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Human foraging responses to climate change

Here Sorot Entapa rockshelter on Kisar Island

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ABSTRACT

This study explores prehistoric human subsistence adaptations within the context of changing marine and terrestrial environments on the tiny Island of Kisar, beginning during the Pleistocene-Holocene transition around 15,000 years ago (ka). We use zooarchaeological data on faunal remains (vertebrates and invertebrates) recovered from Here Sorot Entapa rockshelter (HSE) in temporal relationship to climate data from Flores to document prehistoric human responses to regional sea-level, temperature, and associated habitat changes that occurred after the Last Glacial Maximum (LGM). Human settlement intensity peaked during the colder drier conditions of the Bølling-Allerød period at 14.4-13 ka, and the site was abandoned during a period of unstable sea levels and coastal habitats between 9.4-5 ka. Holocene climate change coincides with increased reefal subsistence, and an increase in crab exploitation over sea urchin use. Rodent abundance increases in the early Holocene, possibly in response to expanding forests during warmer wetter conditions, with a significant increase in the late Holocene as a result of the human introduction of exotic species to the island.

KEYWORDS

Coastal; Wallacea; zooarchaeology; climate change; Younger Dryas; Pleistocene-Holocene transition.

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INTRODUCTION[1]

Evolutionary theoretical models and ethnographic accounts all indicate that hunter-gatherer subsistence strategies are, and were, a series of complex interactions between humans and various environmental and cultural factors. Human behavioural ecology theory typically predicts that humans adapt behaviour to resource availability using technology and strategies to maximize reproductive fitness (Pyke 1984; Gremmillion 2002; Lupo 2007; Allen and O'Connell 2008; O'Connell and Allen 2012). These foraging decisions can affect the availability of edible organisms, inspire changes in hunting methods and technology, cause localized landscape and climate modifications, and can also result in resource competition and the rise of socio-political entities.

On the other hand, climate has arguably been the most critical variable in influencing human evolution, being the dominant factor in determining the biotic composition of an area (Van der Kaars 1995; Hantoro 1997; Wang et al. 1999; Gathorne-Hardy et al. 2002; Hope et al. 2004; Woodruff 2010; Wicaksono et al. 2017). Global climate changes are known to have had significant impacts on faunal distributions (Hewitt 2000) and human survival strategies (Gupta 2004). However, hypotheses that predict the effects of long-term climate change on prehistoric human settlement are difficult to test without a combination of localized archaeological and climatic data.

Changes in climatic conditions after the Last Glacial Maximum (LGM, ~25-21 ka),[2] saw a rapid rise in global sea levels and temperatures during the Pleistocene-Holocene transition (Lambeck and Chappell 2001). This had a dramatic effect on the landscapes and ecologies in Island Southeast Asia (ISEA) (Kealy, Louys, and O'Connor 2016, 2017). These events could have affected human foraging strategies in response to climate-driven changes in the relative abundance of biota (Simanjuntak 2006; Hawkins, O'Connor, and Louys 2017). However, this complex relationship between culture and climate has yet to be examined on the smallest of the islands.

Small islands are significant in human history for their depauperate terrestrial faunas that forced a variety of subsistence adaptations in early human colonizers (O'Connor et al. 2019). Even today, people who live on the island have their own distinct lifeways that differ from people on larger islands

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[2] LGM was the time at which global ice cover reached its greatest extent during last glacial period. The date range varies depending on the location and methods used to obtain the proxy data. For instance, Yokoyama et al. (2000) indicate that the ice was at its maximum extent between 22 to 19 ka. However, here we use the period of lowest sea level to define the LGM as this would have influenced human foraging choices on Kisar (Lambeck and Chappell 2001).

and mainland. Kisar, as one of the smallest habitable islands in Wallacea, has long history of human occupancy. Faunal remains in cave or rockshelter sites (as remnants of the diet of previous inhabitants) that are recovered through archaeological excavation can be used as a proxy to interpret the various subsistence strategies used by people during prehistory. Developments in technology or changing environmental conditions influence resource accessibility, thereby precipitating changes in subsistence over time.

Here we discuss the relationship between environmental and cultural factors on human adaptation to the small Island of Kisar, in the eastern Indonesian region of southern Wallacea, during the Pleistocene-Holocene transition and through into the Holocene. We use zooarchaeological data obtained from the analysis of marine vertebrates (marine fishes, sea turtles), terrestrial micro-vertebrates (small rodents, shrews, bats, birds, lizards), and invertebrates (crustaceans, molluscs, and sea urchins) remains recovered from the Here Sorot Entapa (HSE) rockshelter site (O'Connor et al. 2019) to determine changes in general subsistence strategies and settlement intensity. We then compare our data and associated modelled dates with local Lesser Sunda Islands climate records from nearby Flores Island (Ayliffe et al. 2013) to reconstruct prehistoric human subsistence responses to climate change between 16 ka and 2 ka. We also discuss the potential impact of rapid sea level rise at the end of the LGM on coastal substrates, marine resources, and the human populations using them.

THE WALLACEAN ARCHIPELAGO

The Wallacean islands between the continental landmasses of Sunda (mainland Southeast Asia) and Sahul (Australia – New Guinea) are recognized as a biogeographic transitional zone, characterized by a mixed faunal assemblage originating from both continents (Mayr 1944; Hooijer 1974; Flannery and Boeadi 1995). Faunal diversity is constrained by island size and by isolation from mainland biota (Wallace 1860), as predicted by the *equilibrium theory of island biogeography* (MacArthur and Wilson 1967). The discovery of dwarf stegodons, giant land turtles, giant lizards (Komodo), and giant rats on islands in Wallacea (Aplin and Helgen 2010; Locatelli et al. 201; Louys, Price, and O'Connor 2016; Louys et al. 2018) reflect this dispersal as well as the evolution of endemic faunas as a result of the "Island Rule" (Foster 1964).[3] However, direct evidence that modern humans preyed on these larger bodied animals has yet to be ascertained as, with the exception of the still extant Komodo, overlap with the earliest human settlement in this insular region has not been demonstrated (Louys, Price, and O'Connor 2016; Hawkins, O'Connor, and Louys 2017; Sutikna et al. 2018).

