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Multi-analytical approach to zooarchaeological assemblages elucidates Late Holocene coastal lifeways in southwest Madagascar

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ABSTRACT

The impact of resource exploitation by ancient human communities on Madagascar's environment is an area of intense debate. A fundamental question in the archaeology of Madagascar is the extent to which arrival of settlers, introduction of non-native plants and animals, and subsequent human exploitation of island biota, which catalyzed declines in biodiversity and significantly degraded environmental conditions. Fine-grained datasets, including zooarchaeological, archaeobotanical and other ecological evidence, are needed to assess the relationship between human resource exploitation and environmental change. On Madagascar, the resolution of zooarchaeological datasets is often reduced by poor preservation of faunal remains, making precise taxonomic identifications difficult, and few projects to-date have comprehensively assessed zooarchaeological data. Here, we present zooarchaeological data from three coastal villages in the Velondriake Marine Protected Area in southwest Madagascar, where human occupation spans from ca. 1400 BP to the present. Faunal remains from the Late Holocene sites of Antsaragnangy and Antsaragnasoa were identified using morphological analysis of remains, and a PCR-based bulk bone metabarcoding approach was applied at Andamotibe to molecularly identify fish and other vertebrates in a faunal assemblage that was particularly fragmented. Results were interpreted and contextualized using modern data on local fish diversity, climate and anthropogenic impacts on marine and estuarine habitats, as well as modern fishing practices (including preferred fishing grounds, tackle, taxonomic representation and volume of catch). Our use of multiple analytical and interpretative approaches has provided the most highly resolved view to date of past human subsistence in coastal southwest Madagascar. We contend that future research into human-environment dynamics on Madagascar should make use of diverse analytical methods, in order to more comprehensively evaluate past interactions between human communities and the native biota. Furthermore, we encourage an historical ecological approach, so that long-term perspectives on changing human-environment dynamics may be used to contextualize modern trends.

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1. Introduction

Human-environment interaction on Madagascar remains an intensely debated topic in archaeology. For nearly a century,

scholars from a range of disciplines have studied anthropogenic action on the island's unique biota and landscapes (for recent reviews see [Dewar and Richard, 2012](#); [Douglass and Zinke, 2015](#); [Radimilahy and Crossland, 2015](#)). Previous work on past human-animal interactions by archaeologists, paleontologists, and paleobotanists focused on elucidating the processes by which a large suite of endemic fauna, including the island's giant lemurs, giant tortoises, elephant birds and pygmy hippopotamuses, went extinct. These studies involved paleoecological reconstructions and the

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examination of skeletal remains (Burney, 1987, 1993; Burney et al., 2004; Crowley, 2010; Crowley et al., 2016; Goodman and Jungers, 2014; Goodman et al., 2013; Muldoon, 2010; Muldoon et al., 2009; Perez et al., 2005; Simons, 1995). The southwest coast features prominently in Madagascar's extinction debate, as the highest density of known megafauna sites on the island is located here. These sites, which include limestone caves and coastal marshes, act as taphonomic traps, where large numbers of animal bones accumulate over time (See Table 1 in Crowley, 2010). Interdisciplinary work has yielded evidence that people in the southwest processed carcasses of many now-extinct taxa, including lemurs (Godfrey and Jungers, 2003; Perez et al., 2005) and hippopotamuses (Gommery et al., 2011; MacPhee and Burney, 1991) beginning around 2000 BP (Crowley, 2010). Recent studies have further shown that the disappearance of endemic biota on Madagascar had significant cascading effects across the island's ecosystems and may allow us to predict which taxa and ecosystems are most at risk of extinction today (Federman et al., 2016; Kistler et al., 2015; Virah-Sawmy et al., 2015). Finally, paleoecological reconstructions have attempted to disentangle the relative contributions of climate and anthropogenic action associated with changes in landscape and biodiversity (Burney, 1993; Burns et al., 2016; Crowley et al., 2016; Douglass and Zinke, 2015; Virah-Sawmy et al., 2010).

Despite advances in our understanding of environmental change on Madagascar, the extinction question has overshadowed the need for more comprehensive investigations of past human-animal interactions on the island. Few archaeological projects have systematically analyzed faunal remains, documented in detail the range of taxa people exploited in the past, or described the roles animals played in the lifeways of ancient communities (see Rakotozafy and Goodman, 2005). The data presented in this paper are derived from the most detailed zooarchaeological study to-date of coastal villages in southwest Madagascar. Vertebrate assemblages from three proximal Late Holocene (ca. 1400 BP to ca. 50 BP) fishing villages (Antsaragnangy, Antsaragnaso and Andamotibe) located within the Velondriake Marine Protected Area (Fig. 1) are described using a combination of traditional morphological analyses and ancient DNA PCR-based bulk-bone metabarcoding (Grealy et al., 2016). Results are then contextualized within the backdrop of modern fisheries data. We examine the inter-site variation in exploited taxa observed at sites within a small geographical area, and attempt to discern the diversity of marine and terrestrial fauna exploited by ancient human communities on Madagascar.

2. Previous research in southwest Madagascar

In southwest Madagascar, prior to the Velondriake research presented here, zooarchaeological assemblages were only known from two areas, Rezoky/Asambalahy and Sarodrano. The sites of Rezoky and Asambalahy are located roughly 150 km inland and east of Velondriake, in a region today associated with the Bara pastoralists (Fig. 1). These sites are among the oldest known archaeological sites in Madagascar's interior, dating from ca. 700–400 BP, prior to the ascendancy of the Sakalava empire, from the mid-17th to early 19th centuries AD (Dewar and Wright, 1993; Vérin, 1971). The ancient inhabitants of Rezoky appear to have been cattle pastoralists as evidenced by large quantities of bovid remains collected during the site's excavation (Vérin, 1971). It is clear from the remains of wild endemic animals, including lemurs (Lemuriformes), carnivorans (*Cryptoprocta ferox*), and tenrecs (Tenrecidae), that wild taxa formed part of the staple diet. In addition to cattle and wild game, freshwater mollusks were said to have been a significant part of the diet at Rezoky (ibid), though limited information on mollusks is offered in the site report. The faunal component recovered from a

surface survey of Asambalahy, thought to be the younger of the two sites, is highly fragmented, but the range of taxa present was broadly similar to Rezoky suggesting a combination of cattle herding, hunting and gathering of freshwater mollusks. In addition to the taxa also seen at Rezoky, elephant bird eggshell remains were found at Asambalahy, and the original investigators believed they were contemporary with the site's occupation (ibid). Finally, a limited number of bones of extinct hippopotamuses were identified subsequent to the original report (Rakotozafy and Goodman, 2005).

The lack of information regarding past human-environment interaction is particularly striking when considering ancient coastal communities: given that a considerable proportion of the island's population lives in coastal areas, we know little regarding the contributions of estuarine and marine fauna to past human subsistence (Douglass, 2016b). Until the present study, Sarodrano, a large sand bar peninsula located 20 km south of the city of Toliara, was the best-known coastal archaeological site in southwest Madagascar (Fig. 1). Sarodrano was surveyed in the 1970s and 1980s (Barret, 1985; Battistini, 1995; Battistini and Vérin, 1975; Razafimisa, 1984). A total of 15 archaeological sites—named SAR I through SAR XV—were recorded (Razafimisa, 1984). Limited conclusions about the subsistence economy of Sarodrano were drawn from the excavations at SAR III (Barret, 1985, 1991). The site was likely a seasonal fishing camp, with evidence of ceremonial feasting. Large amounts of fish and shellfish remains were collected, and a list of identified species was presented (Barret, 1991).

In sum, the information regarding past human-animal interactions in southwest Madagascar is limited, despite what we can glean from the work done at Rezoky/Asambalahy and Sarodrano. A significant gap remains between research into Madagascar's extinct fauna (primarily conducted at sites that act as taphonomic traps) and the cause of their disappearance, and research into the interactions between archaeological communities and animals conducted at archaeological sites.

3. Site description

3.1. The Velondriake Marine Protected Area

Velondriake is a region in southwest Madagascar encompassing thirty-two modern-day coastal communities (Fig. 1). Just over a decade ago, in collaboration with Blue Ventures Conservation, these communities formed an association for the sustainable management of fisheries and coastal resources (Harris, 2007). Velondriake was the first locally managed marine area (LMMA) of its kind on Madagascar and today serves as a model for other coastal fisheries throughout the western Indian Ocean (ibid.). Velondriake is home to diverse communities, made up of people who identify as Vezo fishers, Masikoro farmers and herders, and Mikea foragers (Astuti, 1995; Koechlin, 1975; Poyer and Kelly, 2000; Tucker, 2003). Though these subsistence-based identities suggest strict livelihood specializations, most groups in southwest Madagascar today practice a mixed economy (Yount et al., 2001). Oral histories indicate that Vezo, Masikoro and Mikea communities are descendent from the same agropastoral clans that migrated into the region beginning in the 17th century, and recent genetic research confirms this shared ancestry (Pierron et al., 2014, 2017; Tucker, 2003). Further archaeological, ethnohistorical and aDNA research is needed to clarify the identities of earlier inhabitants of the region.

The archaeological research presented here was conducted along approximately 20 km of the central Velondriake coastline (Fig. 2). This area lies on unconsolidated sands with alluvial and lake deposits to the east, and considerable mangrove swamps to the

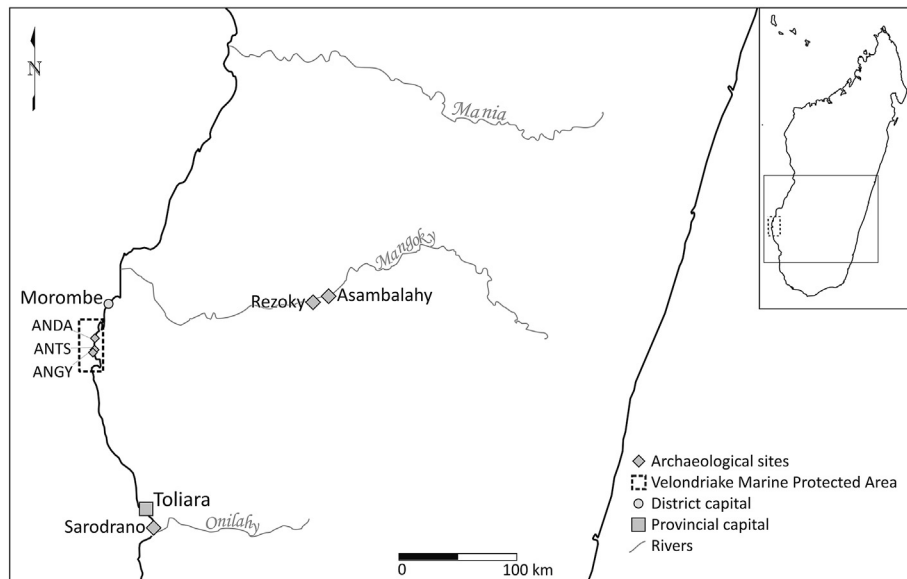


Fig. 1. Map of southwest Madagascar showing archaeological sites mentioned in the text.

north and south. Large stretches of the coastline feature limestone cliffs and outcrops that pepper the karst landscape with rock shelters and sink holes. Many of these sink holes contain archaeological and paleontological materials.

The region is characterized by an arid climate with highly variable rainfall (Dewar and Richard, 2007), and high levels of floral diversity and endemism (DuPuy and Moat, 1996; Jasper and Gardner, 2015; Rakotomalaza and McKnight, 2006; Raselimanana and Goodman, 2004; Raselimanana et al., 2012). The Quaternary dunes that underlie the coastal strip are home to plants of the spiny thicket. Endemic species of *Euphorbia* and endemic families like Didiereaceae make the spiny thicket biome the most highly endemic of Madagascar's diverse biomes (Gautier and Goodman, 2003). The landscape is punctuated by succulent baobabs (*Adansonia*), tamarind trees (*Tamarindus indica*), aloe (*Aloe*), and prickly-pear cactus (*Opuntia dillenii*). The interior of the southwest features Tertiary limestone, with Mesozoic karst outcrops to the north (DuPuy and Moat, 2003). As one leaves the coast, the vegetation shifts from spiny thicket to dry deciduous forest interspersed with grasslands (Gautier and Goodman, 2003). Beyond the borders of the Mikea National Park, a protected area extending over 120 km from north to south, maize and manioc are primary cultigens in the region, and edible wild plants (such as wild tubers and watermelon) remain important to the diets of people in the southwest today (Tucker, 2004). The region faces several conservation challenges today (Blanc-Pamard, 2009; Waeber et al., 2015).

