Late Survivors: Traditional ecological knowledge and the timing of extinction of Madagascar's large-bodied Holocene vertebrates

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Summary

During the Late Holocene, Madagascar experienced the loss of ~50 vertebrate species including mammals, birds and reptiles. Many of these were relatively large-bodied (e.g., "giant" lemurs, hippopotamuses, flightless elephant birds, and horned crocodiles). Many are known to have survived into the past two millennia. Most extinction date estimates fall within a narrow window of ~800 to 1200 CE. There is broad skepticism regarding survival of any of these species into the second half of the last millennium – i.e., the period of European contact. Ethnohistoric (lore and recorded eyewitness) accounts of large vertebrates abound within this period in Madagascar, but they are often fanciful and discounted as mythical. Simultaneously, many new species have been discovered even over the past decade, often spurred by the knowledge of local people. These are typically small species, but examples of the discovery of large vertebrates believed to be extinct exist outside of Madagascar, again aided by local people. **We synthesized data from traditional ecological knowledge of large vertebrate species in Madagascar**, including apparent references to large-bodied lemurs (*Palaeopropithecus, Pachylemur*, and *Archaeolemur*), a large-bodied euplerid, horned crocodiles, hippopotamuses and elephant birds.

Here we map these findings and describe underlying patterns:

- Ethnohistoric records (including eye-witness reports and lore) suggest a much longer extinction window than generally acknowledged.[1]
- Late-20th (or even 21st) century eye-witness reports exist for three of these taxa (a big *Cryptoprocta*, *Hippopotamus*, and *Pachylemur*), all of which have been described as crepuscular or nocturnal. [1,2]
- Rapid deforestation has threatened most last refuges; asynchronous diel activity patterns may have facilitated temporal, if temporary, avoidance of humans. [3-6]
- Traditional ecological knowledge has been undervalued, and can help in our understanding of extinction processes, building research partnerships, and possibly, discovering remote populations of species believed to be extinct.

Figure 1. Timeline of known extant period of seven taxa (dark color), the ^{14}C dates for last occurrence (x;"x" corresponds with date, site in Table 1 and Figure 2), and the period of uncertain persistence (light color) informed by ethnohistoric records (counts and most recent dates in Table 1).