Small, isolated ecosystems (such as islands) are potentially more demanding on human subsistence strategies because of the limited access

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[3] The "Island Rule", "Island Effect", or "Foster's Rule" is a theory in evolutionary biology that explains the evolutionary phenomenon of dwarfism in large animals and gigantism in small animals that become isolated on islands.

to various terrestrial subsistence resources, including fresh water. Access to materials such as wood, bamboo, palms, and shells to make watercraft, fish-hooks, spears, nets, and string (Bednarik 2003; Balme 2013; O'Connor et al. 2017) are also critical to the survival of hunter-gatherer populations on small islands. The abundance of resources on small islands is not, however, solely dependent on land surface productivity, as the length and characteristics of the coastline can often provide a greater diversity of resource zones such as coral reefs, mangrove forests, and estuarine environments (Keegan et al. 2008). Consequently, small islands could in fact support greater resource availability than their size suggests, and provide a significantly greater source of marine resources, proportional to land size, than their larger island neighbours.

The Wallacean Archipelago (Indonesia and Timor-Leste) provides archaeologists with prime research opportunities for investigating early human adaptations to small islands because of the archipelago's continuous isolation (Voris 2000) from mainland Sunda and Sahul. The complexity and accessibility of foraging in these environments can be determined by a comparison between palaeo-landscapes and the proportion and quantity of zooarchaeological remains associated with different ecological resource patches (such as marine versus terrestrial) (Yuwono 2009; Rick 2011) or capture methods (such as netting versus angling), such as the ratio between herbivorous/omnivorous and carnivorous reef fish (Samper Carro et al. 2016). To-date, research on the Wallacean islands has recovered numerous archaeological sites that record evidence for early modern human subsistence practices at various times.

The oldest known early modern human deposits in Wallacea are from the islands of Flores and Timor (Sutikna et al. 2018; Shipton et al. Forthcoming). Laili (Hawkins et al. 2017), Asitau Kuru (previously Jerimalai) (O'Connor 2007; O'Connor, Ono, and Clarkson 2011; O'Connor, Robertson, and Aplin 2014; Shipton et al. Forthcoming), Lene Hara (O'Connor et al. 2010), Matja Kuru 2 (Veth, Spriggs, and O'Connor 2005; O'Connor, Robertson, and Aplin 2014), and Bui Ceri Uato (Selimiotis 2006) all record pre-LGM occupation in Timor-Leste, while the site of Liang Bua on Flores records evidence for early modern human occupation in layers above those containing remains of the diminutive hominin, *Homo floresiensis* (Sutikna et al. 2018). The sites of Laili, Asitau Kuru, and Liang Bua have produced overlapping calibrated radiocarbon age ranges of 43.4-44.7 ka, 43.1-46.5 ka, and 44.13-47.66 ka, respectively, for initial modern human occupation (Hawkins et al. 2017; Sutikna et al. 2018; Shipton et al. Forthcoming). The overlapping 95.4% confidence interval possible range for these dates makes the obtaining of any further determinations of the earliest occupied site between them currently unavailable. Regardless of the exact occupation order between these three sites, their combined results suggest that early modern humans had reached the islands of Flores and Timor, and central-south Wallacea generally, by at least 44 ka (Hawkins et al. 2017; Sutikna et al. 2018; Shipton et al. Forthcoming).

Other early, pre-LGM sites in Wallacea with records of early modern human occupation include; Golo (Bellwood et al. 1998), Leang Sarru (Tanudirjo 2001), Leang Timpuseng and neighbouring rock art sites (Aubert et al. 2014), and Lua Meko (Mahirta 2003), with Tron Bon Lei (Samper Carro et al. 2016; Samper Carro, Louys, and O'Connor 2017; O'Connor et al. 2017) dated to the LGM. With the high ratio of coastline to inland environments, that provide limited ecosystems for terrestrial fauna, the early modern humans who inhabited the Wallacean Archipelago adapted themselves to focus on marine resources to meet their protein requirements (Bowdler 1977; O'Connor, Ono, and Clarkson 2011; Balme 2013; Samper Carro et al. 2016; Samper Carro, Louys, and O'Connor 2017).

Excavation results at Pia Huddle, Roti (Mahirta et al. 2004), Asitau Kuru, Timor-Leste (O'Connor, Ono, and Clarkson 2011; Shipton et al. Forthcoming), Lene Hara, Timor-Leste (O'Connor 2007; O'Connor, Ono, and Clarkson 2011), and Tron Bon Lei, Alor (Samper Carro et al. 2016; Samper Carro, Louys, and O'Connor 2017) all show a high dependence on coastal and marine resources such as fish, shells, crabs, and urchins. A high exploitation of easy-access ecosystems is a common characteristic of the survival strategies employed by coastal communities (Waselkov 1987; Szabó and Amesbury 2011; Boulanger et al. 2019). The discovery of a shell fish-hook made from *Tectus nilocitus* dated to 23-16 ka from Asitau Kuru (O'Connor, Ono, and Clarkson 2011), and the placement of shell hooks as grave goods in Tron Bon Lei around 12 ka (O'Connor et al. 2017), demonstrates the significance of fish and other maritime resources to the early occupants of the Lesser Sunda Islands.

The Lesser Sunda Islands are an insular archipelago of southern Wallacea (Eastern Indonesia, Timor-Leste). The depth of the marine channel that separates each of these islands is also a factor in the biogeographic dispersal of biota from mainland and other island sources (Maryanto and Higashi 2011). As the distance from mainland Sunda increases, the terrestrial vertebrate diversity on these islands declines exponentially. Therefore, in addition to the domination of marine and coastal faunas, Pleistocene subsistence strategies in this region are characterized by only a limited consumption of terrestrial fauna such as reptiles, birds, and small mammals. Medium- to large-sized mammals are absent from the Pleistocene records of modern human occupation in the Lesser Sunda Islands, only appearing in the late Holocene as a result of human introductions (Mahirta et al. 2004; Heinsohn 2010; O'Connor, Ono, and Clarkson 2011; Samper Carro et al. 2016).

Almost all Wallacean sites show a high dependence on marine resources, even the more inland sites such as Laili and Matja Kuru 2 still preserve a record of marine exploitation including marine shellfish, fish, turtle, crabs, and sea urchins (although notably reduced compared to the coastal sites), indicating the value of this resource zone even when procurement distances exceeded four km. Archaeological records on smaller islands including Roti, Gebe, Talaud, and Alor indicate heavy dependence on marine resources in the face of their depauperate terrestrial faunas. Hence Kisar, the smallest (approximately 80 km2) Wallacean island with a known archaeological record (O'Connor et al. 2019, 2018), is the ideal location for the study of human adaptation to insular environments.

KISAR ISLAND

Kisar is a small island that is part of the Lesser Sunda Islands chain of Wallacea, an insular archipelago that has never been connected to the continental landmasses of Sunda or Sahul. It is located north-east of the Island of Timor, in the Indonesian province of Maluku Barat Daya (Figure 1). Kisar and other islands of the Lesser Sundas, such as Timor, Moa, Leti, Wetar, and Romang, formed as a result of the collision between the Australian and Eurasian Plates (Kadarusman et al. 2010). Of these islands, Kisar is located on the border between the non-volcanic area of the Outer Banda Arc (that consists of the islands of Timor, Moa, and Leti) and the volcanic area that lies on the Inner Banda Arc (including Wetar, Romang, and Damar) (Kadarusman et al. 2010; Major et al. 2013).