In contrast to the diversity of plant life in the southwest, land mammal diversity is moderate. Madagascar's extant mammal groups are all found in the region—including bats (Chiroptera), tenrecs (Tenrecidae), carnivores (Eupleridae), lemurs (Lemuriformes), rodents (native Nesomyidae and introduced Muridae), possibly introduced bush pigs (*Potamochoerus larvatus*) and feral cats (*Felis sylvestris*) (Garbutt, 2007; Mittermeier et al., 2010). In the region today, the spiny tenrecs (*Tenrec ecaudatus*, *Setifer setosus* and *Echinops telfairi*) are an important bush meat, and are hunted primarily during the wet season when they emerge from hibernation (Tucker, 2004, 46). Feral cats, and the increasingly rare lemurs and bush pigs, are also hunted.

Surprisingly, for an island with such high overall levels of biodiversity, Madagascar's avifauna is relatively poor in species

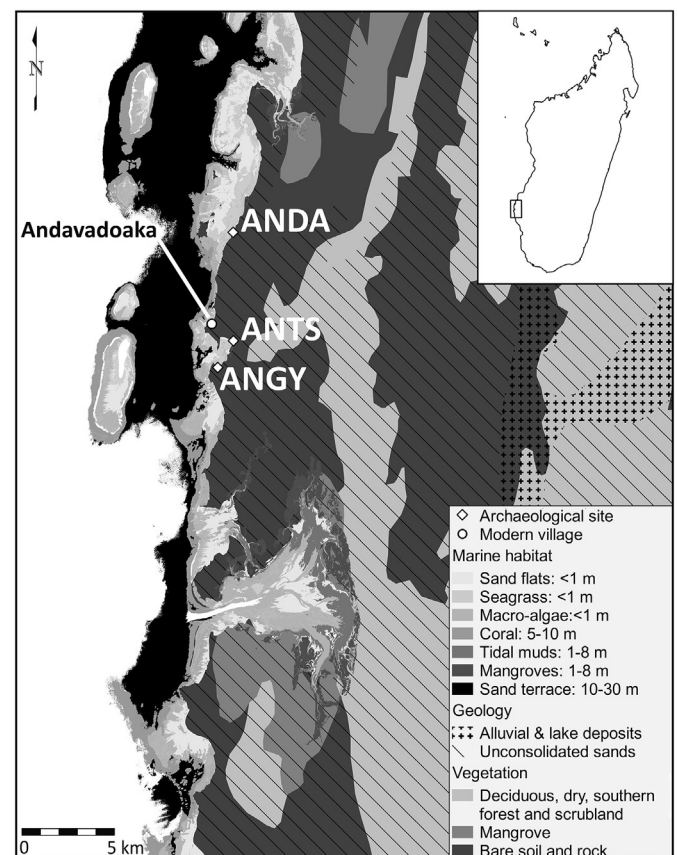


Fig. 2. Map of the Velondriake Marine Protected Area, showing ANDA, ANTS and ANGY archaeological sites, vegetation, geology and marine habitats (Roy et al., 2009; DuPuy and Moat, 1996).

diversity (Langrand, 1990). The avifauna of southwest Madagascar includes 118 species (Langrand, 1990). Of the endemic species, eight are forest dwellers—including the subdesert mesite (*Monias benschi*), the running coua (*Coua cursor*) and the long-tailed ground-

roller (*Uratelornis chimaera*)—and three are marine species—the wedge-tailed shearwater (*Puffinus pacificus*), the red-tailed tropicbird (*Phaethon rubricauda*) and the kelp gull (*Larus dominicanus*).

Prior to their extinction in the Late Holocene several large animals were also native to the Velondriake area. Based on detailed inventories of the remains of extinct taxa from the sites of Belo-Sur-Mer, Taolambiby and Ankilitelo, the southwest was home to several now-extinct animals (Goodman and Jungers, 2014). These include several species of elephant birds of the Aepyornithidae family, the goose *Alopochen sirabensis*, the cuckoo *Coua primavea*, the giant tortoises *Aldabrachelys grandidieri* and *A. abrupta*, the crocodile *Voay robustus*, the aardvark-like *Plesiorycteropus madagascariensis*, the carnivorous *Cryptoprocta spelea*, the pygmy hippo *Hippopotamus lemerlei*, and families and species of the order Lemuriformes, including Archaeolemuridae, Palaeopropithecidae, Megalapidae, Daubentonidae, and *Pachylemur insignis* of the family Lemuridae.

The marine environment of the southwest features high levels of biodiversity and extensive coral reefs: the wide and gently sloping continental shelf of southwest Madagascar features the longest continuous reef system in the western Indian Ocean, approximately 300 km in length (Le Manach et al., 2012). This environment consists of different bathymetric zones (Fig. 2), the shallowest of which are sand flats and macro-algae and seagrass beds (<1 m). Sand flats typically encircle small offshore islands, and also occur near fringing reefs and in tidal embayments. Macro-algae and seagrass communities are predominated by *Sargassum*, *Thalassodendron ciliatum* and *Thalassia hemprichii*. Tidal embayments (1–8 m) are especially common in southern Velondriake and are home to diverse species of mangrove (*Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Rhizophora mucronata* and *Sonneratia alba*). Stony corals (5–10 m), including *Acropora*, *Echinopora*, *Favia*, *Favites*, *Fungia*, *Pavona*, *Porites* and more, grow on top of large beds of dead and fossil corals. The sandy continental shelf (10–30 m) extends between the shallow fringing reefs and deeper reef systems.

In response to severe threats like overfishing, deforestation, and climate change, scientists have intensively surveyed the marine environment along Velondriake's coastline; changes in the location, condition and extent of a number of marine habitats (including diverse coral, seagrass and algal communities, mangrove swamps, and tidal muds) have been closely monitored over the last decade (Cripps, 2009; Cripps et al., 2015; Hantanirina and Benbow, 2013; Harris, 2007; Nadon et al., 2007; Roy et al., 2009).

3.2. Archaeological context of Antsaragnangy, Antsaragnasoa and Andamotibe sites—dating and material culture

The archaeological sites examined herein—Antsaragnangy (ANGY), Antsaragnasoa (ANTS) and Andamotibe (ANDA)—were excavated between 2012 and 2014 (Douglass, 2016a). Although preliminary evidence suggests that the Velondriake region may have been settled as early as ca. 3000 BP (ibid.), this current paper focuses on more securely dated occupation phases spanning from ca. 1400–100 BP (Table 1).

The sites of ANGY and ANTS are located on a small bay situated 1 km south of the modern village of Andavadoaka (Fig. 3). The bay is framed to the northwest by a long arm of limestone (featuring several small rock shelters), and to the southeast by a large mangrove stand. ANGY is located on the southwestern rim of the bay on an established foredune (22°5'38.61"S; 43°14'26.81"E). The site covers at least 1 ha. The vegetation consists of grasses and low-lying shrub, with seasonal marshes and dense spiny brush to the south, a limestone terrace to the west, and the modern village of Antsaragnangy to the northeast. Surface materials included dense concentrations of ceramics, fish bone, shellfish and glass

beads. ANGY featured multiple occupation phases and the deepest deposits of any site excavated in Velondriake to-date. The surface and Level 1 featured “Vezo-Antavelo” ceramics with combed exteriors, which are assigned to ca. 300–100 BP from coastal sites further north (Vérin, 1975). Levels 2–4 yielded incised ceramics with some similarities to ceramic assemblages from Rezoky and Asambalahy (ca. 700–400 BP), but bearing some distinct features as yet unknown from other parts of Madagascar. A charcoal sample from Level 4 yielded dates across a range of 900–727 cal BP (2 σ), possibly placing the beginning of the most active phase at ANGY a few centuries earlier than the occupations at Rezoky and Asambalahy. A drilled *Turbo coronatus* shell collected in Level 10 returned a range of 1425–1177 cal BP (Douglass, 2016a, b). The shell was associated with fish bone, and an ash lens with small flecks of charcoal. This range currently represents the oldest date for an open-air archaeological settlement on the southwest coast of Madagascar. ANGY may have been an occasional fishing camp at the beginning of the sequence and become a progressively larger fishing village by ca. 1000 BP.

ANTS lies on the eastern rim of the bay (22°4'52.88"S; 43°14'57.03"E), approximately 100 m away from a mangrove stand and roughly 2 km from ANGY. The site extends over about 1.5 ha. Surface materials were spread evenly across the site, and consisted primarily of shellfish remains and coarse-grained ceramics with combed exteriors. The site featured a single relatively shallow occupation layer dated by the prevalence of “Vezo-Antavelo” combed ceramics and oral histories (Nahoda Noely, pers. comm.) to ca. 300–100 BP. However, a radiocarbon date from charcoal in a hearth feature at the bottom of the occupation layer returned a range of 431–152 cal BP (2 σ), suggesting occupation of the site may have begun as early as ca. 400 BP, and that the “Vezo-Antavelo” ceramic phase may begin earlier than previously thought (Vérin, 1975).

Seven kilometers north of ANGY and ANTS is ANDA (22°1'39.90"S; 43°14'56.14"E), the largest of the three sites, covering roughly 4.5 ha along a shallow inlet across from the offshore island of Nosy Ve (Fig. 4). Surface materials included abundant 19th century imported British ceramics, combed local ceramics of the “Vezo-Antavelo” type, bottle glass and shellfish. ANDA featured a single, relatively shallow occupation layer, dated by the presence of imported materials and local combed ceramics to ca. 400–100 BP. The occupations at ANTS and ANDA, and the final occupation at ANGY may thus be contemporary settlements.

4. Methods

Vertebrate remains from ANGY and ANTS were analyzed following established zooarchaeological standards and methods (e.g. Lyman, 2005, note that the identification and analysis of shellfish remains are detailed in Douglass, 2016b). Bags of animal bones from each context were initially sorted by fragment size through a nested sieve (2 mm, 1 mm, 0.5 mm). Sorted materials were weighed and recorded according to size class.

Taxonomic identifications were made using comparative collections at the Ditsong National Museum of Natural History in Pretoria, osteological atlases, and the analysts' experience with southern and eastern African faunal assemblages (Froese and Pauly, 2015; Pedrono, 2008; Quintana Morales, 2012, 2013; Tercerie et al., 2015; S. Goodman, pers. comm.) The Number of Identified Specimens (NISP) is reported, and, unless otherwise stated, all taxonomic groups identified from the bone remains from ANGY, ANTS and ANDA still occur in the region. Unidentified mammal, bird and herpetofauna bones were recorded and grouped into the following categories: enamel, rib, bone flake (i.e. longbone shaft pieces) and miscellaneous fragments (i.e. bones that could not be assigned to

Table 1
Radiocarbon dating and occupation phases for ANGY, ANTS and ANDA archaeological sites.

Site and Occupation Phase	Occupation Dates	Radiocarbon Sample ID	Sample Description	Context Description	Radiocarbon Age	$^{13}\text{C}/^{12}\text{C}$	Calibrated Date BP (2 Sigma 95.4%)
ANGY I	ca. 1400–900 BP	ANGY1B-10-1 ^a	Worked marine shell	Open air site, Level 10	1954 \pm 27	2.9	1425–1177
ANGY II	ca. 900–700 BP	ANGY1-4-1 ^b	Charcoal	Open air site, Level 4	915 \pm 25	–28.1	900–727
ANGY III	ca. 700–400 BP	Dated based on the presence of Rezozy/Asambalahy style ceramics					
ANGY IV	ca. 400–100 BP	Dated based on the presence of Vezo-Antavelo style ceramics and 19th century glass trade beads					
ANTS I	ca. 400–100 BP	ANTS 817 ^b	Charcoal	Open air site, Level 1	279 \pm 22	–9.8	431–152
ANDA I	ca. 400–100 BP	Dated based on the presence of Vezo-Antavelo style ceramics, 19th century British stoneware, and glass trade beads					

Notes:

^a Dates calibrated using Marine13 marine curve with estimated ΔR of 200 years \pm 50 (Southon pers. comm.).

^b Dates calibrated using SHCal13 atmospheric curve. All AMS determinations made by the Direct AMS Laboratory.

