scant local human presence. Our new data allowed us to document the hydroclimate of the subarid Southwest during the Holocene, as well as shifts in faunal composition—including local extirpations, large-vertebrate population collapse, and the appearance of introduced species. These records affirm that climate alone cannot have produced the observed vertebrate turnover in the Southwest. Human



BROOKE CROWLEY AND LAURIE GODFREY

Last occurrence dates for Pachylemur, Archaeolemur, *and* Megaladapis *at sites in the spiny thicket and succulent woodland ecoregions of the dry South. All dates are calibrated, and all major terrestrial ecoregions of Madagascar are shown.*

activity, including the introduction of cattle, as well as associated changes in habitat exploitation, also played an important role.

Our paleontological mission began in 2014 with an initial exploration and survey of both TNP and Antsirafaly. In 2015, we began a limited collection of subfossil bones from the surface of the submerged floor of Vintany Cave to determine how well organic matter was preserved in the flooded caves. Our first large-scale effort to collect subfossils was launched in 2016, when team divers collected bones from the floors of Vintany and two additional flooded caves–Mitoho and Malazamanga. In addition, we collected bones from three dry sites within the park: Soarano, Anjohimpaty, and Ambolely. In 2018 and 2019, we followed different collection methodologies for each TNP locality, and, for the first time, dug into the waterlogged sediments on the bottom of Vintany Cave. We found that Vintany Cave sediments preserved abundant subfossils, and we mapped and recorded all collection localities within the cave. We collected microfaunal bones (rodents, bats, and birds) from eolian deposits on the floor of Anjohimpaty Rock Shelter, on a submerged bat guano deposit in Mitoho Cave, and on the floor and in sediments at Vintany Cave. In 2019, our team returned to Antsirafaly where we extracted subfossils from an isolated dried pond. Subfossils had been retrieved at this site previously by local villagers. Some of these bones articulated with the bones that we collected, suggesting that they belonged to the same individuals.

Separated by about forty-five kilometers direct distance and differing in depositional habitat, the sediments of the Antsirafaly pond and TNP caves show striking differences in faunal composition. In total, we found sixteen extinct species, eight at Antsirafaly and thirteen at Tsimanampesotse, with five species occurring at both sites. At Antsirafaly, we only recovered extinct species. These included three primates (*Megaladapis edwardsi*, *M. madagascariensis*, and *Archaeolemur majori*), two elephant birds (*Mullerornis modestus* and the largest-bodied species, *Vorombe titan*), two reptiles (*Voay robustus* and *Aldabrachelys* sp.), and a hippo (*Hippopotamus lemerlei*). Delicate bones of small vertebrates were either not preserved or may have been missed because we did no fine sieving of sediments.

At TNP, the extinct species included three primates (*Pachylemur insignis*, *Mesopropithecus globiceps*, and *Megaladapis edwardsi*), two euplerid carnivorans (*Cryptoprocta* new sp. and *C. spelea*), the hippo (*Hippopotamus lemerlei*), an elephant bird (*Mullerornis modestus*), four volant birds (*Alopochen sirabensis*, *Coua* cf. *berthae*, *Coua* cf. *primaeva*, and *Vanellus madagascariensis*), and two reptiles (the giant tortoise, *Aldabrachelys grandidieri* and the crocodile, *Voay robustus*). Comparing the extinct taxa at Antsirafaly and TNP, the two extinct primate species most common at TNP (*Pachylemur insignis* and *Mesopropithecus globiceps*) are notably absent at Antsirafaly. Crocodiles are much more common at the TNP sites than at Antsirafaly. In contrast, the extinct *Megaladapis*, which is relatively common at Antsirafaly, is extremely rare at TNP. *Megaladapis edwardsi* is represented by a single skull at Malazamanga Cave and two specimens found at the entrance to Mitoho Cave; *M. madagascariensis* is absent entirely at TNP. Similarly, *Hippopotamus* is extremely rare at TNP, represented by just two (likely associated) specimens from Malazamanga Cave that were found together under the *Megaladapis* skull. Elephant birds are far more common at Antsirafaly than at TNP.