Kisar's geology consists predominantly of metamorphic rocks surrounded by a series of limestone terraces formed as surrounding coral reefs were uplifted over time (Figure 1; Major et al. 2013). The island has undergone a tectonic uplift of about 0.5 m per 1000 years as the result of its geological location (Chappell and Veeh 1978, Major et al. 2013). The present climate on Kisar is classified as dry with rainfall ranging between 900-1200 mm/pa and its vegetation is dominated by savanna and plantations. Occasional large trees are still found in valley bottoms along river channels, but dense patches of forest exceeding 2-5 ha are absent (Trainor and Verbelen 2013).

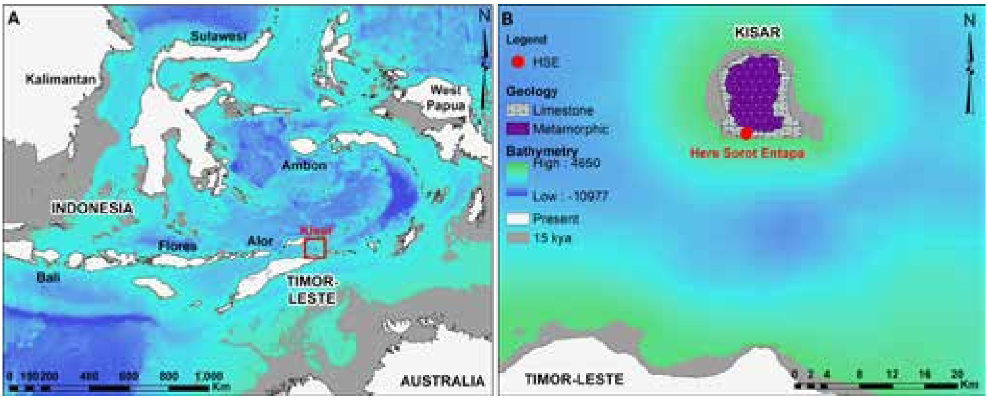

Figure 1. Map showing the regional location of Kisar and the Here Sorot Entapa (HSE) rockshelter. A) Island Southeast Asia and the location of Kisar. Light grey shows the present extent of the islands, dark grey indicates the extent at 15 ka. B) Geology of Kisar (based on Kadarusman et al. 2010) and location of HSE rockshelter.

Evidence of the high archaeological potential on Kisar can be seen from the discovery of numerous caves and rockshelters containing rock art (O'Connor et al. 2018) and also from the results of the small excavations conducted at

HSE located at Wosi/Posi Beach, Kiomanumere Hamlet, Wonreli Village (O'Connor et al. 2019). The beach is on the southern coast of Kisar directly facing towards the northern side of the Island of Timor.

HERE SOROT ENTAPA (HSE) ROCKSHELTER

HSE consists of a rockshelter in a limestone terrace with a smaller cave chamber at the back (Figure 2). The shelter lies at a height of about 24 m above present mean sea level and is located approximately 80 m from the modern shoreline (O'Connor et al. 2019). Archaeological evidence from HSE suggests Kisar was occupied from 15.5 ka calibrated Before Present (cal BP) with settlement terminating around 2 ka cal BP (O'Connor et al. 2019). Hence, Kisar is the smallest Wallacean island with a Pleistocene record of modern human occupation and its chronology spans the post-LGM period that saw significant climate and sea level changes during the Pleistocene-Holocene transition and into the Holocene.

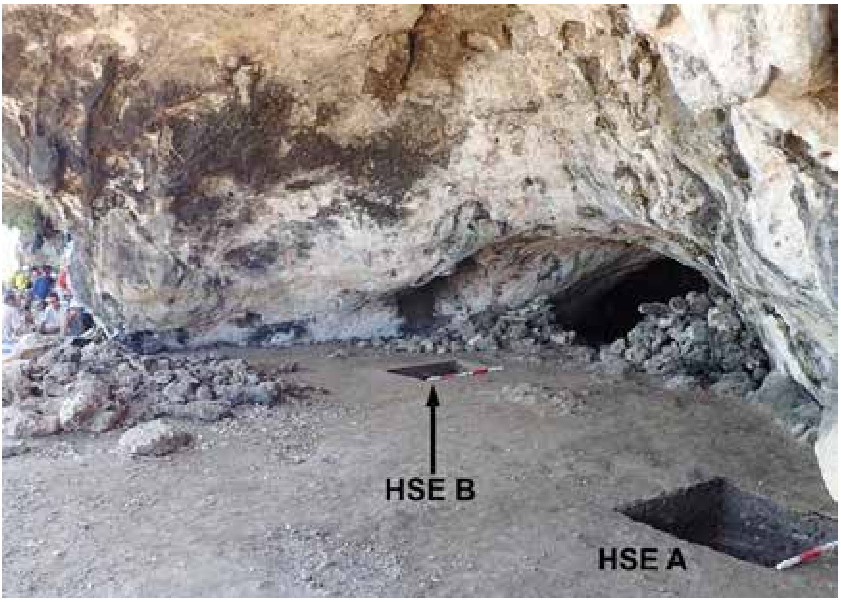

Figure 2. Photograph of HSE rockshelter showing the two excavated pits; Square A in the foreground and Square B indicated by the arrow.

HUMAN RESPONSES TO PALAEOCLIMATE IN THE LESSER SUNDAS

Ayliffe et al. (2013) detailed the closest palaeoclimate record to Kisar at Gua Liang Luar on Flores for the period 18 ka – present; coinciding with human settlement at HSE. Previous research indicating that the tropics were affected by global climatic shifts such as the Younger Dryas[4] is supported by the

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[4] The Younger Dryas was a period of abrupt climate change and rapid cooling with a return to more glacial conditions following the warming of the post-LGM period. The end of Younger

speleothem records at Liang Luar that record evidence for Heinrich Stadial 1 - Bølling-Allerød - Younger Dryas climatic events (Ayliffe et al. 2013). Post-LGM, the Pleistocene-Holocene transition is marked by a series of significant long-term global climate events that lasted several millennia. Climate data in the Northern Hemisphere splits this final deglaciation period into two sudden cooling phases (Heinrich Stadial 1 and the Younger Dryas) separated by one warm period (Bølling-Allerød). Conversely, the climate record in the Southern Hemisphere does not necessarily adhere closely to these climate patterns. Some evidence even indicates the trend was the opposite, commonly known as the "bipolar see-saw" (Dubois et al. 2014; Zhang et al. 2016).