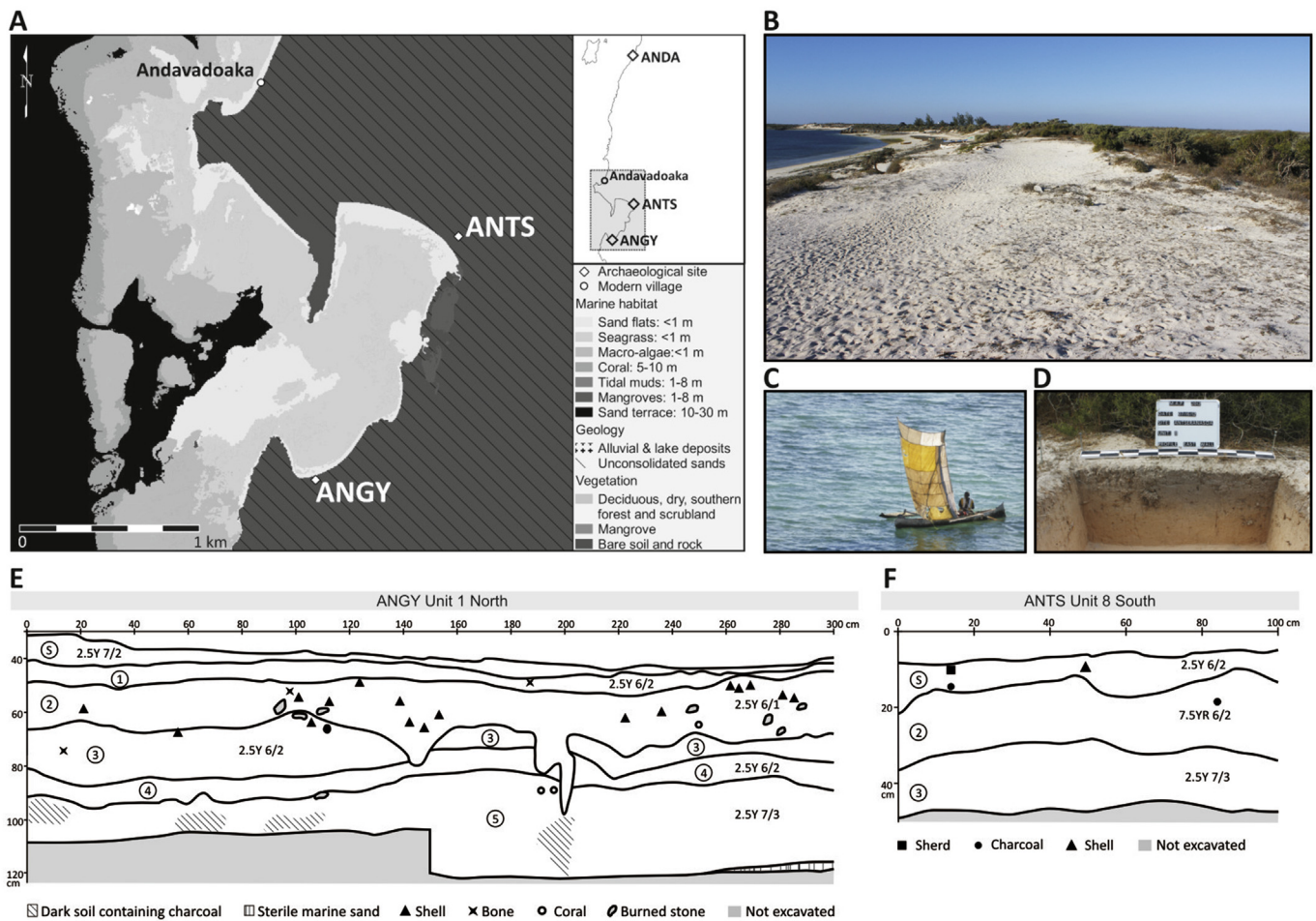


Fig. 3. A) Map of vegetation, geology and marine habitat showing the location of ANTS and ANGY archaeological sites; B) view of surface of ANGY looking northeast; C) small local outrigger canoe, used for fishing in shallow inshore waters; D) view of ANTS Unit 8 wall; E) sample profiles from ANGY Unit 1 and F) ANTS Unit 8.

any skeletal element). Identifiable fish remains were sorted by family, while non-identifiable fish bones were sorted in the following categories: spine, proximal spine and burnt spine fragments; rib, pterygiophore, and branchiostegal ray fragments; vertebra and urostyle fragments; teeth, otoliths, scutes, and other identifiable elements. The Minimum Number of Individuals (MNI) was calculated for each excavation level by considering size and laterality. In addition to taxonomic identification, provenance, size range, age, element, side/position, number of remains, and weight were recorded, whenever possible.

Taxonomically identifiable and unidentifiable bones were all

analyzed for taphonomic traces. Modifications such as burning, butchery marks, and gnawing (carnivore and rodent) were recorded, as was weathering of the bone surface (Fisher, 1995). For non-fish, weathering was recorded by noting the presence of fine line fractures, flaking, erosion, root etching and sun bleaching. For fish, degree of weathering was recorded on a scale of 1–3 (1 = smooth, 2 = cracked and 3 = flaking/eroded; see Campbell, 2005). Burning was recorded on a scale from “brown” (slightly heat-exposed), to “black” (carbonized) and “white” (calcined). Calcined bone was sometimes difficult to distinguish from sun-bleached bone.

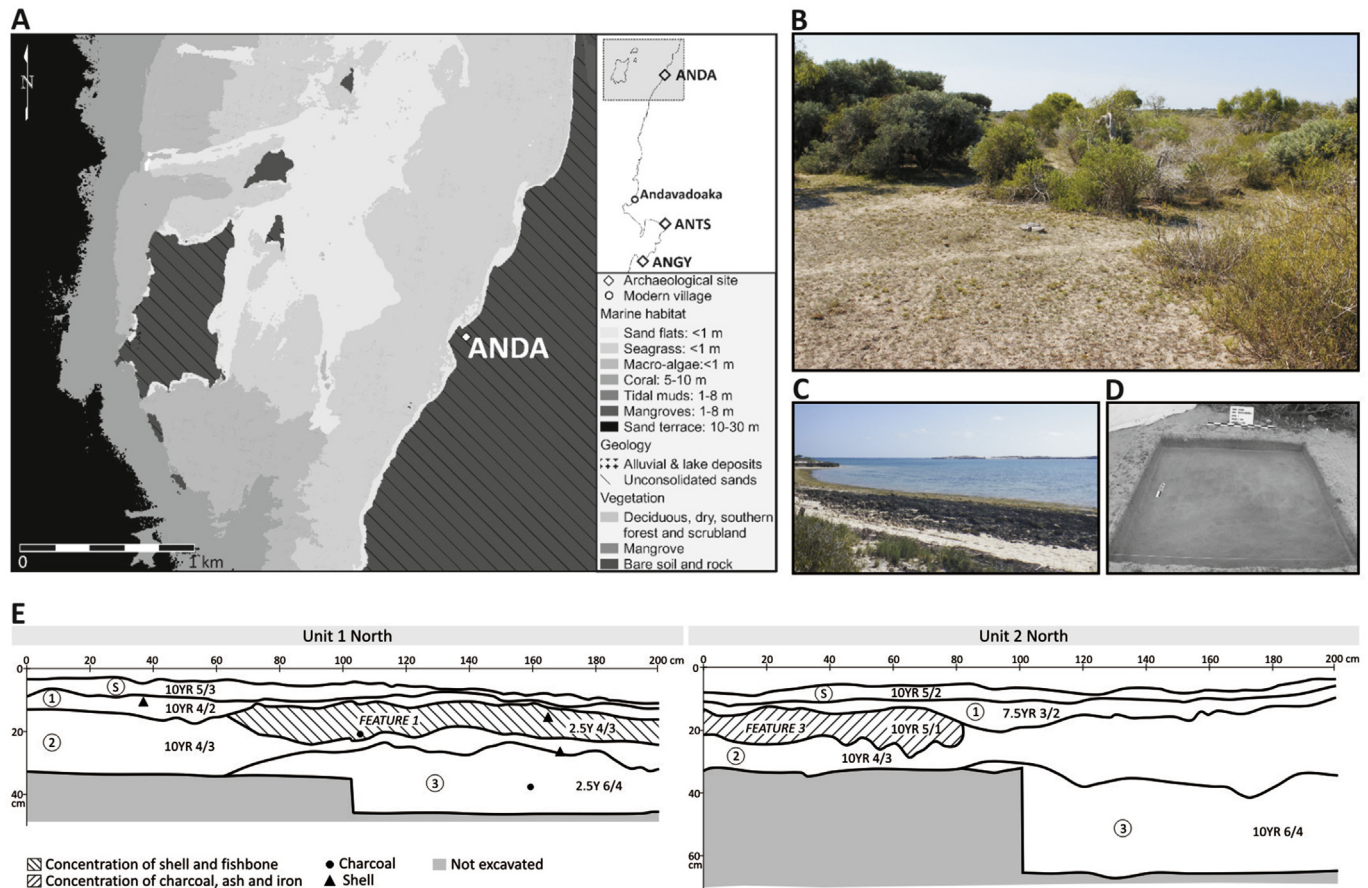


Fig. 4. A) Map of vegetation, geology and marine habitat showing the location of ANDA archaeological site; B) view of surface of ANDA looking northeast; C) view of ANDA coastline looking southwest; D) ANDA Unit 1 excavation; E) sample profiles from ANDA units 1 and 2.

Bone fragments retrieved from ANDA were identified through aDNA bulk metabarcoding (Murray et al., 2013): in addition to the samples previously described by Grealy et al. (2016), nine pools of 50 bones each from the most bone-dense layers were also analyzed (three additional pools from Level 1 Unit 1, three additional pools from Level 1 Unit 2, one additional pool from Level 2 Unit 1, one additional pool from Level 2 Unit 2, and one additional pool from Feature 1, Level 2, Unit 2), resulting in the analysis of 28 samples (a total of 1307 bones; three layers contained less than 50 bones). DNA was extracted from bulk bone pools according to Grealy et al. (2016). Primers targeting four different barcoding regions of mitochondrial 16S rRNA and 12S rRNA genes were used to amplify both vertebrate and fish aDNA from each extract following the methods described by Grealy et al. (2016) with minor changes (S1).

We predominantly targeted fish because these make up the greatest proportion of morphologically unidentifiable fragments from the assemblage; however, targeting vertebrates in general allowed us to gain a broader view of the vertebrate assemblage (Table S1). The choice of metabarcoding assay was constrained by the fragmented nature of endogenous aDNA that occurs in biomolecules post-mortem (particularly in warm-temperate environments); consequently, we targeted gene regions from 56 bp in length to 200 bp. These longer gene regions were expected to provide greater taxonomic resolution but capture fewer taxa, while shorter gene regions were expected to capture a greater diversity of taxa but with a reduced taxonomic resolution. Next-generation sequencing, trimming, quality control, and taxonomic assignments were carried-out as per Grealy et al. (2016) with minor

changes (S2).

Finally, the organization Blue Ventures Conservation collected data on catch by local fishers in Velondriake from 2010 to 2013. These data offer information on many aspects of the modern Velondriake fisheries, including catch volume, fishing ground locations and taxonomic representation. The raw data shared by Blue Ventures were analyzed to generate a modern fisheries taxonomic list and catch habitat provenience for comparison with taxa recorded in the archaeological record. Modern taxon-specific catch location data were used to code fish species recovered in the archaeological record in terms of their likely habitat provenience (i.e., seagrass, coral, etc.).

5. Results

5.1. ANGY assemblage

By far, the largest assemblage of faunal remains comes from the multiple-occupation site of ANGY (Tables 2–3). A total of 1617 mammal, bird, amphibian and reptile, and 1784 fish bones were analyzed from ANGY (Table 4). Of these, only 13% of non-fish and 36% of fish remains were identified to family, genus or species level (Tables 2–3). Of the unidentified non-fish bones, 88% are classified as miscellaneous fragments, which is a reflection of the overall degree of fragmentation of the zooarchaeological assemblage (Table 4). Though preservation of all bone at ANGY was poor, 58% of identified fish bones featured over half of the complete element. As is the case at ANTS and ANDA, the high degree of fragmentation and

bone surface abrasion greatly impeded taxonomic identification (Fig. 5). The effects of animal gnawing on the assemblage were minimal (Table 4). Bones with gnawing were primarily mammal and bird longbones, though one sea turtle phalanx was also gnawed. Bleaching from sun exposure and heavily abraded bone surfaces were common.