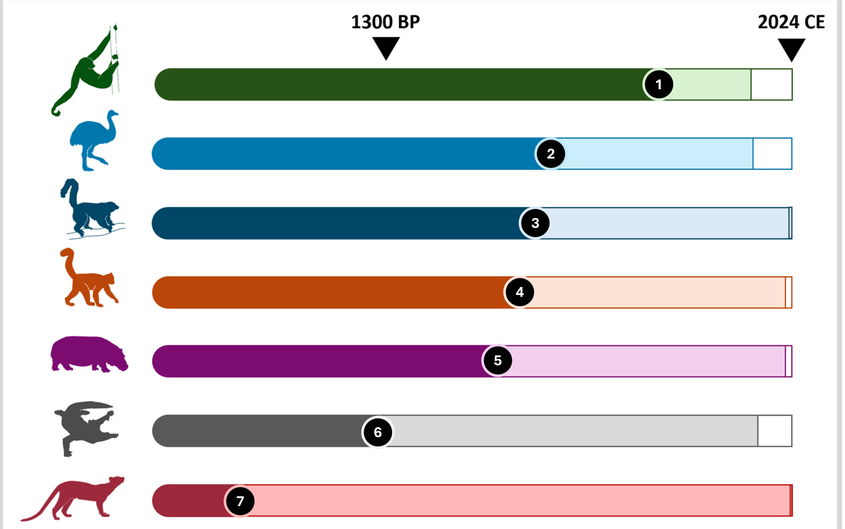
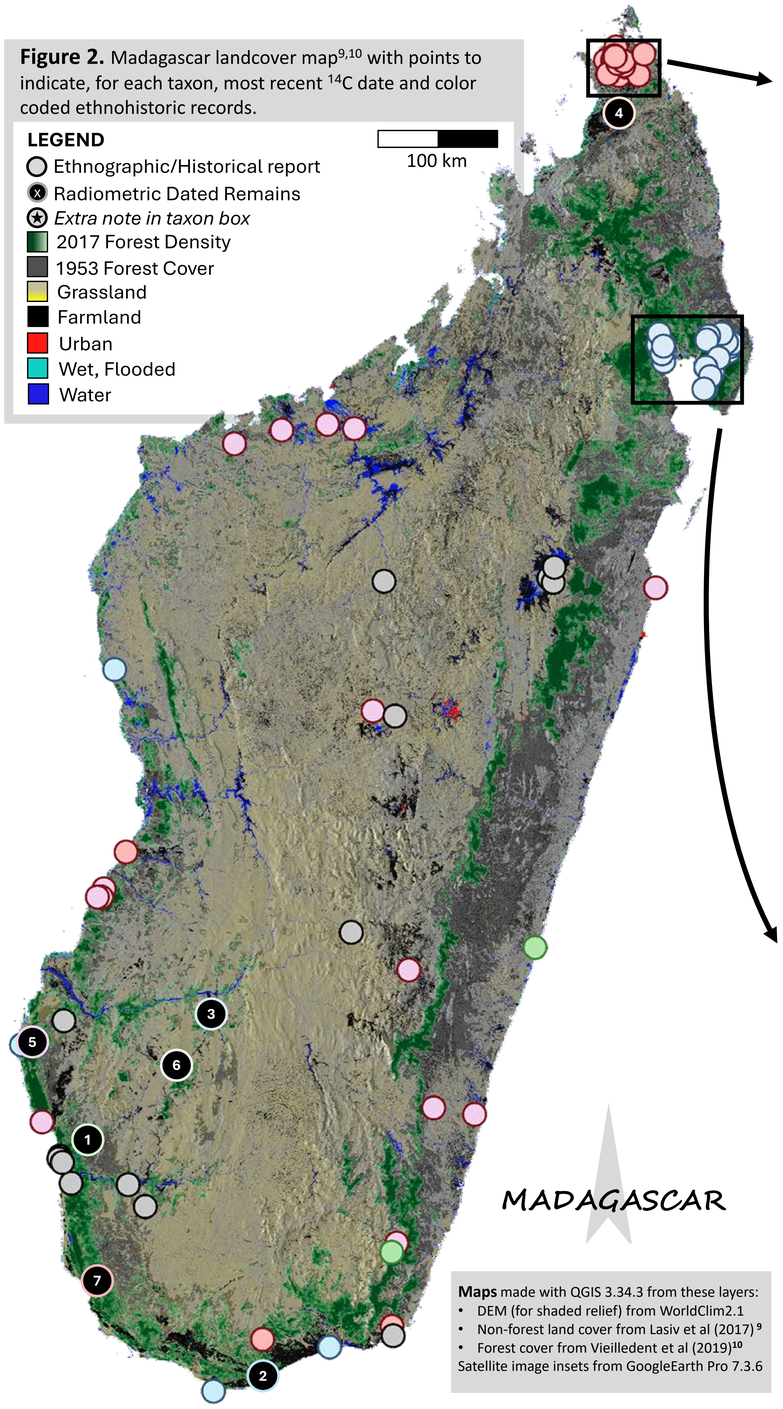


Table 1. Last occurrence within the period of megafaunal decline for those extinct taxa that apparently survived into the last half of the 2nd millennium CE (*Last occurrence dates older than 2000 cal yr BP are excluded);* Counts of non-paleontological records that, apparently, describe the persistence of these fauna. Colored numbers link site and date information to Figures 1 & 2; moon icon indicates crepuscular/cathemeral/nocturnal habit reported in Taxon Boxes.

