

Late Quaternary Mammal Introduction and Extinction Records from Archaeological Cave Deposits in Timor-Leste

JULIEN LOUYS^{1,2} , SUE O'CONNOR^{2,3} , SHIMONA KEALY^{2,3} , STUART HAWKINS^{2,3} ,
AND KENNETH P. APLIN^{4†} 

¹ Australian Research Centre for Human Evolution, Griffith University, Brisbane, Australia

² Archaeology and Natural History, College of Asia and the Pacific,
The Australian National University, Acton ACT 2601, Australia

³ ARC Centre of Excellence for Australian Biodiversity and Heritage,
The Australian National University, Canberra ACT 2601, Australia

⁴ Australian Museum Research Institute,
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

† Ken Aplin 1958–2019, deceased.

ABSTRACT. Humans have influenced island biotas in the last few millennia through widespread forest clearances and the introduction of commensals and pest species, causing the extinction of island endemics around the world. This is particularly evident in Timor, where more than 40,000 years of human habitation produced few if any extinctions until the last few thousand years when Timor lost most of its endemic murids. We present new records and dates for endemic rodents and introduced fauna from archaeological cave deposits in Timor-Leste that captures this human-mediated transition. We discuss the chronology of faunal introductions and losses at these sites, and compare the Timor records to other records in surrounding islands. We find no directly dated evidence for significant overlap between the introduction of exotics and extinction of murid endemics at ecological timescales, although determining true extinction and introduction ages will require direct dating and modelling of taxon occurrences, which may bring extinction and introduction closer together in time. Nevertheless, we suggest that, based on current data, the almost complete loss of Timor's endemic forests were the primary driving force in rodent extinctions.

ABSTRAK [Bahasa Indonesia]. Manusia telah memengaruhi keragaman biota pulau dalam beberapa milenya terakhir melalui pembabatan hutan yang luas dan introduksi spesies komensal dan hama, yang menyebabkan kepunahan hewan endemik pada beberapa pulau di seluruh dunia. Hal ini terutama terlihat di Timor, di mana lebih dari 40.000 tahun umur hunian manusia yang hanya menyebabkan sedikit atau hampir tidak ada kepunahan, sampai beberapa ribu tahun terakhir ketika Timor kehilangan sebagian besar tikus endemiknya. Kami menyajikan data dan penanggalan baru terkait tikus endemik dan fauna yang diintroduksi ke dalam pulau berdasarkan pada temuan dari gua arkeologi di Timor-Leste yang merekam perubahan yang disebabkan oleh manusia. Kami membahas kronologi introduksi fauna dan dampak negatif di lokasi-lokasi ini, dan membandingkan data di Timor dengan data lain di pulau-pulau sekitarnya. Kami

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ORCID ID: Louys <https://orcid.org/0000-0001-7539-0689>, O'Connor <https://orcid.org/0000-0001-9381-078X>, Kealy <https://orcid.org/0000-0002-0646-1313>, Hawkins <https://orcid.org/0000-0001-8838-2856>, Aplin <https://orcid.org/0000-0003-0403-8690>

Corresponding author: Julien Louys j.louys@griffith.edu.au

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tidak menemukan bukti penanggalan yang dapat dicocokkan korelasinya antara waktu pengenalan fauna eksotis dan kepunahan tikus endemik dalam skala waktu ekologis, walaupun menentukan usia kepunahan dan introduksi fauna yang sesungguhnya akan memerlukan penanggalan secara langsung dan pemodelan kemunculan taksonomi, yang mungkin dapat menunjukkan waktu kepunahan dan introduksi lebih dekat. Meskipun demikian, berdasarkan data yang ada saat ini, kami berpendapat bahwa hampir hilangnya hutan endemik di Timor merupakan faktor utama dalam kepunahan tikus.

REZUMU [Tetum language]. Emar fó ona influénsia ba biota insulár sira iha miléniu hirak liubá, liuhusi tesi ai no hamate floresta (ai-laran) iha fatin barak no liuhusi hatama espésie komensál sira no kuit (praga), hodi provoka estinsaun ba espésie endémika insulár iha mundu tomak. Prosesu ida ne'e ita bele haree liuliu iha Timor, iha ne'ebé, durante tinan rihun 40 resin ho prezensa emar nian, estinsaun sira la iha, ka iha uitoan de'it, maibé iha tinan rihun balun ikus ne'e, Timor lakon maioria husi ninia murídeu (balada maktohik ka roedór) endémiku sira. Ami aprezena rejistu no data foun sira kona-ba roedór endémiku sira no kona-ba fauna ne'ebé hatama ona. Dadus sira ne'e ami rekolle iha depózitu arkeolójiku sira iha fatuk-kuak Timor-Leste nian, ne'ebé hatudu tranzisaun ida ne'e, ne'ebé akontese tanba prezensa emar nian. Ami diskute kronolojia kona-ba introdusaun (hatama) no perda (lakon) sira fauna nian iha fatin sira ne'e, no ami kompara rejistu sira husi Timor ho rejistu husi illa sira ne'ebé besik. Ami la hetan prova sira ho data ne'ebé bele hatudu duni sobrepozisaun (akontese iha tempu hanesan) maka'as entre introdusaun (hatama) espésie ezótika sira no estinsaun (lakon nafatin) husi murídeu endémiku sira iha eskala tempu ekolójika nian sira, maske definisaun ho loloos kona-ba idade estinsaun no introdusaun prezisa data saun (atribui data) direta no modelasaun konaba okorrénsia (mosu) *táxones* (grupu ka divizaun iha sistema biolójiku) nian, no definisaun ida ne'e bele hatudu katak estinsaun no introdusaun akontese iha tempu besik. Maske nune'e, ami sujere katak, bazeia ba dadus ne'ebé oras ne'e daudaun iha, lakon kuaze total husi floresta (ai-laran) endémika Timor nian maka razaun prinsipál ba estinsaun roedór sira nian.