The majority of identifiable non-fish bones from ANGY were attributed to the order Testudines, which includes turtles, terrapins and tortoises (Table 3). These remains were, for the most part, shell fragments, though a few longbone fragments were also recovered. Although fragmentation and surface burning impeded taxonomic identification, most of the remains resembled tortoise (terrestrial) and/or terrapin (freshwater) features. At least one shell fragment was identified as belonging to a tortoise, as opposed to a terrapin or turtle. Six phalanges and one vertebra fragment were identified to the Cheloniidae family, and are likely the remains of a single green sea turtle (*Chelonia mydas*), based on habitat distribution and size range (Glaw and Vences, 1994). The reptile and amphibian remains at ANGY are from small individuals, which may have died after burrowing into the deposits. No alterations were noted on these remains.

Mammals of the family Bovidae were also identified in the ANGY assemblage (Table 3). Fragmentation and weathering impeded identification to species, however, based on the size of the specimens and lack of native bovids on Madagascar, these are identified as domesticates (i.e. sheep, goats and cattle). A maxilla fragment and incomplete premolar is probably from a sheep or goat, though the latter may also be from a small cow. Two large longbone shafts are probably cattle, and several unidentified shaft fragments from medium to large mammals may also be bovid remains.

Primates appear to be minimally represented in the ANGY assemblage; probable lemur phalanx, radius and rib fragments were only recovered from the latest occupation layer (Table 3). The phalanx could be that of *Lemur catta* (S. Goodman, pers. comm. 2015). These remains suggest that coastal communities may have hunted lemurs during the last few centuries, though none of these bones feature butchery marks and no evidence of intensive hunting has been documented thus far. Furthermore, the size range of the ANGY specimens is within the range represented by extant lemur species; no evidence of the exploitation of large, now-extinct lemurs was recorded.

Carnivora elements include two lower molars identified as a small species (likely Eupleridae, subfamily Galidiinae) and a metacarpal fragment of a juvenile (possibly from the same individual) (Table 3). A larger tarsal may belong to taxa that are no longer found in Velondriake. Remains radiocarbon dated to ca. 500 BP of *Galidia elegans* (ring-tailed vontsira) and *Galidictis grandieri* (Grandidier's vontsira) were recovered at Ankilitelô Cave, a paleontological site on the Mikoboka Plateau, roughly 100 km southeast of the research area (Muldoon et al., 2009). The former has not been recorded anywhere else in southwest Madagascar, and the latter has a restricted range. Confirming the identification of these species at ANGY through aDNA analysis would extend their known historical range. Other carnivoran remains include a small tooth and ulna. These smaller specimens may be *Mungotictis decemlineata*, the narrow-striped mongoose, which still occurs in southern Mikea Forest today, though it is rarely seen (Goodman et al., 2005).

Six mandible and longbone fragments of small mammals could not be further identified morphologically (Table 3). These may represent taxa whose current or past habitat ranges extend into Velondriake, such as bats, tenrecs and a variety of lemurs. Further possibilities are the Asian musk shrew (*Suncus murinus*) and the pygmy musk shrew (*S. etruscus*) — species introduced to Madagascar probably during the Islamic era (Boivin et al., 2013; Hutterer and Trainer, 1990). Again, aDNA would allow for further

taxonomic assignment.

Bird remains, excluding eggshell of extinct elephant birds, were more common at ANGY than at ANDA or ANTS, and were represented by longbones, phalanges and eggshell. 17 of the 23 bird identifications could not be confirmed due to the lack of diagnostic features and heavy weathering of bone surfaces. Despite poor preservation, the size range provides some indication of possible species present (Table 3): two “chicken-sized” specimens were recorded along with one small galliform bone. The “chicken-sized” bones may be *Gallus gallus* (chicken) or *Numida meleagris* (helmeted guinea fowl). A longbone fragment from the surface of ANGY may be from *Phoeniconaias minor* (lesser flamingo). These birds still occur in the region today and live in flocks on coastal mudflats and along river mouths (Griveaud and Albignac, 1972; Langrand, 1990). Thin eggshell fragments recovered are tentatively identified as sea bird eggshell, pending further analysis using a bulk aDNA approach and/or Zooarchaeology by Mass Spectrometry (ZooMS; cf. Stewart et al., 2013).

The ANGY fish assemblage is primarily made up of bony fish (97% NISP—Class Osteichthyes—Table 2). Of the bony fish identified in the assemblage, the large majority are reef-dwelling species: emperors (Lethrinidae, 34%), parrotfish (Scaridae, 11%), surgeonfish (Acanthuridae, 10%), groupers (Serranidae, 7%), and rabbitfish (Siganidae, 8%). These families include herbivorous fish that feed on algae (Scaridae, Acanthuridae, and Siganidae) and bottom-dwelling carnivorous fish (Lethrinidae and Serranidae). The 13 other reef-dwelling families represented in the sample (<5% NISP) include Haemulidae (*Plectorhynchus* sp.), Muraenidae, Balistidae, as well as families associated with shallow inshore embayments, like Beloniformes, Gerreidae and Mugilidae. Cartilaginous species (Class Chondrichthyes), especially shark, were also represented, but in very small quantities. Only four shark teeth were recovered along with a few calcified vertebrae of cartilaginous species (Table 2).

Body part representation reveals that over half of the identified fish remains (63%) are postcranial elements (Fig. 6), and primarily made up of vertebrae, though a total of 18 cranial elements and nine postcranial elements were used to identify bony fish taxa (Table S 3–4). Body part representation varies somewhat across fish families, where some taxa were identified solely from vertebrae—like Beloniformes, Gerreidae, Mugilidae, Mullidae and Muraenidae—and others (such as Scaridae) were identified primarily from cranial elements (Table S 3–4). Rates of preservation of different elements differ by taxon, which can impact overall body part representation. Different methods and locations for processing and discarding different species can also have an effect on which elements end up in archaeological deposits. At ANGY, for example, parrotfish were primarily identified through cranial elements, but because parrotfish vertebrae bear distinctive morphological features and usually preserve well in archaeological deposits, their relative absence in the assemblage is likely due to processing strategies.



















Signs of cultural alteration include rare butchery marks (observed on only three bones) and burning. The heavy degree of bone surface weathering may have masked evidence of butchery and other signs of cultural alteration. 26% of the non-fish bones and 13% of the fish bones were burnt (Table 4). Burnt bones were primarily recovered from Unit 1 and included Testudine shell and several unidentifiable fragments. Though some of the bones were indirectly exposed to heat (as might occur when a hearth is placed on top of older deposits), other bones, and especially Testudine fragments, seem to have been deliberately burnt. Testudine carapace and plastron fragments exhibited varying degrees of burning, a pattern that suggests that shells were cooked upside down on an open fire and periodically turned. Some fragments were burnt on

Table 2
Morphological taxonomic identifications of fish bones from all occupation phases at ANGY and ANTS.

NISIP by Site and Occupation Phase									
	Taxonomic ID	Common name	ANGY	ANGY	ANGY	ANGY	ANGY	ANTS	Total
			All	I	II	III	IV	I	
Osteichthyes	Acanthuridae	Unicorn fish,	60	17	21	6	16	7	67
	cf. Acanthuridae	Surgeonfish	8		8				8
	Balistidae	Triggerfish	9	6	1	1	1	17	26
	cf. Balistidae		1		1				1
	Beloniformes	Needlefish and	24	2	19		3	1	25
	Belonidae	related families						8	8
	Carangidae	Pompanos, Scads,	3	3					3
	cf. Carangidae	Trevallies	2		2				2
	Gerreidae	Biddies	18	2	9	4	3	4	22
	Haemulidae	Grunts, Sweetlips	17	1	7	3	6	4	21
	Holocentridae	Soldierfish						1	1
	cf. Labridae	Wrasses						3	3
	Lethrinidae	Emperors, Breams	213	87	84	17	25	20	233
	cf. Lethrinidae		8	6	2				8
	Lutjanidae	Snappers	18	4	7	2	5	11	29
	cf. Monodactylidae	Moonyfish	1	1		1			2
	Mugilidae	Mulletts	22	5	5	1	11		22
	Mullidae	Goatfish	10	1	5		4		10
	Muraenidae	Moray eels	14	9	4		1		14
	Ostraciidae	Cowfish	1			1		2	3
	Scaridae	Parrotfish	74	14	27	15	18	4	78
	cf. Scaridae		1			1			1
	Serranidae	Groupers	42	11	20	5	6	7	49
	cf. Serranidae		3	1	2				3
	Siganidae	Rabbitfish	50	10	17	8	15	9	59
	Sparidae	Breams	12	4	6		2		12
	Sphyraenidae	Barracuda	1		1			2	3
	Terapontidae	Terapons	1	1					1
	Not Identified	Bony fish	1133	471	289	91	282	243	1376
Chondrichthyes	ray		3	2			1		3
	cf. ray		6		4		2		6
	shark	Rays and Sharks	13	2	2	2	7	4	17
	cf. shark		14	2	8	3	1		14
	cf. shark/ray		1		1				1
Fish Total			1784	662	552	161	409	347	2131

Table 3

Morphological taxonomic identifications of bird, mammal and herpetofauna bones from all occupation phases at ANGY and ANTS.

NISP by Site and Occupation Phase										Total
Taxonomic ID	Size range	Common name		ANGY All	ANGY I	ANGY II	ANGY III	ANGY IV	ANTS I	
Bird	Aves	S		5	1	1		3		5
	cf. Aves	S		10	10					10
	Aves	M		1				1		1
	cf. Aves	M	Chickens, Guinea fowl, Flamingos	2	1			1		2
	cf. Aves	S/M		5	5					5
Mammal	Mammalia	S		6	1			5	1	7
	Mammalia/Aves	S/M		1	1				2	3
	cf. Lemuriformes	M		2	1			1		2
	cf. Lemuridae	S		1				1		1
	Carnivora	S		1		1				1
	cf. Carnivora	S		3	1			2		3
	cf. Carnivora	M/L		1		1				1
	cf. Eupleridae	S		1				1		1
	Bovidae	S/M		1		1				1
	Bovidae	M/L		1			1			1
	Bovidae	L	Sheep/Goats	1				1	1	2
	cf. Bovidae	L	Cattle	1		1				1
Herpetofauna	Testudines	S		11	1	6	2	2		11
	Testudines	S/M		31	23	2	2	5		32
	Testudines	M		120	59	54	2	5	4	124
	Testudines	M/L							3	3
	Cheloniidae	M		7				7		7
	Amphibia	S		2	1			1		2
	cf. Squamata	S		2			2			2
Non-fish Total				217	105	67	9	36	11	228

the interior and exterior (burnt through), and the presence of calcined fragments suggests prolonged heat exposure, such that shells may have been left on the fire after the meat was removed (Weiner, 2010). On Madagascar today, it is common to cook turtle and tortoise meat by placing the animal in its shell upside down on an open fire. This may have been the case in the past as well (see Thompson and Henshilwood, 2014).

5.2. ANTS assemblage

The bone assemblage from ANTS is relatively small. A total of 124 non-fish and 347 fish bones were recovered from the eight excavation units and 9% of non-fish and 30% of fish bones were identified to taxon (Table 4). The 113 non-fish bones that could not be identified were primarily longbone shaft and other

Table 4

A) Summary of ANGY and ANTS vertebrate assemblages; B) summary of alterations for ANGY and ANTS vertebrate assemblages.