Based on faunal changes seen in the archaeological records, in the tropical Indonesian archipelago beginning around 30-25 ka and peaking between 25-15 ka, a colder and dryer climate has been postulated to have occurred during the LGM (O'Connor et al. 2005; O'Connor and Aplin 2007). Temperatures reached 3-7°C below present (Gathorne-Hardy et al. 2002) and summer precipitation was reduced by at least 30% as a result of a weaker summer monsoon (Chabangborn, Brandefelt, and Wohlfarth 2014). Indonesia's climate fluctuated between these colder, dryer conditions to wetter and warmer climes at approximately 17-16 ka, and again at 15-14 ka (Williams et al. 2009). Lower global temperatures during the Late Pleistocene caused sea levels to drop on account of increased polar ice. The lowest sea level reached during this period in ISEA is estimated to have been about 135 m below current sea levels (Lambeck and Chappell 2001).

The Flores record also indicates localized climactic events following the LGM that would have influenced the early inhabitants of the Lesser Sunda Islands including Kisar. These include increases in temperature, sea levels, and hydrology (Ayliffe et al. 2013). Ayliffe et al. (2013) found a negative correlation between the stalagmite data from the Liang Luar Cave on Flores and the record of Hulu Cave in China. The cold and dry climate of Heinrich Stadial 1 (around 17.6 to 14.7 ka) in the Northern Hemisphere, recorded at the Hulu Cave, was instead recorded as warm and wet in Flores because of the stronger Australian-Indonesian Summer Monsoon (AISM). A warm period during the Bølling-Allerød (around 14.6 to 12.9 ka) and a stronger East Asian Summer Monsoon (EASM) in China, is instead indicated as a cooler period in the Flores record, on account of a weaker AISM in the region. The Younger Dryas interval (around 12.9 to 11.5 ka) is marked by a stronger AISM in Flores, resulting in warmer conditions, but cooling in China on account of a weakening EASM (Ayliffe et al. 2013).

These long-term fluctuations in climate probably had a significant impact on human settlement of Kisar in the form of responses to changes in resource availability that would have influenced the success or failure of human

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Dryas also marks the start of the Holocene period. While the phenomenon of the Younger Dryas is much more pronounced closer to the poles, particularly in the north, the Flores record (Ayliffe et al. 2013) adds evidence supporting the claim that the tropics were not free of its impact (see also Maloney 1995; Partin et al. 2015; Kuhnt et al. 2015).

populations on such a small island. Global climate changes appear to have generated a variety of responses by the early inhabitants in neighbouring sites. Changes in human settlement during the LGM varies considerably between sites, even sites on the same island. Asitau Kuru and Matja Kuru 2 in Timor-Leste show little evidence for occupation during the LGM (O'Connor 2007; Shipton et al. Forthcoming), while at Laili human settlement persisted during the LGM but with marked changes in resource use and increased dramatically during the terminal Pleistocene to early Holocene (Hawkins et al. 2017). The variety of shellfish species recovered from Leang Sarru (Talaud Islands) is also noted to have expanded during the LGM (Ono, Soegondho, and Yoneda 2009).

Additionally, several sites throughout Wallacea, including Tron Bon Lei (Samper Carro et al. 2016; Samper Carro, Louys, and O'Connor 2017), Uai Bobo (Glover 1969), Daeo 2 (Bellwood et al. 1998), and Lua Manggetek (Mahirta 2003), were occupied for the first time as the LGM began to subside. Changes in faunal subsistence strategies following the Pleistocene-Holocene transition have also been found by Samper Carro et al. (2016) and Samper Carro, Louys, and O'Connor (2017) at Tron Bon Lei, Alor Island, indicating a shift from the exploitation of larger carnivorous to smaller herbivorous (shallow/reef) fish taxa, possibly as a consequence of the stabilisation of sea levels and reef communities in the Holocene. Based on the calibrated radiocarbon dates, occupation on Kisar began shortly before 15.5 ka (O'Connor et al. 2019) as sea levels began to rise at the end of LGM. This data indicates enduring subsistence and mobility adaptations on the islands of Wallacea during the LGM, and into the Pleistocene-Holocene transition, as reflected in the variability in human occupation strategies at different locations.

METHODS

SITE EXCAVATION

The 2015 excavation of HSE was conducted in two separate 1 x 1 m test pits (HSE-A and HSE-B; Figure 2), dug in 5 cm spits to respective depths of 1.3 m and 1.2 m (O'Connor et al. 2019). At these depths, cultural materials were no longer present, and excavation ceased when sterile beach sand and coral deposits were encountered. All excavated material was weighed for each spit prior to processing, allowing accurate weights for each excavation removal (spit) to be recorded. The excavated material was then sieved in two stages, first dry followed by wet sieving, both using 1.5 mm mesh to ensure the recovery of small bones and artefacts (O'Connor et al. 2019).

We analysed the faunal materials from HSE-B; the square with the greatest concentration of faunal remains. HSE-B is located inside the dripline in the centre of the rockshelter floor (Figure 2), an area that tends to have higher rates of sedimentation due to human activity (Louys et al. 2017). This is supported by the sedimentation rates and stratigraphy recorded at HSE; especially HSE-B; in which numerous dense ash and charcoal layers from human activities were identified (Figure 3).

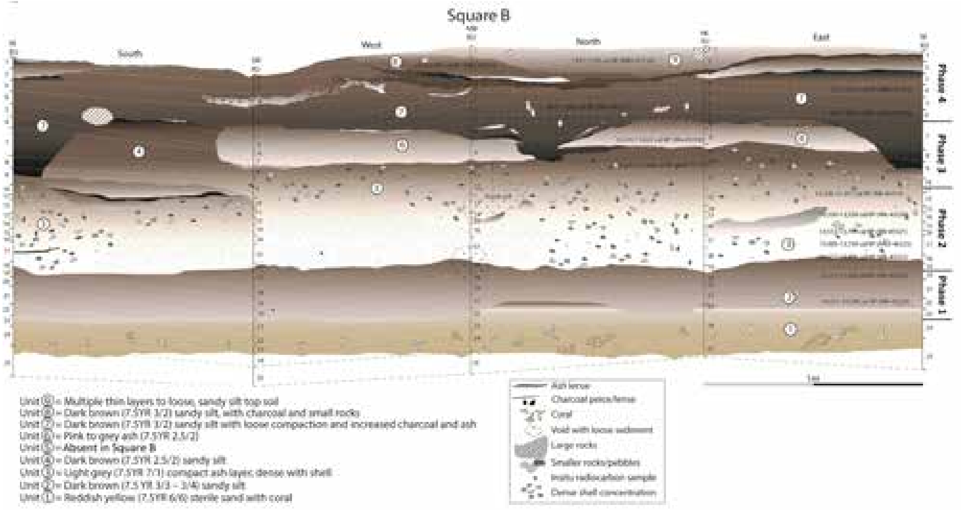

Figure 3. Stratigraphy of HSE-B showing spits (Sp.), units, and phases. Modified from Figure 4 of O'Connor et al. (2019).