Introduction

Humans have had a disproportional impact on island biotas over the last few millennia (Ceballos & Ehrlich, 2018; Louys *et al.*, 2021; Nogué *et al.*, 2021), and the widespread introduction of commensals and pest species have been implicated in the extinction of island endemics around the world (Wood *et al.*, 2017; Castilla-Beltrán *et al.*, 2021). However, based on current archaeological and palaeontological records, humans and other hominins may have had more limited impacts on island ecosystems prior to the widespread adoption of agriculture, maritime trade, and domestication (Leppard, 2014; Rozzi *et al.*, 2023; Louys *et al.*, 2021; Wood *et al.*, 2017), but this record is not well resolved for earlier periods of the Pleistocene. On the island of Timor, more than 40,000 years of human habitation produced very few extinctions (Hawkins *et al.*, 2017; Louys *et al.*, 2021); although an example of the latter includes a crane (*Grus* sp.) that likely became extinct in the Late Pleistocene (Meijer *et al.*, 2019). It was only in the last few thousand years that Timor lost a disproportionate amount of its endemic biota (Aplin & Helgen, 2010).

Prehistoric excavations on Timor documenting some of these losses began in rockshelters near Nikiniki, southwest Timor (Fig. 1), by Alfred Bühler in 1935 (Sarasin, 1936) (no local names of the rockshelters are provided and they are referred to as “Abri” [rockshelter] I, II, and III). Bühler uncovered pottery fragments and domestic animals that were likely Holocene in age, as well as giant rat fragments from Abri II which were subsequently described by Schaub (1937) as the extinct species *Coryphomys buehleri*. In 1938, Willems of the Oudheidkundige recovered relatively recent archaeological material from Ulnam Cave on the slopes of Gunung Mutis located NW of Nikiniki (Oudheidkundig Verslag, 1939: 12). Two additional caves, Liang Leluat II and Liang Djenilu, excavated by Verhoeven in 1954, produced more Holocene material, including blades, scrapers, and worked points (Verhoeven, 1959).

Older deposits on Timor were first identified at Lene Hara cave in the eastern part of the island by the Portuguese anthropologist Antonio de Almeida in 1963. The site contained an 80 cm deep cultural assemblage with marine shells and stone artefacts found throughout the sequence, but with pottery fragments restricted to the surface (Fig. 1). A brief report on the stone artefacts described them as typologically “pre-Neolithic” (Almeida & Zybszweski, 1968). However, the site was never dated, and none of the fauna was properly described. In 1966, Glover visited the site and photographed Almeida’s trench, which was still open (Glover, 1969). Glover made a small cutting on the edge of the trench, which confirmed Almeida’s observation that pottery was absent below the surface (Glover, 1969).

Glover conducted additional excavations between 1966–1967 at Uai Bobo 1 and 2, Lie Siri, and Bui Ceri Uato in eastern Timor and found large amounts of prehistoric terrestrial faunal remains that, together, provided a baseline cultural sequence for the island (Glover, 1986) (Fig. 1). Glover (1986: appendix 2) presented new giant murids from his excavations, with initial identification of murid cranial remains made by Dan Witter, with further work and tabulation undertaken by Jack Mahoney, as described in Glover’s (1986) Appendix 2. Mammalogist Guy Musser of the American Museum of Natural History subsequently agreed to take over the study of the fossil rodents, and he later passed on the material to Kristofer Helgen, who studied the collection with mammalogist and zooarchaeologist Kenneth P. Aplin (KPA). In addition to *Coryphomys*, three undescribed genera of giant rats were recognized in Glover’s monograph. Pending formal description, these were designated “Large murid, genus A” (Glover, 1986: plate 49), “Large murid, genus B” (Glover, 1986: plate 50), and “Large murid, genus C” (Glover, 1986: plate 51). These are hereafter referred to as Genus A, B, and C, respectively. Genus C is absent from Bui Ceri Uato but otherwise all three genera are present in all of Glover’s sites.

Following the annexation of Timor-Leste by Indonesia