A										
Vertebrate assemblage summary					ANGY			ANTS		
Total non-fish identified					217			11		
Total non-fish unidentified					1400			113		
Enamel fragments					2			0		
Vertebra fragments					0			1		
Rib fragments					6			2		
Bone flakes					152			20		
Miscellaneous fragments					1240			90		
Total fish identified					651			104		
Total fish unidentified (spines, fragments, etc)					1133			243		
Total sample					3401			471		
Mass of identifiable non-fish bones (g)					184			35		
Mass of unidentifiable non-fish bones (g)					415			103		
Mass of identifiable fish bones (g)					108			14		
Mass of unidentifiable fish bones (g)					133			30		
Total mass (g)					840			182		
B										
Alteration - ANGY and ANTS	NISP		Burnt		Butchered		Gnawed (carnivore)		Gnawed (rodent)	
	ANGY	ANTS	ANGY	ANTS	ANGY	ANTS	ANGY	ANTS	ANGY	ANTS
Identified										
Bird	23						1 ^a		1	
Mammal	19	2	2	1			1	1	1	
Mammal/Bird	1	2						1		
Amphibian	2									
Reptile	172	7	51	1			1	1		
Fish	651	104	48	6	2	1				
Unidentified										
Enamel fragments (non-fish)	2	1	1	1						
Rib fragments (non-fish)	6	2	1							
Bone flakes (non-fish)	152	20	15	3	1	1		2		
Miscellaneous fragments (non-fish)	1240	90	353	37		1 ^a		1		
Spines, fragments (fish)	1133	243	189							
Total NISP	3401	471	660	49	3	2	2	6	2	0

Note:

^a Denotes possible identifications.

miscellaneous fragments, reflecting the high degree of fragmentation of the assemblage. Due to time constraints, a sample of fish bones from Unit 6 was prioritized, as this unit likely represented a food preparation area.

The ANTS fish assemblage is characterized by light to medium weathering, caused by wind and sand exposure, and a high degree of fragmentation (Figs. 5 and 7). Overall, weathering did not have as much of an impact on taxonomic identification as fragmentation. Carnivorous activity – signs of which were observed on six bones – may well have contributed to the high degree of fragmentation seen in the assemblage. Fish remains from ANTS were significantly better preserved than those from ANGY. The majority (78%) consisted of over half of the complete element and showed limited to no signs of surface weathering.

Identified bones include a large bovid longbone shaft fragment, probably of cattle. Several unidentified shaft fragments of another large mammal may be from cattle as well. Six turtle/tortoise shell fragments from medium to large individuals and a longbone were also identified (though some of these come from disturbed deposits and may be of more recent origin). The only other identifiable

specimens were two longbone fragments of a small mammal or bird.

Bony fish (Class Osteichthyes) made up 98% NISP of the ANTS fish assemblage (Table 2). Like at ANGY, cartilaginous species like shark were rare. Bony fish were primarily reef-dwelling species: triggerfish (Balistidae; 18%), emperors (Lethrinidae, 17%), snapper (Lutjanidae; 11%), rabbitfish (Siganidae; 9%), surgeonfish (Acanthuridae, 7%), groupers (Serranidae, 6%) and parrotfish (Scaridae, 3%). Other reef-dwelling families identified (9% NISP) include wrasses (Labridae), grunts (Haemulidae), barracuda (Sphyraenidae), and squirrelfish (Holocentridae), as well as families associated with shallow inshore embayments (13% NISP), like needlefish (Belontiiformes) and silver biddies (Gerreidae). Of these families at ANTS, only Labridae and Holocentridae were not identified at ANGY, but both are recorded in modern catch data.

As at ANGY, only three bones in the entire assemblage yielded evidence of butchery in the form of cut or chop marks, and limited evidence of carnivorous gnawing was recorded (Table 4). Burning was recorded on 34% of non-fish bones (Table 4). Heat exposure varied somewhat, but a majority of the burnt bones were exposed to heat for prolonged periods and were either carbonized or calcined (Fig. 8). Some bones were carbonized on the interior and calcined on the exterior, suggesting they were exposed to temperatures above 650 °C. This is within the temperature range of flames in an open fire (Weiner, 2010, 117). Localized burning was also recorded on the large mammal bone from Unit 4 and the Testudine longbone from the same context. This localized charring may be the result of cooking meat directly on an open fire, so that only portions of bone not covered by meat are carbonized. Disposal of bones in a hearth can also lead to localized charring. In contrast to the non-fish assemblage, evidence of burning on fish remains was very rare—only three fish vertebrae were calcined—which may indicate that fish was cooked or discarded in a different way than other animals. Body part representation suggests that most fish were discarded whole since both cranial and postcranial elements are present in the assemblage (Fig. 9). Certain fish families represented entirely by postcranial elements, such as rabbitfish, surgeonfish, and silver biddies, tend to have smaller, more fragile cranial elements that are less likely to preserve.

5.3. ANDA assemblage

Given the extreme weathering and fragmentation observed in the ANDA assemblage as compared to other sites in Velondriake, bone samples from ANDA were submitted for DNA bulk bone metabarcoding. Results from a first round of aDNA analysis of bone pools from ANDA were presented in Grealy et al., (2016). Since the time these results were published, the genetic reference database (GenBank's nucleotide database) has been expanded allowing for improved molecular identifications. An additional nine pools of 50 bones from ANDA were also analyzed, and multiple independent metabarcoding regions were targeted in order to identify more taxa with higher credibility (Table S6). These recent analyses revealed previously undetected taxa; 32 credible to highly credible fish families were identified, compared with the 23 credible/highly-credible family-level identifications presented in Grealy et al. (2016) (Table 5), i.e., nine additional families were identified, eight with high credibility (taxonomic assignments were considered highly credible if the percent similarity of the sequence to the reference was above 90% across its entire length, if the taxa is found in the area according to FishBase, and if all genera within the family are represented in GenBank). These families include Ambassidae, Belontiidae, and Holocentridae, as well as Chaetodontidae, Gobiidae, Lutjanidae, Pleuronectidae, Platycephalidae, and Myliobatidae (which were detected in more than one sample, adding to their

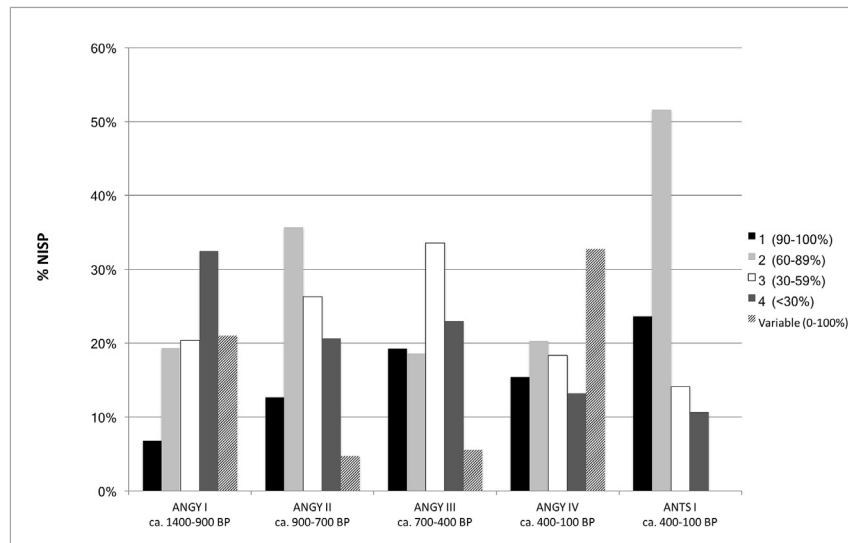


Fig. 5. Degree of fragmentation of fish bone across occupation phases at ANGY and ANTS. Note: Variable fragmentation recorded in groups of non-diagnostic bones (esp. spines and pterygiophores).

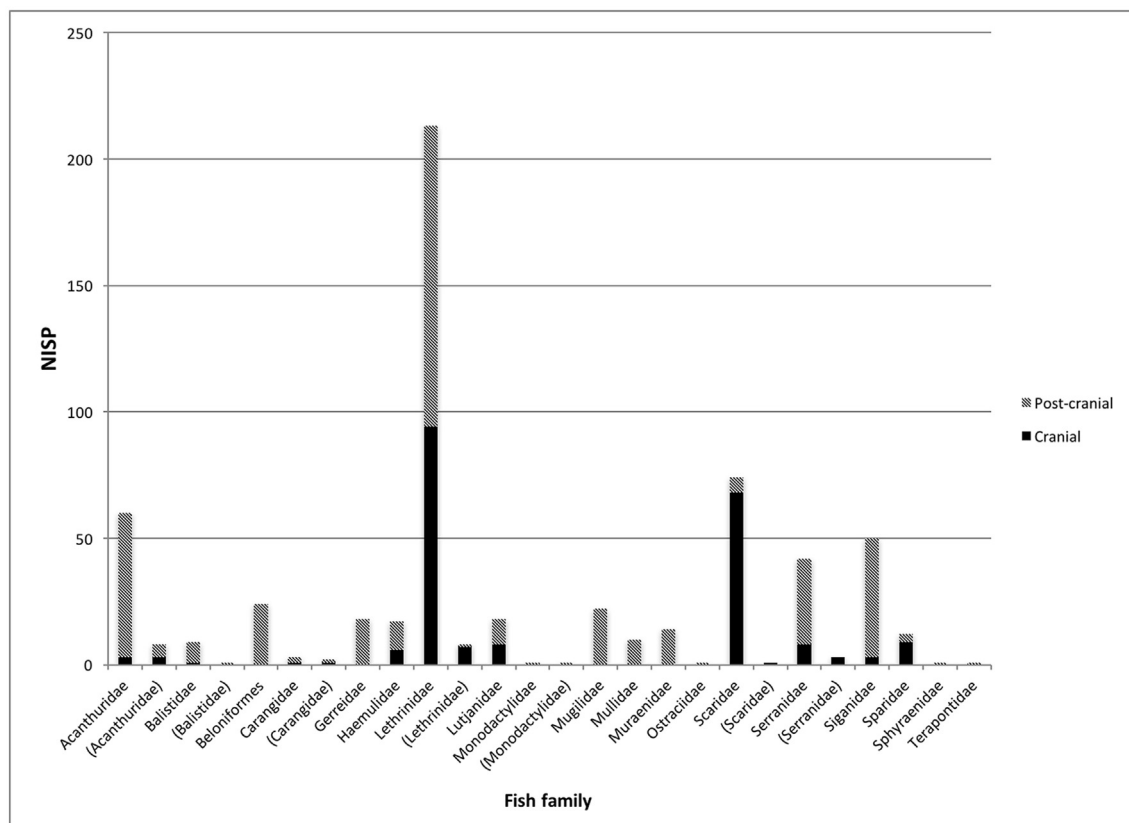


Fig. 6. Relative abundance of fish cranial and post-cranial elements at ANGY. Parentheses denote possible identifications.

credibility). In addition, more highly credible genus and species-level identifications were obtained: an additional 18 highly credible genera (36 total) and ten highly credible species (32 total) of fish were detected within the highly credible family identifications. New highly credible genera include *Rhabdosargus*, *Selar*, *Chlorurus*, *Triaenodon*, *Tylosurus*, *Nebrius*, and *Rhinoptera*, with *Caranx*, *Lutjanus*, *Chelon*, *Balistapus*, and *Papilloculiceps* being detected in more

than one sample, and *Naso*, *Trachinotus*, *Scarus*, *Rhinecanthus*, and *Plectorhinchus* being detected in more than one sample with more than one primer set. New highly credible species include *Selar crumenophtalmus*, *Epinephelus coeruleopunctatus*, *Tylosurus crocodilus*, and *Rhinoptera javanica*, along with *Epinephelus multi-notatus*, *Naso lituratus*, *Balistapus undulatus*, *Plectorhinchus gaterinus*, and *Papilloculiceps longiceps*, which were detected in

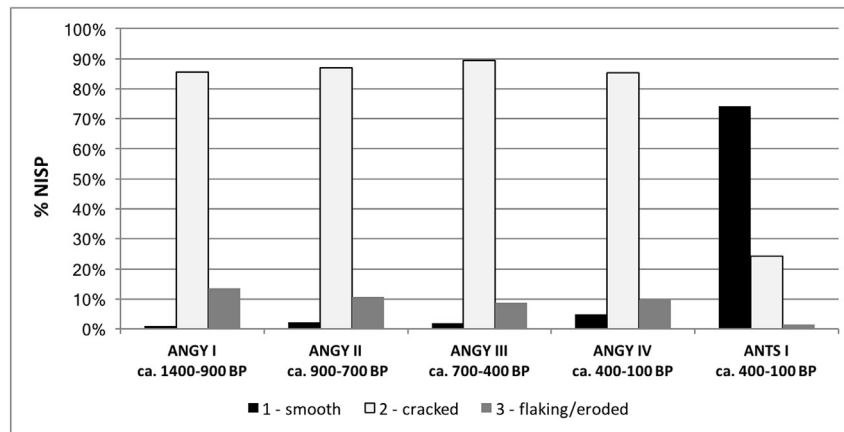


Fig. 7. Weathering of fish bone across occupation phases at ANGY and ANTS.