We recovered bones from over forty endemic extant taxa at TNP. Many

of these still live within the park, but five are locally extirpated. The latter include a rare and poorly known nesomyid rodent (Petter's big-footed mouse, *Macrotarsomys petteri*), a Vulnerable euplerid (the fanaloka, *Fossa fossana*), and three Endangered or Critically Endangered birds (Humblot's heron, *Ardea humbloti*, the Madagascar sacred ibis, *Threskiornis bernieri*, and the Madagascar fish-eagle, *Haliaeetus vociferoides*). *Fossa fossana* subfossils have never previously been collected in the dry West or subarid Southwest; this euplerid is restricted today to the humid eastern rainforest and parts of the Central Plateau. *Haliaeetus vociferoides* is of interest because it would have presumably exploited freshwater fish from Lake Tsimanampesotse, which no longer exist due to the lake's current salinization.

Neither TNP nor Antsirafaly was an early human settlement site. However, there are clear signs of minimal human presence over the past 800 years, or so, derived from introduced taxa. Radiocarbon dates for the introduced domestic cat (*Felis catus*) from a dry second entrance to the flooded Mitoho Cave called Andranohilova span much of the past millennium. They suggest that feral cats at least occasionally used Andranohilova.

We found specimens of the helmeted guinea fowl (*Numida meleagris*, long assumed to be introduced to Madagascar) in association with nearly 2,000-year-old plant remains and over 2,000-year-old subfossil *Pachylemur* within the sediments of the deep section of Vintany Cave. However, there are findings of guineafowl at Ankilitelo in southwest Madagascar over 13,000 years ago, raising the possibility that this species colonized Madagascar from Africa prior to, and independently of, the initial colonization of the island by humans.

To develop a long-term record in southern Madagascar of pluvial (more rainy) versus arid (non-pluvial, or interpluvial) conditions, we used the growth phases of speleothems (i.e., the formation of cave stalactites and stalagmites). Speleothems require calcium ion supersaturation in percolating drip waters. For southwest Madagascar, with annual rainfall near the minimum required for speleothem growth (approximately 250–300 mm per year, depending on evaporation and the seasonality of rainfall) periods of stalagmite deposition and non-deposition can be used to infer pluvial versus arid climate.

ZACHARY KLUKKERT

Fossils of the extinct horned crocodile from Vintany Cave, shown by one of the cave explorers, conservation geneticist Evon Hekkala, of Fordham University and the American Museum of Natural History

Our records show that the differences in mean annual rainfall between pluvial and interpluvial periods in the southwest were not necessarily very large, and certainly were smaller than the differences across ecoregions at any single point in time. We also found that, in southern Madagascar, the Holocene was largely drier than it is today, and through most of the dry Holocene, the rich community of large vertebrates endemic to this region thrived. That said, we can assume that if there is any place in Madagascar where dry climate would have been most likely to trigger the extinction of vertebrate species, it would be the subarid Southwest. Indeed, there is evidence that after a long, dry interpluvial, vertebrate populations were impacted. At both TNP and Antsirafaly, local extirpation occurred without evidence of a human trigger. However, our data also suggest that climate alone cannot have caused their extinction. Our profiles of local decline, coupled with regional data on the late survival of endemic large vertebrates and the timing of appearance of introduced species, present a picture that is more complex.

We contend that it was the introduction and spread of agropastoralism that transformed what had been a series of local biogeographic shifts into wholesale population collapse and species extinction. The introduction of domesticated animals and cultivated plants from Asia and Africa spread to Madagascar during the late first millennium CE. Between 1200 and 900 years ago, it spread across the island. This was long after people had settled on Madagascar. People were present at least intermittently in the Southwest during the Early and Middle Holocene and certainly prior to 2,000 years ago. But these hunter/foragers and fisher/foragers had minimal impact on endemic large-bodied vertebrate populations.

Adapted from "Teasing Apart Impacts of Human Activity and Regional Drought on Madagascar's Large Vertebrate Fauna: Insights From New Excavations at Tsimanampesotse and Antsirafaly" by Laurie R. Godfrey, et al. Published in *Frontiers in Ecology and Evolution*, 23 September 2021 doi: 10.3389/fevo.2021.742203.

***Laurie Godfrey**, biological anthropologist and paleontologist, is Professor Emerita at the University of Massachusetts, Amherst.*