Taxon	Paleontological Record of Last Occurrence			Ethnohistoric Records (most recent date)
	Site	Calibrated age BP*	Source	
Palaeopropithecus	**Ankilitelo** 1	**442.5 ± 122.5**	Simons 1997	**2 (1893 CE)**
Elephant Bird *(Aepyornis)*	**Manambovo** 2	**767.5 ± 137.5**	Battistini *et al.* 1963	**4 (1900s CE)**
Pachylemur	**Tsirave** 3	**820 ± 85**	Godfrey *et al.* (n.d.)	**22 (2015 CE)** ☾
Archaeolemur	**Antsiroandoha** 4	**872.5 ± 87.5**	Simons *et al.* 1995	**5 (2004 CE)**
Hippopotamus	**Lamboharana** 5	**942.5 ± 17.5**	Hixon *et al.* 2021	**20 (2005 CE)** ☾
Voay	**Ampoza** 6	**1322.5 ± 42.5**	Hekkala *et al.* 2021	**17 (1915 CE)**
Cryptoprocta**	**Ankazoabo** 7	**1767.5 ± 67.5**	Crowley 2010	**32 (2019 CE)** ☾

*(mean ± 1s cal yr BP); Conventional ^{14}C dates were calibrated or recalibrated to calendar years before present (cal yr BP) using Calib 8.2 [7] and the southern hemisphere calibration curve (SHCal20) [8]. **Exclusive of extant *C. ferox*.

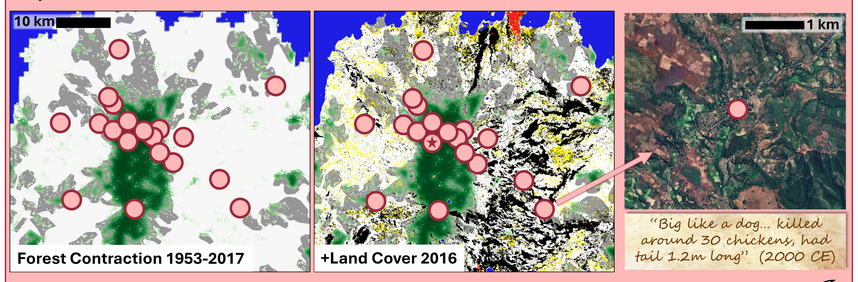
Figure 2. Madagascar landcover map[9,10] with points to indicate, for each taxon, most recent ^{14}C date and color coded ethnohistoric records.



Maps made with QGIS 3.34.3 from these layers:
- DEM (for shaded relief) from WorldClim2.1
- Non-forest land cover from Lasiv et al (2017) [9]
- Forest cover from Vieilledent et al (2019)[10]

Satellite image insets from GoogleEarth Pro 7.3.6

Reports from Mt d'Ambre



***Cryptoprocta* spp.** [1,2,11]

- There are multiple types of fosa (larger and smaller)
- The big one is dog-sized or bigger; Est. body mass >20 kg (as large as 25-30 kg)
- Long trunk, very long tail, short forelimbs and long hind limbs
- Dark pelage (variously described as very black, blackish, ash, dark red)

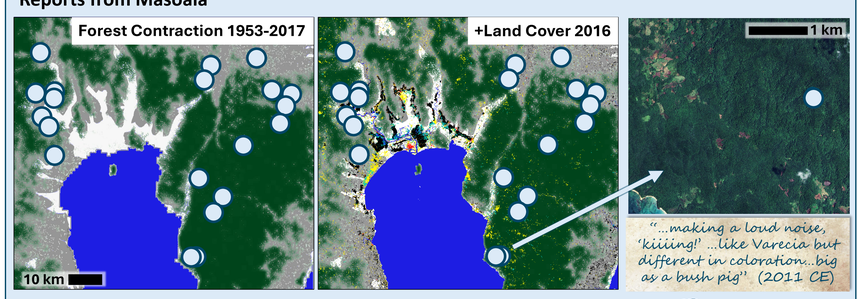
- Dwells in the forest; Can climb trees
- Preys on lemurs, certain wild birds, raids chicken coops
- Will attack larger animals like bush pigs or cows (especially if the intended prey is compromised, sick, wounded, young, old)

- *Dangerous*, especially during its breeding season
- Will attack, can kill a person
- Can kill a dog; dogs are afraid of this animal

- **Called the fosa, fosa be, fosa maventy, fosa tamana, joby tombotomboloha, fosa joby, fosa mainty, fosa jobijoby**