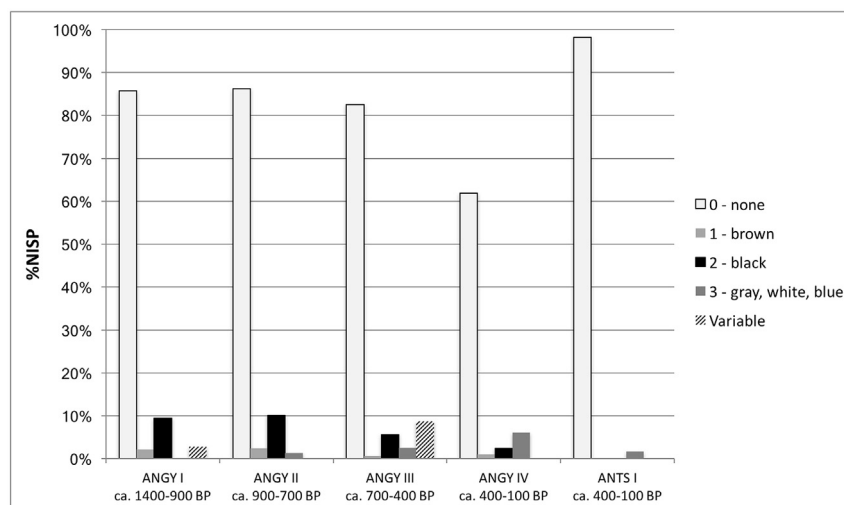


Fig. 8. Degree of burning of fish bone across occupation phases at ANGY and ANTS. Note: Variable burning recorded in groups of non-diagnostic bones (esp. spines and pterygiophores).

more than one sample. The identification of fish taxa that have not been previously recorded in the area (*Oplegnathidae*, *Siniperca*, *Knipowitschia*, *Haemulon aurolineatum*, *Himantura gerrardi*, *Diplomystidae*, *Urotrygonidae*, *Callichthyidae*, and *Cottidae*) could be the result of: (1) error, either from aDNA damage or sequencing error (for instance, *Urotrygonidae* occurs only in the same samples as the closely-related family *Myliobatidae* but at much lower abundance). *Urotrygonidae* sequences also differ from *Myliobatidae* sequences at one base that is a cytosine in *Myliobatidae* but thymine in *Urotrygonidae*. This change supports the idea that *Urotrygonidae* sequences may be a result of aDNA damage, which is typically results in C-to-T substitutions); (2) these taxa are present but have not been observed before, are not recorded in FishBase, or are locally extirpated; (3) some species may have been reclassified, be synonymous with others, or have been misassigned when generating the genetic reference; and (4) the family may be closely related to another that is not represented in GenBank but is known to occur on Madagascar.

Highly credible identifications within other animal classes include one mammal family (*Tenrecidae*), one bird family (*Anatidae*) and two reptile families (*Colubridae* and *Pseudoxyrhophiidae*). The latter two are likely the result of animals burrowing into deposits and dying, particularly given the presence

of these taxa in superimposed layers (Table 5). These identifications confirm the predominantly marine orientation of resource exploitation at ANDA described previously. The detection of the whistling duck (*Anatidae*) and tenrec (*Tenrecidae*) provide some evidence that the people of ANDA were also exploiting, at least occasionally, inland areas, including seasonal marshes. Introduced taxa such as *Felis*, *Canis lupus*, *Sus scrofa*, *Bos taurus*, and *Equus caballus*, as well as human were also detected; however, the authenticity of this DNA as ancient is questionable—it is likely it may be of modern origin as these animals frequent the area today. Although it is possible that such contaminants arose from the laboratory environment, no extraction controls or PCR no-template control amplified DNA suggesting that it is more likely this DNA, if modern, originated from the field.

Though the bulk bone metabarcoding method cannot provide definitive data on the relative abundance of detected taxa, a rough estimate of relative abundance can be gleaned from the number of bone pools/layers each taxon is found in (Fig. 10). It should be noted that differential DNA preservation rates across bones warrant caution in interpreting abundance from bulk bone sequences. An accurate estimation of abundance is further hindered by PCR bias. However, families that were detected in the most pools/layers include reef-dwelling fish, such as emperors (*Lethrinidae*),

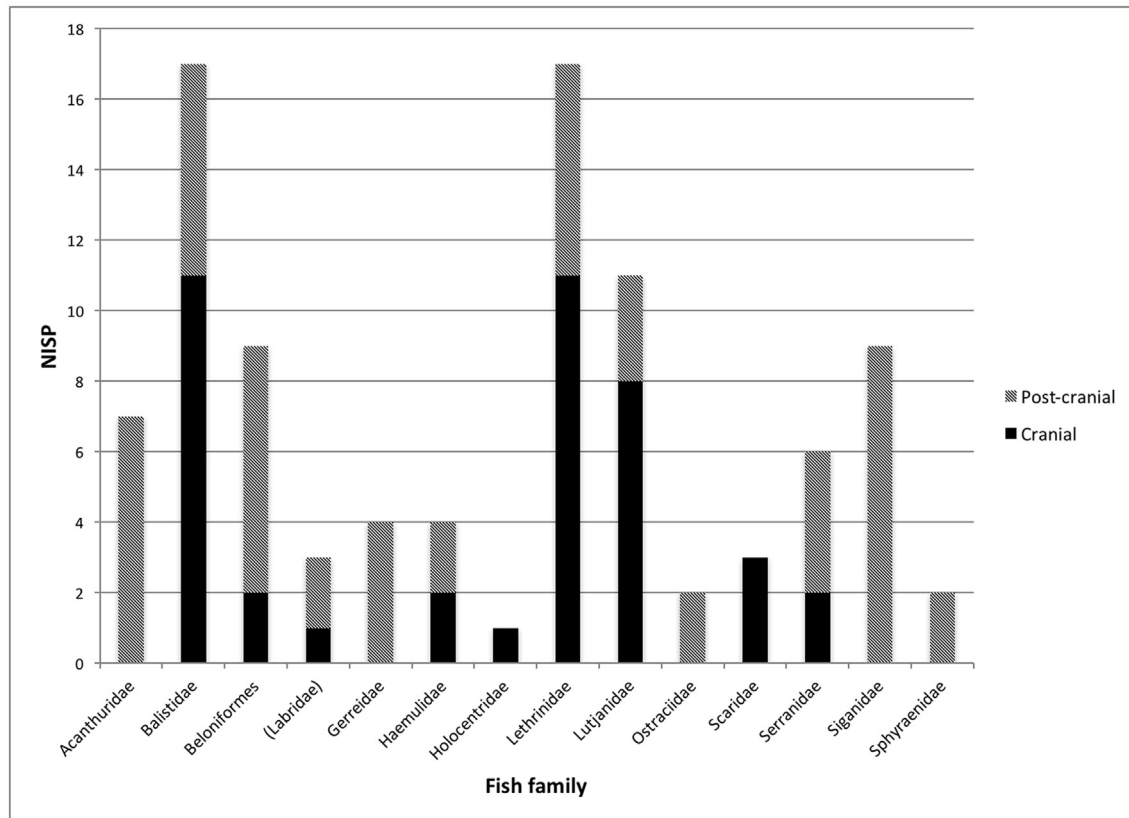


Fig. 9. Relative abundance of fish cranial and post-cranial elements at ANTS. Parentheses denote possible identifications.

parrotfish (Scaridae), rabbitfish (Siganidae), surgeonfish (Acanthuridae), groupers (Serranidae), breams (Sparidae), wrasses (Labridae), grunts (Haemulidae), triggerfish (Balistidae), and pompanos and trevallies (Carangidae). Additionally, mullets (Mugilidae), which are associated with freshwater and estuarine environments, were also frequently detected. Cartilaginous families (Class Chondrichthyes) were detected (Table 5), and include taxa that have not been recorded in recent fisheries data (Table S5). The presence of several nocturnal taxa, including carpet (or nurse) sharks (Ginglymostomatidae), requiem sharks (Carcharhinidae) and bony fish like soldierfish (Holocentridae), snappers (Lutjanidae), and scads (Carangidae), provides evidence of night fishing or leaving nets out overnight.

When compared with morphological taxonomic identifications at ANGY and ANTS, the bulk bone method identified 35% more family-level diversity (Table S5). For further comparison, the modern Velondriake fisheries data record a total of 68 exploited fish families, roughly twice as many families as detected in the ANDA samples (Table S5). The ANDA bulk bone samples, however, were collected from relatively small-scale excavations (two 2×2 m units), and still yielded a significant snapshot of the diversity of taxa exploited in the past. The success of this aDNA method in capturing taxonomic diversity in a tropical environment should encourage its application to other contexts in the future, including contexts older than ANDA's relatively young assemblage (ca. 400–100 BP). Further expansion of genetic databases will continue to improve these results.

6. Discussion

This study provides the first comprehensive zooarchaeological study of coastal villages in southwest Madagascar. Results from the

sites of ANGY, ANTS and ANDA reveal predominantly marine lifeways, though inter-site and diachronic variations in marine resource exploitation were observed. Analysis of faunal assemblages from these sites offers insights into the human history of southwest Madagascar, and should encourage further integration of multiple analytical approaches, including aDNA, ZooMS, isotopic analyses, food-web modeling and ethnozoarchaeology. These techniques will in turn improve the resolution and extent of taxonomic identifications and paleoenvironmental reconstruction, and expand our thinking on the nature of human-animal interactions in the island's past.












6.1. Differences in lifeways across occupation phases and sites







It is clear from vertebrate assemblages across all occupation phases at ANGY, ANTS and ANDA that the inhabitants of these communities primarily exploited marine resources. However, in the earlier human history of Velondriake from ca. 1400–700 BP, represented by phases I and II at ANGY, there may have been a more diversified subsistence economy. Though still predominantly marine in orientation, the people associated with ANGY I and II exploited a greater range of terrestrial taxa than during later periods. In addition to the diversity of terrestrial taxa in ANGY I and II deposits, there is evidence for more intensive exploitation of turtles than in later periods. This trend for increased taxonomic diversity in ANGY I and especially ANGY II is also apparent in the shellfish assemblage (Douglass, 2016b), where the large diversity of taxa from ANGY II in particular includes non-comestible species whose presence in the assemblage is linked to craft production and perhaps other activities.














By the ANGY III phase, ca. 700–400 BP there is a decline in the abundance and diversity of exploited taxa that may be concurrent

Table 5

Molecular taxonomic identifications obtained through bulk bone metabarcoding of remains from ANDA units 1 and 2. Taxa in bold were not previously detected in Grealy et al. (2016). Taxa are recorded according to credibility where † refers to highly credible taxa (within the cut-off ID across 100% of the query, found in the area according to FishBase, and all subtaxa of the family or genus having a reference in GenBank), ‡ refers to credible taxa (within the cut-off ID across 100% of the query and found in the area according to FishBase but where not all subtaxa within family or genus are represented in GenBank), bolded symbols indicate the taxa was detected in more than one subsample, and * indicates that data was identified by more than one primer set.