Stratigraphic Unit	Spit	Lab No.	Material Dated	Δ¹³c	C¹⁴ Age	Calibrated Date (calBP)	
						From	To
Unit 9	2	ANU 47724	Charcoal	-29	2,050 ± 29	1,931	2,114
Unit 8	2	ANU 46323	Charcoal	-26.312	2,250 ± 24	2,158	2,340
	Hearth feature between 2 & 3	ANU 46324	Charcoal	-4.3569	2,250 ± 31	2,155	2,344
Unit 7	4	ANU 47725	Charcoal	-27	3,858 ± 32	4,157	4,410
	6	ANU 47726	Charcoal	-29	4,209 ± 37	4,622	4,852
	6	ANU 46321	Charcoal	-17.623	4,314 ± 26	4,837	4,960
--HIATUS--							
Unit 6	7	Wk 43317	Turbo sp.	-667.7	8,849 ± 20	9,455	9,538
	9	Wk 43318	Turbo sp.	-709.1	9,920 ± 20	10,741	11,023
Unit 3	11	ANU 47727	Charcoal	-28	10,354 ± 45	12,019	12,400
	12	Wk 43319	Turbo sp.	-775.5	12,000 ± 26	13,336	13,537
	14	Wk 43320	Turbo sp.	-775.2	11,991 ± 26	13,330	13,528
	16	Wk 43321	Turbo sp.	-781.1	12,204 ± 27	13,512	13,791
	17	ANU 46325	Charcoal	-15.335	11,802 ± 41	13,485	13,750
	18	Wk 43322	Turbo sp.	-781.5	12,217 ± 27	14,001	14,222
Unit 2	20	Wk 43323	Turbo sp.	-806.9	13,211 ± 30	15,117	15,409
	22	Wk 43324	Turbo sp.	-797.4	12,824 ± 29	14,212	14,796

Table 1. Radiocarbon dates with calibrations for HSE-B, showing spit and stratigraphic unit assigned to each sample and the location of the hiatus; as published by O'Connor et al. (2019: Table 1). Carbon-13 isotope fractionation is expressed as $\Delta^{13}C‰$. The conventional radiocarbon ages are listed under the C^{14} Age column with corresponding error values.

Based on dating of coral in the sterile sand and coral unit underlying the occupation deposit at HSE (O'Connor et al. 2019), combined with estimated uplift rates (Major et al. 2013), it is predicted that the shelter would have been dry and available for occupation shortly after 45 ka (O'Connor et al. 2019). However, the oldest possible date for human settlement at the shelter, based on radiocarbon dated age-depth models, suggests that HSE was not inhabited until around 16 ka (O'Connor et al. 2019). Cultural material was recovered from spits 1 to 23 of the 25 spits excavated. Cultural remains found in the excavation include stone artefacts, charcoal, pottery, ochre, plant remains, fish-hooks, and beads, while the upper late Holocene spits included small amounts of earthenware pottery (O'Connor et al. 2019). The age-depth model suggests HSE experienced relatively continuous occupation from around 16 ka until the early Holocene, with a hiatus (possibly indicating site abandonment) between 9.5 ka (Unit 6) and 5 ka (Unit 7) after which settlement resumed during the late Holocene between 5 ka and 1.6 ka (Table 1; O'Connor et al. 2019). The presence of glass fragments consistent in the uppermost spits indicates that occasional use of the shelter continued into the colonial period (O'Connor et al. 2019).

PHASES OF OCCUPATION

O'Connor et al. (2019) divided HSE into two phases; an initial occupation/ pre-hiatus phase from about 15.5 ka – 9.5 ka, and a latter/post-hiatus from about 4.9 ka. The stratigraphy was divided into nine units with the cultural units beginning at Unit 2 (O'Connor et al. 2019: Figure 4).

Looking closer at the zooarchaeological record for HSE-B, the density of faunal remains suggests that HSE-B can be further divided into four occupation phases (Figures 3 and 4), based on the extent and patterns of faunal deposition:

PHASE 1	Initial occupation (16-14.5 ka); spits 23 to 20
PHASE 2	The peak of occupation/ Late Pleistocene (14.5-12.8 ka); spits 19 to 11
PHASE 3	Younger Dryas and Early Holocene (12.7-9.5 ka); spits 10 to 7
- Record Hiatus -	
PHASE 4	Holocene Phase (5-1.6 ka); spits 6 to 1

Based on the overall weights of zooarchaeological remains, occupation intensity at HSE increased steadily after initial occupation until around 14 ka (Figure 4). An occupation peak between 14.5-12.8 ka is identified based on the high density of faunal remains alongside much more rapid sedimentation when compared to other periods, about 40 cm/ka vs just 5-10 cm/ka. The peak in occupation intensity in the terminal Pleistocene is followed by a notable decline in occupation continuing through to about 10 ka, followed by site abandonment. Occupation resumes in the mid-Holocene as represented by significant concentrations of faunal remains, charcoal, as well as pottery in the upper spits, but the intensity of occupation never again approaches that seen in the terminal Pleistocene at HSE (O'Connor et al. 2019: Figure 4).