☆ "I awoke at about 0600h (**before light**) to a strange noise coming from the supply tent… I descended slowly from my tent to see a long black tail… I took a step closer to the tent, the animal turned around, bumping its head against the rain fly, then its long head looking directly at me… it looked like a fosa… but its head was solid black, as were its body and tail… much larger than *C. ferox*… maybe 20-25kg… it ran off very fast away from me." Ampamelonabe main camp, Dec. 1989 -Benjamin Z. Freed [10]

Reports from Masoala



***Pachylemur* spp.** [1,2,12]

- A lemur, similar to *Varecia* but much larger
- Tricolored, like *V. rubra*, but red, black and grey rather than red, black and white
- Forelimbs are not as short relative to the hind limbs as those of *Varecia*

- Makes very loud, piercing sounds
- **Active at night (Cathemeral?)**
- **Sleeps high in the canopy in the tallest trees; Descends from the tall trees at dusk to forage**
- Tends to confront perceived predatory threats aggressively, moving toward the predator rather than freezing or fleeing (Note: *Varecia* has an unusual reproductive strategy, giving birth to a litter of up to four altricial young that are stashed in nests high in the canopy, and not carried unless moved to a new nesting location. Their highly aggressive anti-predator tactics make sense considering their inability to flee from a predator with altricial infants; infants can't cling to parents for transport.)

- **Called the "kisoala" – knife of the forest – a reference to the extremely loud noises it makes.**

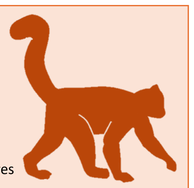
***Palaeopropithecus* spp.** [1,2]

- Short (human-like) face
- Long digits
- No tail
- Rounded ears
  (Note: indriids have rounded ears, lemurids have pointy ears; palaeopropithecids are sister to indriids)

- Cannot move on a smooth rock (sloth-like)

- **Called the "tretretretre" or "tratratratra"**

***Archaeolemur* spp.** [1,2]



- A lemur
- Around the body mass of a 7-year-old child

- Commonly observed on the ground (semiterrestrial quadruped)
- Fond of foraging for crabs in the coastal mangroves

- **Called the "kidoky" or "kindoky" on the west coast.**

Voay robustus [1,2]

- Robust and potentially very large: can be >6 meters in length.
- Teeth can be huge (up to 60 mm in circumference)

- Inhabits caves near fresh water, stagnant bodies of fresh water, marshes and coastal lagoons (the Nile crocodile prefers rivers)

- **Called "mamba" except in the central highlands where it is called "voay" and Mamba refers to the Nile crocodile**

Elephant birds (*Aepyornis, Mullerornis*) [1,2,13]

- Enormous bird whose eggs large enough to contain a newborn human

- Strong, dangerous, aggressive, capable of killing a man as powerful as a king. Ostrich-like threat response recorded

- 1600s, people of the south used their eggs as vessels to carry different types of liquids
- Known to the local people at the Cap Sainte-Marie in 1866, and identified as the bird that laid the abundant eggs littering the ground as broken shell in the region (A. Grandidier, 1867)

- **In southern Madagascar, called the 'vouron (voron) patra' (the bird of the Ampatres, or the land of the people of the semidesert). Also called 'Vorombe' or 'Ivorombe' (= 'big bird')**

***Hippopotamus* spp.** [1,2]

- Water cow, roughly the size of a small cow, but hornless
- Skin is dark but there is pink coloration around the mouth and eyes
- Footprint reveals webbed toes (not distinctly separated)
- Eyesight is poor
- Floppy tissue obscures the chin (likely transverse neck folds misinterpreted by Etienne de Flacourt as ears)

- **Feeds at dusk or dawn**; will raid village crops, such as corn
- Emerges from and retreats to bodies of fresh water (volcanic crater lakes, rivers, water holes)
- Makes threatening, frightening roars
- Charges perceived threats blocking its path through the forest; aggressive, dangerous, can kill people
- Sprays urine at perceived threats

- **Called the "tsy-aomby-aomby" = 'a little cow-like' or, 'the cow that isn't a cow,' and other names that describe hippos**

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