				Unit													
				1	2	1	2	1	2	1	2	1	2	2	1	2	
				Level	S	S	1	1	2	2	2	2	2	2	2	3	3
				Feature							1	1	2	2	3		
Fish	Family	Genus	Species	(98-100%	Common name												
	(90-94% ID)	(95-97% ID)	ID)														
	Dasyatidae			Stingray			†										
		<i>Himantura</i>					†										
	Latidae							†									
		<i>Psammoperca</i>		Waigeo barramundi				†									
		<i>waigiensis</i>						†									
	Ginglymostomatidae			Carpet sharks													†
		<i>Nebrius</i>		Tawney nurse shark													†
		<i>ferrugineus</i>															†
	Carcharhinidae			Requiem sharks			†	†		†							
		<i>Carcharhinus</i>		White tip reef shark				†									
		<i>Trienodon</i>					†										
		<i>obesus</i>					†										
	Mullidae			Goatfish			†*		†*	†	†*						
		<i>Mulloidichthys</i>					†*			†							
	Mugilidae			Mullet			†*	†*	†*		†	†	†	†*	†	†	
		<i>Chelon</i>		Largescale mullet			†*	†*	†*		†	†	†	†		†	
		(syn. <i>Liza</i>)					†*	†*	†*		†	†	†	†		†	
		<i>macrolepis</i>					†										
	Myliobatidae			Eagle rays				†									
		<i>Rhinoptera</i>		Cownose rays				†									
		<i>javanica</i>		Flapnose ray				†									
	Platycephalidae			Flathead					†		†						
		<i>Papillolociceps</i>		Tentacled flathead					†		†						
		<i>longiceps</i>							†		†						
	Carangidae			Pompano			†*	†*	†	†*	†*	†*	†	†*		†	
		<i>Trachinotus</i>					†*	†	†				†			†	
				Snubnose pompano			†		†								
		<i>blochii</i>					†										
		<i>Alectis</i>		Threadfish								†					
		<i>Selar</i>		Scads				†									
			<i>crumenophthalmus</i>	Bigeye scad				†									
		<i>Caranx</i>		Trevallies			†				†	†		†		†	
			<i>melampygus</i>	Bluefin trevally										†			
	Lethrinidae			Humpnose big-eye bream			†*	†	†*		†*	†*	†*	†*	†	†	†*
		<i>Monotaxis</i>										†*					
		<i>grandoculis</i>										†					
		<i>Lethrinus</i>		Emperors			†*	†	†*		†*	†*	†*	†*	†	†	†*
				Pink ear emperor			†	†	†		†	†	†	†	†		†
		<i>lentjan</i>					†	†	†		†	†	†	†	†		†
		<i>harak</i>		Thumbprint emperor					†		†		†				
		<i>mahsena</i>		Sky emperor			†	†	†		†	†		†			
		<i>obsoletus</i>		Orange-striped emperor				†			†						

					Unit														
					1	2	1	2	1	2	1	2	1	2	2	1	2		
					Level	S	S	1	1	2	2	2	2	2	2	2	3		
					Feature	/		/		/		1	1	2	2	3	/		
Family	Genus	Species	(98-100% ID)	Common name															
(90-94% ID)	(95-97% ID)	ID)																	
Fish	Acanthuridae						†*	†	†*		†*	†	†	†			†		
	Naso			Unicorn fishes			†*	†	†		†*	†	†	†			†		
			lituratus		Orange-spine unicorn fish			†				†		†	†				
			(syn. elegans ?)				†				†		†						
	Acanthurus			Surgeonfish			†*		†*								†		
			triostegus		Convict surgeonfish			†*		†*								†	
	Chaetodontidae								†			†	†	†					
	Gerreidae								†		†*		†	†					
	Gerres			Mojarras			†						†		†				
			oyena		Common silver biddy								†						
	Scaridae						†*	†*	†*	†*	†*	†*	†	†*	†	†	†	†	
	Scarus			Parrot fishes			†	†	†	†	†*	†		†				†	
			Chlorurus												†				
	Labridae										†*		†	†	†*	†		†*	
	Hemigymnus			Wrasses					†*				†	†	†*	†		†*	
			melapterus		Blackeye thicklip				†*						†			†	
	Novaculichthys								†*						†				
			taeniourus		Rockmover wrasse								†					†	
	Sparidae												†					†	
	Rhabdosargus			Sea breams			†*	†	†*				†*	†	†*				
			sarba		Goldlined seabream					†									
Serranidae																			
Epinephelinae																			
Epinephelus			Groupers			†	†*	†*				†*	†*	†*	†	†*			
						†	†*	†				†	†	†*	†	†			
		coeruleopunctatus		White-spotted grouper											†				
	multinotatus		White-blotched grouper					†								†			
Balistidae																			
Balistapus			Triggerfish			†*	†*	†*	†*				†*						
		undulatus					†		†										
	Rhinecanthus					†	†	†*	†				†						
Belonidae																			
Tylosurus			Needlefish					†											
		crocodilus						†											
Siganidae																			
Siganus			Rabbit fishes			†*	†*	†*				†*	†	†	†	†	†*		
						†*	†*	†*				†*	†	†	†	†	†*		
Cichlidae																			
Lutjanidae			Snapper			†	†			†		†				†			
	Lutjanus					†	†			†		†				†			
			argentimaculatus		Mangrove red snapper					†									

					Unit	1	2	1	2	1	2	1	2	1	2	2	1	2	
					Level	S	S	1	1	2	2	2	2	2	2	2	3	3	
					Feature							1	1	2	2	3			
					Family	Genus	Species	(98-100%											
					(90-94% ID)	(95-97% ID)	ID)												
					Common name														
Fish	Megalopidae			Tarpons			†*		†*										
		<i>Megalops</i>					†*		†*										
			<i>cyprinoides</i>	Indo-Pacific tarpon			†*		†*										
	Gobiidae			Gobies			†			†				†					
	Kyphosidae			Sea chubs						†			†						
		<i>Kyphosus</i>								†			†						
			<i>bigibbus</i>	Brown chub						†			†						
	Pleuronectidae			Flounder			†		†										
	Pomacentridae			Sergeant-majors						†*									
		<i>Abudefduf</i>								†*									
			<i>sordidus</i>	Blackspot sergeant						†									
	Chanidae			Milk fish					†*								†		
		<i>Chanos</i>															†		
			<i>chanos</i>														†		
	Haemulidae			Grunts					†*	†*	†		†	†*		†	†*	†*	
		<i>Plectorhinchus</i>		Sweetlips					†*	†*	†		†	†		†	†	†	
			<i>sordidus</i>	Sordid rubberlip												†			
			<i>gaterinus</i>	Blackspotted rubberlip					†	†	†		†	†		†		†	
			<i>gibbosus</i>	Harry hotlips												†			
	Ambassidae			Asiatic glassfishes					†										
		<i>Ambassis</i>		Commerson's glassy					†										
	Holocentridae			Ray finned fish									†						
		<i>Myripristis</i>		Solider fishes									†						
	Ostraciidae			Boxfishes					†										
		<i>Ostracion</i>							†										
Reptile	Lamprophiidae															†			
		<i>Dromicodryas</i>															†		
			<i>bernieri</i>	Bernier's striped snake													†		
	Colubridae			Snakes				†					†						
Avian	Anatidae			Whistling duck									†						
		<i>Dendrocygna</i>											†						
Mammal	Tenrecidae			Lesser								†		†					
		<i>Echinops</i>		hedgehog								†		†					
			<i>telfairi</i>	tenrec								†		†					

with a shift in regional social and political dynamics. At this time, new groups of people were migrating into the area and competing kingdoms were jostling for territory and tribute (Fagereng, 1947a, b; 1981; Fanony, 1986; Rengoky, 1988; Stiles, 1991; Yount et al., 2001). The resultant political insecurity may have had an impact on patterns of resource exploitation and further investigation of sites from this time period is needed to understand how

communities may have responded to heightened stress and insecurity. In Madagascar's far south, where warfare between competing kingdoms was also occurring, this period of increased political insecurity is marked by the fortification of sites, a closing off of social engagements and a more austere material culture (Parker Pearson, 2010).

Finally, the last 100–400 years are well represented at several

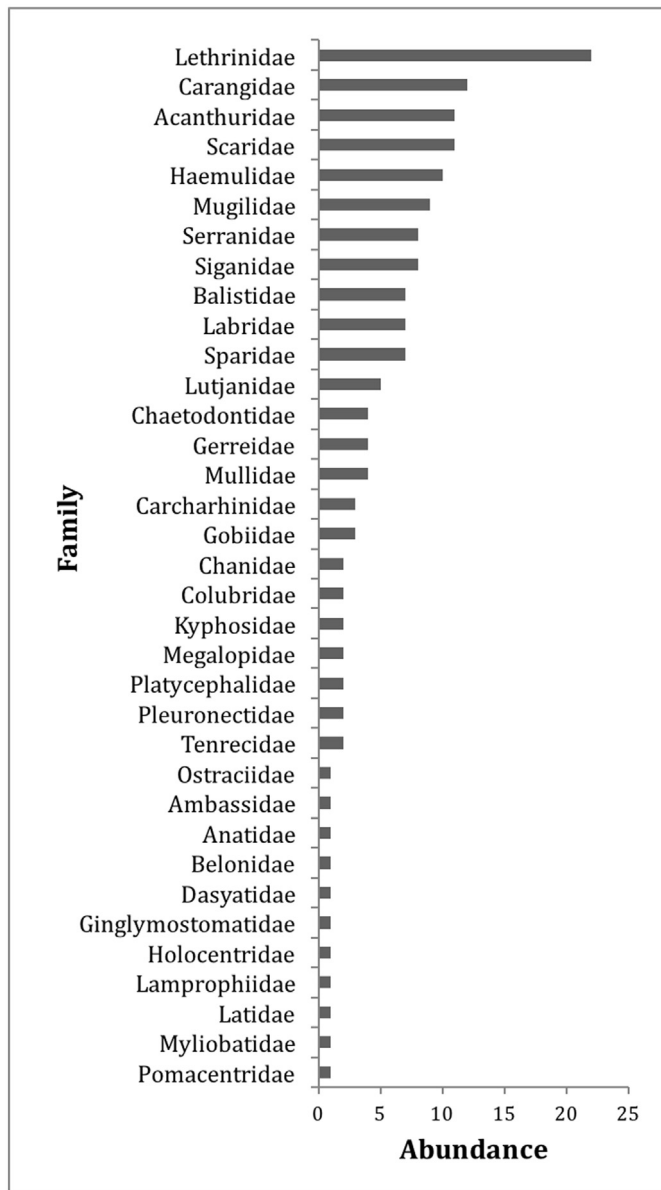


Fig. 10. Estimate of relative abundance based on number of layers each family was detected in.

sites in Velondriake. Many sites surveyed and all excavated sites showed evidence of occupation within the last 400 years, perhaps as a result of population growth during this time. The data from ANGY IV and ANTS I suggest differences in the fishing practices of these likely contemporary and geographically proximal communities. For example, ANGY IV yielded far more remains of reef-dwelling herbivores, like surgeonfish (Acanthuridae), parrotfish (Scaridae) and rabbitfish (Siganidae), than ANTS I. These herbivorous fish are most effectively caught with traps. In turn, ANTS I and ANDA I seem to include more demersal carnivorous fish that require different fishing strategies, like nets, hooks and lines. Though apparently more common at ANTS I and ANDA I, the presence of demersal fish at all three sites throughout the record suggests the use of bottom trawling nets on the reef and surrounding sand flats. The possibility of this fishing strategy is supported by shellfish remains, which included a large number of medium-sized drilled shells (esp. *Turbo coronatus*) that probably served as net weights, appropriate for the gauge nets needed to

catch these taxa (Douglass, 2016b). Overall, when viewed alongside shellfish data, it appears that the communities of each site and time period preferentially exploited certain habitats, while sometimes ignoring other nearby resource bases.

Though preliminary in terms of the extent of the excavations carried out to-date, the data presented here suggest that archaeological communities in southwest coastal Madagascar selectively exploited faunal resources, such that even contemporary communities within the same small area likely had differential impacts on distinct habitats and faunal populations.

6.2. Human interactions with extinct and endangered fauna

Considering the intense debate over anthropogenic impact and megafauna extinctions on Madagascar and the abundance of paleontological sites in southwest Madagascar, it is noteworthy that no megafauna bones have been identified at any of the excavated sites in Velondriake. Dates of final occurrence of many extinct megafauna taxa in southwest Madagascar (Crowley, 2010) indicate chronological overlap with archaeological communities in Velondriake, however no evidence for megafauna exploitation was found. It is possible that carcasses of megafauna taxa were processed at kill sites further inland and that only meat was brought back to settlements, thus rendering this activity invisible in the archaeological record. Future fieldwork must target areas inland from the coast, in order to evaluate the possibility of off-site processing of megafauna carcasses. Madagascar's interior southwest remains critically underrepresented in archaeological investigations.

Chelonian remains at ANGY and ANTS were relatively abundant and undoubtedly represent exploited taxa. However, the small size range of these remains excludes the giant, now-extinct genus *Aldabrachelys* (Goodman and Jungers, 2014). Five species of sea turtle occur along Madagascar's coastline. Many taboos in the far south prohibit the consumption of sea turtle meat, but it is considered a delicacy among the Vezo of the southwest. There seems to be a preference in the southwest for the common *Chelonia mydas* (green turtle), which feeds primarily on seagrass and algae (Glaw and Vences, 1994, 229). Some of the remains identified at ANGY and ANTS likely represent the critically endangered *Geochelone* (*Asterochelys*) *radiata* (radiated tortoise) and *Pyxis arachnoides* (spider tortoise), whose habitat ranges are increasingly restricted and populations are rapidly declining with the onslaught of hunting for bush meat and illegal exportation for the pet trade (Glaw and Vences, 1994).