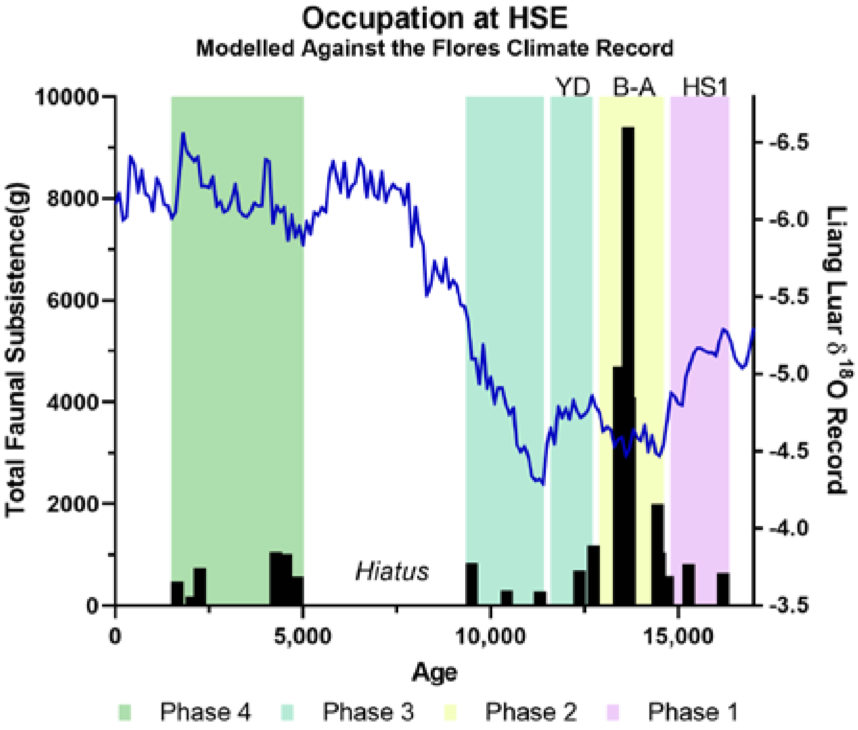

Figure 4. Climate change at Liang Luar since 18 ka (from Ayliffe et al. 2013) graphed (blue) against total foraging intensity at HSE-B (column). Phases 1-4 as defined in this paper shaded according to the key. The Younger Dryas (YD), Bølling-Allerød (B-A), and Heinrich Stadial 1 (HS1) delimited by the white lines.

As radiocarbon ages were unavailable for each spit within the HSE-B excavation, we performed an age-depth model in OxCal v.4.3 (Ramsey 2009), based on the available C^{14} dates (Table 1) to interpolate the gaps in our record (Table 2). This depositional model assumes a Poisson (or random) accumulation of sediment (Ramsey 2008), calculated from the available age data by averaging the model over many values of *k* (Ramsey and Lee 2013). The model interpolation rate was set to a single date per spit, and the unit of depth used was total sediment weight in grams (g) as a proxy for spit volume (Table 2). We used default priors and an outlier probability of 5% (Ramsey 2008; Ramsey and Lee 2013). The model was constructed as PHASES within two SEQUENCES corresponding to the nine units and two phases of O'Connor et al. (2019), respectively. Radiocarbon dates within the model were calibrated using the IntCal13 (for charcoal) and Marine13 (for marine shell) calibration curves (Reimer et al. 2013). The mean modelled and interpolated dates were then calculated from the model results and applied to the corresponding spit data throughout this study.

Spit	Sediment Weight (G)	C^{14} Age	Modelled Date	Mean Modelled Date	Convergence
1	64840	-	1999 – 1303	1651	99.8
2	64245	2,050 ± 29	2115 – 1935	2025	99.9
3	63960	2,250 ± 24 2,250 ± 31	2340 – 2159	2249.5	99.9
4	46450	3,858 ± 32	4411 – 4157	4284	99.9
5	39980	-	4867 – 4237	4552	97.6
6	64230	4,209 ± 37 4,314 ± 26	4867 – 4830	4848.5	99.9
7	28885	8,849 ± 20	9540 – 9452	9496	99.9
8	44445	-	11390 – 9454	10,422	93.5
9	29860	9,920 ± 20	11390 – 11246	11,318	99.8
10	49240	-	13470 – 11250	12,360	47.7
11	42150	10,354 ± 45	13494 – 11962	12,728	50.4
12	41465	12,000 ± 26	13499 – 13332	13,415.5	99.7
13	43975	-	13519 – 13345	13,432	99.6
14	41495	11,991 ± 26	13540 – 13370	13,455	99.6
15	37565	-	13690 – 13402	13,546	97.3
16	41390	12,204 ± 27	13720 – 13515	13,617.5	99.6
17	74710	11,802 ± 41	13732 – 13560	13,646	99.6
18	40450	12,217 ± 27	13791 – 13584	13,687.5	99.6
19	50825	-	15327 – 13577	14,452	96.4
20	32095	13,211 ± 30	15368 – 13627	14,497.5	71.1
21	82770	-	15801 – 13657	14,729	83.2
22	68430	12,824 ± 29	16403 – 14142	15,272.5	92.7
23	36080	-	18175 – 14203	16,189	91.7

Table 2. Results of the depositional model based on radiocarbon data from HSE-B. Recorded sediment weight (g) (excluding large rocks) is shown per spit alongside uncalibrated radiocarbon ages with the corresponding modelled and interpolated dates. The *Aoverall* agreement index = 97.68%, that in addition to generally high convergence values suggests the model is robust and a good approximation of available data.

FAUNAL ANALYSIS

The zooarchaeological findings in each spit were classified according to their habitat into three distinct ecological zones: 1) marine fauna: bony fishes (*Actinopterygii*), cartilaginous fishes (*Chondrichthyes*), and turtles (*Testudines*); 2) coastal/tidal zone fauna: shells (*Molluscs*), barnacles (*Maxillopoda*), crabs (*Malacostraca*), and sea urchins (*Echinodermata*); and 3) terrestrial fauna: snakes (*Serpentes*), lizards (*Lacertilia*), birds (*Aves*), bats (*Chiroptera*), rodents (*Rodentia*), shrews (*Soricidae*), and dogs and their relatives (*Carnivora*). A total of 16.84 g of vertebrate remains could not be identified to any of these groupings. The majority of these (10.26 g) could be identified at least to the superclass Tetrapoda and therefore tentatively ascribed to the terrestrial fauna zone as the only likely marine tetrapods (turtles) are known for their distinctive morphology (Wyneken and Witherington 2001). The other 6.58 g of unidentified vertebrates are included in the measures of overall occupation intensity but excluded from the zonal analyses because of the uncertainty of their classification. Nine compare to human bones identified previously (O'Connor et al. 2019) were excluded from this analysis as they are unrelated to human subsistence strategies.

The vertebrate faunal remains were classified using the reference collection in the Department of Archaeology and Natural History at the Australian National University. Fauna, once classified, was weighed and then adjusted by weight to account for variability in spit volume, thereby detecting true changes between spits (see Appendix Table A1). The adjusted weight is the weight of one faunal classification divided by the weight of the sediment from the entire spit (excluding large rocks) adjusted to 50 kg for every spit. The calculation is as follows:

$$\text{Adjusted weight} = \frac{5000\text{ g}}{\begin{array}{c}\text{Total sediment weight (g)}\\ \text{from spit x}\end{array}} \times \begin{array}{l}\text{Faunal group weight (g)}\\ \text{from spit x}\end{array}$$

For example; spit 3 recovered 1.41 g of identified serpent remains. The total volume of sediment excavated for spit 3 weighed 63,960 g. 50,000/63,960 = 0.78174. Hence, the adjusted weight for serpents in spit 3 is: 0.78174 × 1.41 = 1.10 g (to 2 decimal p).