The only indication of the exploitation of megafauna in Velondriake is abundant elephant bird eggshell debris, primarily at rock shelter sites (Douglass et al., in prep). Study of the eggshell may reveal that the exploitation of eggs was intensive enough to have an impact on elephant bird populations and contribute to their local extinction. Even if this is the case, however, the lack of evidence of hunting—let alone of intensive hunting—of adult birds stands in sharp contrast to other examples of island ratite extirpation, as in the case of New Zealand's moa (Anderson, 1989; Steadman, 2006). In the case of ANGY, which was certainly occupied prior to the complete extinction of elephant bird populations, there is no evidence of egg consumption and only one piece of eggshell—a unique perforated disk—was recovered from the entire site. Meanwhile, several relatively dense eggshell scatters, which may have been nesting sites, occur in the vicinity of ANGY and the other open-air sites, making it all the more intriguing that no evidence of elephant bird egg consumption was recorded at these sites. As it is the only ratite eggshell recorded at ANGY, the perforated disk may have been made from a discarded eggshell fragment found in the area, instead of from an egg that was consumed at ANGY. The disk

may also have been a trade item exchanged between foraging groups and ANGY villagers.

6.3. Introduction of exotics

The Velondriake assemblages offer some perspectives on the introduction of non-endemic fauna into the region. The exact timing of the introduction of bovids to Madagascar is unknown though there is some consensus that these animals arrived sometime in the second millennium BP via different Indian Ocean trade routes (Boivin et al., 2013; Fuller and Boivin, 2009). The probable presence of cattle was recorded in ca. 900–700 BP deposits at ANGY, providing a *terminus ante quem* for the introduction of cattle into the Velondriake region and making ANGY potentially one of the earliest known sites in southern Madagascar with cattle remains (see Parker Pearson, 2010).

The introduction of chicken and helmeted guineafowl to Madagascar is still not sufficiently confirmed either. Guinea fowl may have been introduced to the nearby Comoros as early as ca. 1000–800 BP (Boivin et al., 2013). They may, however, be native to Madagascar, as a guinea fowl bone was dated to ca. 9000 BP at Ankiliteho Cave in southwest Madagascar, a date which is considerably earlier than any confirmed human presence on the island (Goodman et al., 2013). Their possible presence at ANGY cannot be confirmed prior to ca. 400 BP. Pending further research, it may be that domesticates, including cattle, sheep, goats and chickens, were introduced at different times and by different cultural groups into the region.

Small mammal remains from ANGY and ANTS, as yet unidentified beyond class, also merit further efforts at taxonomic identification through aDNA analysis or Zooarchaeology by Mass Spectrometry (ZooMS), as well as direct dating. Among the possible identifications at these sites, the Asian musk shrew (*Suncus murinus*), cat (*Felis sylvestris*), dog (*Canis familiaris*), and African bush pig (*Potamochoerus larvatus*) are candidates for early introductions to Madagascar from the African mainland, but evidence on the timing of these introductions has been elusive.

Further investigations in the Velondriake region may thus contribute to the debate over the impact of introduced species on endemic fauna (Burney et al., 2004). Though it is possible that domesticates contributed to environmental change and competed with endemic grazers, like pygmy hippos, ratites and giant tortoises, past populations of cattle and small stock in Velondriake appear small based on the number of identified specimens at ANGY and ANTS and the lack of credible identifications at ANDA.

6.4. Archaeological and modern fisheries

Modern Velondriake fisheries data indicate that modern fishers exploit a wide range of fish taxa (Table S5). Ancient DNA analyses detected close to half of the taxa recorded in the modern fisheries, as well as a few families not recorded in the modern data (e.g. Ambassidae, Ginglymostomatidae, Cichlidae). In turn, morphological identifications at ANGY and ANTS identified roughly one third of the diversity recorded in the modern data. Given the high degree of fragmentation and smaller samples sizes, it is likely that further sampling of archaeological assemblages will yield evidence of the exploitation of a greater diversity of taxa in the past.

Both the archaeological assemblages and modern fisheries data indicate reliance on primarily shallow water habitats close to coral communities. Inhabitants of ANGY, ANTS and ANDA in all periods likely had access to similar resources. However, despite overlap in taxonomic lists, the relative abundance of taxa varies. For example, the ANTS fish taxa are more evenly distributed compared to ANGY, where emperor fish are dominant except in the most recent phase

(ANGY IV). This pattern could be related to chronological changes in the local ecology and/or fishing strategies since much of the ANGY assemblage represents older occupations. Throughout the archaeological record, the ANGY assemblage suggests minimal targeting of pelagic species, such as tuna (Scombridae) and jacks (Carangidae), which generally require larger crews and different fishing strategies than reef-associated species living in shallow waters (Wheeler and Jones, 1989). The taxonomic diversity represented by the identified remains suggests that the people of all three archaeological communities made use of a variety of fishing methods. Some taxa, such as groupers and emperors, are most effectively caught using fishing lines and hooks, while traps baited with algae work well for herbivorous fish, like parrotfish, surgeonfish and rabbitfish (Quintana Morales, 2013). In Velondriake today, traps are not used and some herbivorous fish (i.e. rabbitfish) are caught using lines baited with octopus ink. Nets can be used to catch a variety of fish, and their use can lead to by-catch; the cowfish (Ostraciidae) identifications at ANGY and ANDA may represent unintentional catch using a net, since this is not a species that is typically consumed as food today. No other uses of cowfish are known in modern-day Velondriake.

Despite the dominance of coral reef-associated taxa in both archaeological and modern data, it appears past communities relied more heavily on coral habitats, with small variations in reliance through time (Fig. 11). ANGY III and ANDA I feature the highest degree of reliance on corals noted in archaeological assemblages. The decline in reliance on coral communities in the modern fisheries data may be linked to more recent degradation in coral reefs observed along the southwestern coast of Madagascar (Harris et al., 2010). Among other factors, the heavy exploitation of apex predators like shark has likely had cascading effects across trophic levels that lead to impoverished reef biodiversity (Ruppert et al., 2013).

Contrary to recent hypotheses (Grealy et al., 2016), additional sampling of archaeological sites in Velondriake yielded little evidence for the past exploitation of large apex predators, suggesting that the intensive fishing of species like shark is a recent phenomenon in southwest Madagascar (Barnes-Mauthe et al., 2013; Cripps et al., 2015; Iida, 2005; McVean et al., 2006). Based on our rough estimate of abundance of shark at ANDA and the results from ANGY and ANTS, cartilaginous families made up a very small fraction of the overall archaeological assemblage. This may be partially due to their inferior preservation, but may also indicate limited

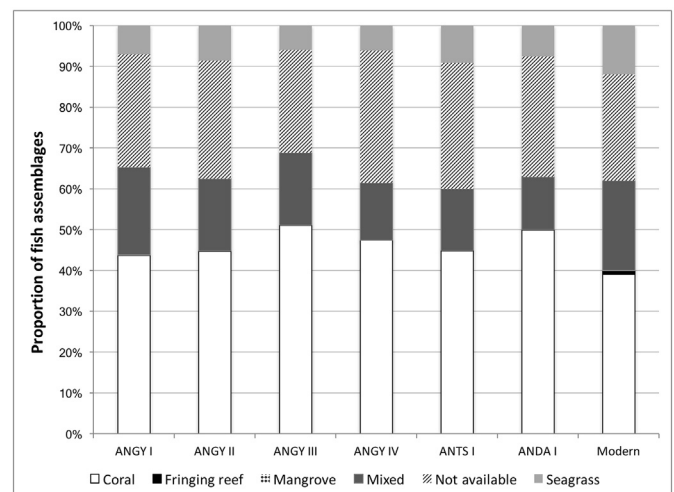


Fig. 11. Habitat associations of fish assemblages by site and occupation phase.

Table 6

Total Catch Volume in metric tons by habitat type and by survey year (Blue Ventures Conservation).

Survey years	Tidal muds	Coral	Fringing reef	Mangrove	Mixed	N/R	Seagrass beds	Channel	Total
2010	0.00	21.63	0.00	0.00	0.00	0.86	4.53	0.00	27.02
2011	0.00	63.21	0.00	0.00	0.00	13.85	0.41	0.00	77.47
2012	0.00	56.25	0.17	0.19	4.89	48.40	1.96	0.10	111.96
2013	0.00	0.77	0.00	0.00	0.29	18.71	0.16	0.00	19.93
Total	0.00	141.86	0.17	0.19	5.18	81.82	7.06	0.10	236.38

exploitation of these taxa in the past. Again, the shellfish remains provide an additional line of evidence. A relatively small number of shell net weights of sufficient size and weight to be used with heavier gauge nets capable of taking shark were recovered from ANDA, ANGY and ANTS, suggesting that shark were minimally fished in the archaeological past. In the case of carpet sharks (Ginglymostomatidae), which were detected at ANDA, older members of the Velondriake community recall these animals being present in the area in their lifetime (Nahoda Noely pers. comm.). This suggests that some of these taxa may have been extirpated quite recently.

Annual variation in habitat reliance patterns and taxonomic diversity of catch was observed in the modern fisheries data (Table 6). This variation may be partially due to annual climatic variation and major weather events, such as Cyclone Haruna, which devastated Velondriake in early 2013. The cyclone had an effect on benthic habitats of many of the reefs, reducing hard coral cover significantly in a number of affected reefs (Blue Ventures Conservation, pers. comm.). Beginning in 2013, exploitation patterns appear to shift, warranting further assessment of factors affecting people's choice of fishing ground, fishing strategy and tackle, and the resilience of marine habitats, in the past and present. Seasonality and diachronic changes in exploitation patterns in the archaeological record necessitate further analysis and additional samples. Otoliths, calcified biominerals located in the inner ears of fish, may offer information on the season in which the specimens were caught through comparison of the growth rings with reference collections. In the analyzed remains from ANGY Unit 1, two complete otoliths were recovered from Level 3 and one otolith fragment was recovered from Unit 1B, Level 10; however, these otoliths have yet to be taxonomically identified. The more intensive exploitation of mesopredators of the reef in the archaeological past, combined with minimal targeting of apex predators may have made the ancient reef more resilient and quicker to recover during climatic events like cyclones.

7. Conclusion

The results presented here offer a first glimpse of resource exploitation patterns throughout the recorded archaeological sequence of Velondriake, based on the analysis of faunal remains. Traditional morphological analyses were combined with bulk bone DNA metabarcoding and the results were interpreted alongside modern local fisheries data. Vertebrate faunal assemblages recovered from survey and excavations in Velondriake were limited in size and often highly fragmented, but their analysis serves as an important first step in establishing a fine-grained zooarchaeological record for the region. The sites of ANDA, ANGY and ANTS have a distinct maritime identity based on the predominance of marine species in their faunal remains. Overall, all three villages demonstrated a strong reliance on reef communities, but taxonomic representation also appears variable across occupation phases and sites, suggesting unique human-environment interaction scenarios.

Zooarchaeological research thus remains an essential area for

the development of new projects on Madagascar, with great potential to elucidate ancient lifeways, and the patterns of resource use and human-environment interaction that may have contributed to changes in island landscapes and biodiversity. Future work should emphasize the recovery of macro and micro, terrestrial and marine faunal remains, even in contexts with poor preservation, and should leverage multi-analytical approaches for maximum data collection. Whenever possible archaeological data should be integrated with other lines of evidence, including modern conservation data, to improve our understanding of diachronic changes in human-environment interaction. Given today's concerns about environmental degradation, gaining long-term historical ecological perspectives on human resource use may offer insights that are applicable to today's conservation efforts.

Author contributions

KD organized and directed archaeological fieldwork in the Velondriake Marine Protected Area. KD performed taxonomic identification and morphological and taphonomic analysis of shellfish remains. ARA performed taxonomic identification and morphological and taphonomic analysis of mammal, bird and herpetofauna bones. EMQM performed taxonomic identification and morphological and taphonomic analysis of fish bones. AG assisted in the field collection of bulk bone samples for aDNA analysis. AG conducted genetic analysis with assistance from MB. CG organized collection of modern Velondriake fisheries data. KD drafted the manuscript with contributions from ARA, EMQM and AG and comments from MB, CB and CG. CB rendered maps and figures.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.quaint.2017.09.019>.

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