Sediment weights include soil, artefacts, and fauna, but do not include large rocks (Table 2). Thereby, accounting for any variation in faunal weights between spits caused by differences in spit volume; either as a result of less sediment because of large rock accumulations in the spit or changing spit depth because of excavation variability. By adjusting the individual weights to a normalised spit average weight of 50 kg, the abundance of the different faunal groups can be accurately compared between spits (Table A1). The 50 kg amount was selected based on the volume of a perfect 100 x 100 x 5 cm cube (one 5 spit in the 1 x 1 m square).

Quantification methods such as Number of Identified Specimen (NISP) and Minimum Number of Individuals (MNI) are more popular methods than weight for analysing archaeological fauna (see Samper Carro et al. 2016; Samper Carro, Louys, and O'Connor 2017; Hawkins, O'Connor, and Louys 2017; Hawkins et al. 2017). However, each of these methods has advantages and disadvantages (Grayson 1984; Barrett 1993). For example, each species has a different skeletal structure, corresponding butchering patterns, and processes of fragmentation (Gilbert and Singer 1982).

By using NISP, there is a high risk of counting the same individual more than once, across multiple spits. Moreover, when we compare two different species with distinct skeletal structures, such as a fish and a mammal, fish bones tend to be more numerous because of a greater number of individual bones within their skeleton and the ease with which they are fragmented (Stahl 1996). The MNI method works to counteract this risk, however it can result in significant overestimations of rare taxa and an underestimation of others. For example, a single MNI count of sea urchins requires the identification of five "teeth" (Gutierrez Zugasti 2011), while vertebrates are regularly identified by a variety of cranial or postcranial elements whose use in MNI identifications can be selected on the basis of specific preservation patterns at the site (see Worthy et al. 2015). Certain MNI methodologies used by different researchers such as different levels (spits, layers, squares) of aggregation and elements identified, can also lead to ambiguity in the separation of individuals, resulting in quite different results (Gilbert and Singer 1982).

We use weight of fauna in grams (g) as a proxy for relative potential of meat yields from the different animal groups (Barrett 1993). This aims to reduce the quantification issues generated by the NISP and MNI methods while to some degree taking into account the variability in size of animals deposited. While variability in species morphology and taphonomy still leads to disparities within the weight dataset, for a general comparison between subsistence strategies over time, across all faunal classifications, the use of adjusted weights was deemed the most appropriate for this study.

RESULTS

Invertebrates

A total of 44.9 kg of invertebrate remains were recovered from the HSE-B excavation. Grouped under the four classifications of shell (*Mollusca*), barnacle (*Maxillopoda*), sea urchin (*Echinodermata*), and crab (*Malacostraca*), the bulk of the invertebrate fauna of HSE-B are considered to have been sourced from the Tidal Ecological Zone. The adjusted weight comparison suggests a correlation in the exploitation of shells and crabs during each phase of occupation at HSE-B (Figure 5). This trend indicates moderately high exploitation of shell and crab in the first phase of occupation with a dramatic increase during the second phase, followed by a marked decline during the early Holocene. In contrast, high rates of sea urchin exploitation are documented for the initial occupation phase, followed by a noticeable decline into the second half of the following phase (Figure 5). Sea urchin deposition at HSE increases once again during the fourth phase, following the hiatus.

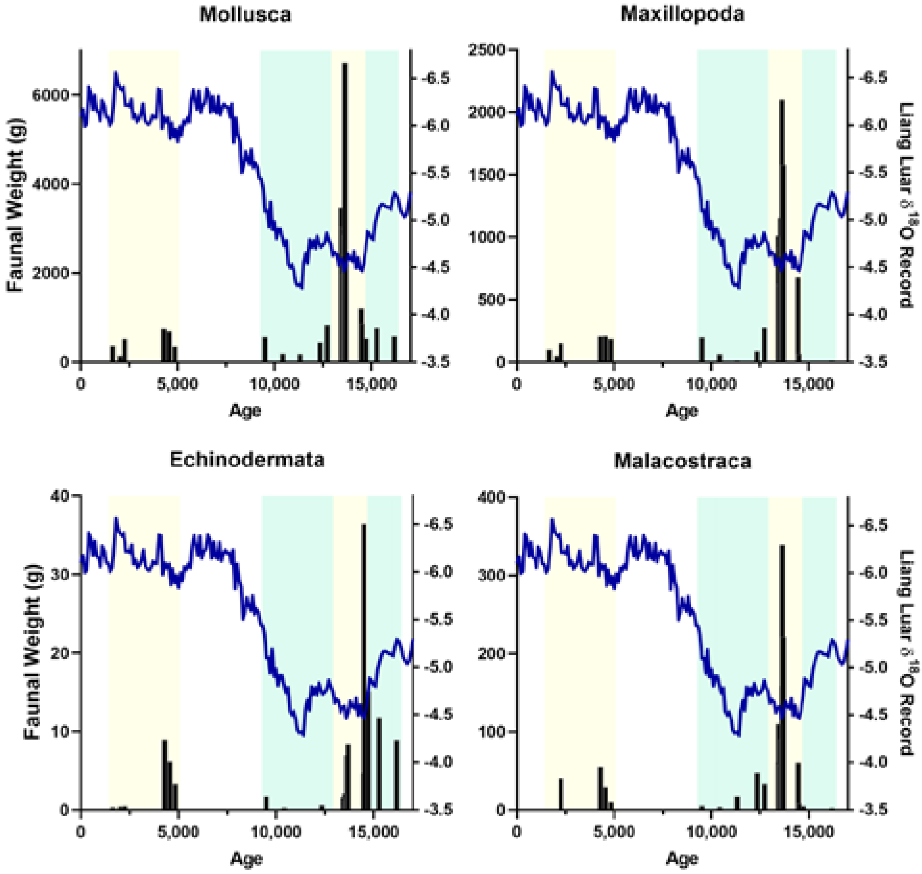

Figure 5. Tidal zone faunal record from HSE-B. Adjusted weight (g) for each spit graphed over time following modelled depositional ages (Table 2). The different phases are shaded, and the Flores climate record is drawn in blue.

Vertebrates

A total of 1.736 kg of identified marine and terrestrial vertebrate remains were recovered from the HSE-B excavation. Our data indicates that marine vertebrate subsistence was dominated by bony fishes (*Actinopterygii*), indicating significant human maritime adaptations to this specific ecological zone. A total of 1614.1 g of bony fish remains were recovered from HSE-B, peaking in the second occupation phase, around 13 ka (Figure 6).

During the initial occupation of HSE (16-14.5 ka), marine exploitation was at its height with fish dominating the assemblage that also contained small amounts of turtle and shark (Figure 6). Most of the shark remains were identifiable to the family *Carcharhinidae* (requiem sharks) (O'Connor et al. 2019), and first appear in the initial phase of occupancy, increasing in the second phase (Figure 6). HSE-B preserves evidence for turtle hunting in each phase of occupation, with the highest proportion recorded from spit 17 in Phase two (Figure 6).

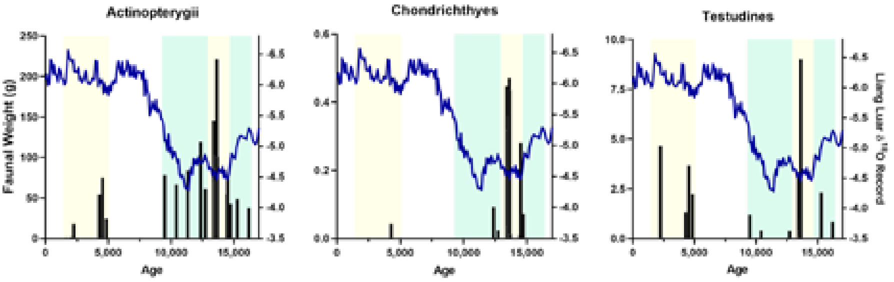

Figure 6. Marine zone faunal record from HSE-B. Adjusted weight (g) for each spit graphed over time following modelled depositional ages (Table 2). The different phases are shaded, and the Flores climate record is drawn in blue.

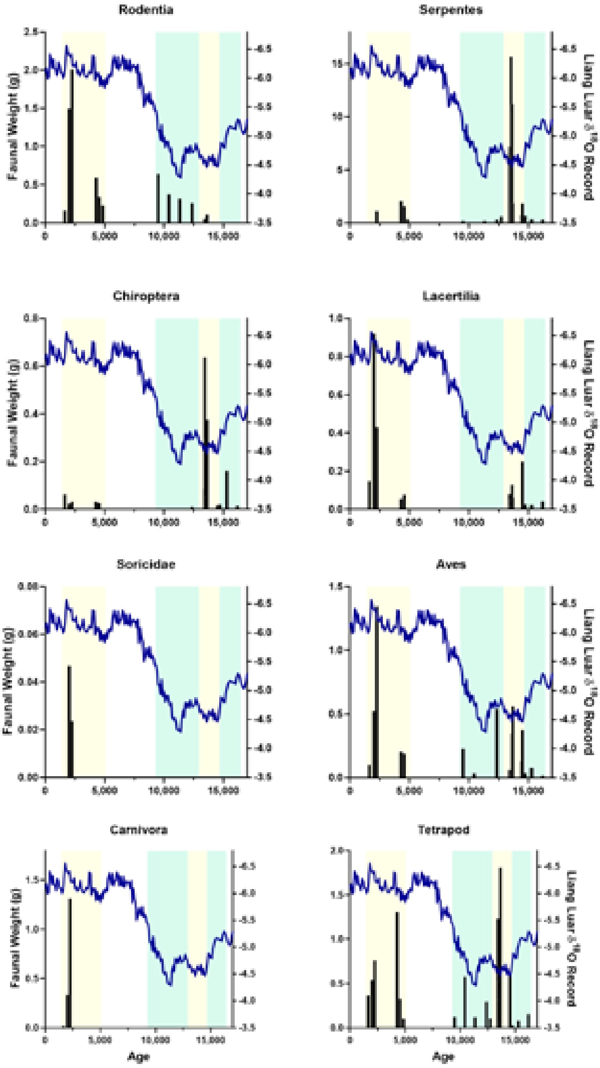

Figure 7. Terrestrial zone faunal record from HSE-B. Adjusted weight (g) for each spit graphed over time following modelled depositional ages (Table 2). The different phases are shaded, and the Flores climate record is drawn in blue.

Only small quantities of terrestrial micro-vertebrates[5] were recovered from HSE. In the initial phase of occupation, the terrestrial faunal assemblage is dominated by snakes, lizards, and birds. Bones of rats and bats also occur but in much smaller amounts (Figure 7). At the end of the Pleistocene, a dramatic increase in the deposition of snakes occurs across every spit of Phase 2 (Figure 7). The diameters of the vertebrae (between 0.5-1 cm) suggest the majority of snake remains were from small to medium individuals, with the larger bones probably belonging to some type of python. The majority of lizard remains are vertebrae and mandible elements and also suggest small-sized individuals.

During the early Holocene, there appears to have been a decline in occupation intensity and a change in the pattern of terrestrial faunal remains deposited at the site (Figure 7). Rodent abundance increases significantly compared to snakes and other terrestrial fauna. This trend continues until the termination of the site record. The deposition of snakes, lizards, and birds during the final phase was also high; however the relative weights for these three groups are still far less than that for rodents (Figure 7). Shrews are only found in the latter half of the last phase (4) in low proportions.

Discussion

Human occupation at HSE on Kisar Island began as sea levels were rising at the end of the LGM, coinciding with other archaeological evidence throughout Wallacea that indicates increased human habitation and activity during this period (Bellwood et al. 1998; Mahirta 2003; Samper Carro et al. 2016; Samper Carro, Louys, and O'Connor 2017; Hawkins et al. 2017; O'Connor et al. 2019; Shipton et al. Forthcoming). It has been suggested that falling sea levels and narrowing water gaps between islands during the LGM might have promoted human movement between islands (O'Connell, Allen, and Hawkes 2010). In some cases, such as in the Talauds, the larger land areas created by lower sea levels could have sustained occupation in areas that were previously marginal for human habitation (Tanudirjo 2001; Ono, Soegondho, and Yoneda 2009).

However, rising sea levels (Lambeck and Chappell 2001) and warmer climates during the Heinrich Stadial 1, notably the most prominent and longest climate event in the terminal Pleistocene (Ayliffe et al. 2013), provide a viable alternative hypothesis to explain why the post-LGM period sees an increase in human activity in the region (Chappell 1993; Shipton et al. Forthcoming). Increased coastal occupation has been linked with rising seas as this change supports more reefs, lagoons, swamps, beaches, and estuaries that themselves support a greater abundance and diversity of marine life and resources (Chappell 1993, 2000). Additionally, although islands might

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[5] Recovery of micro-vertebrate faunas in archaeological contexts often provides a significant contribution to the interpretation of human subsistence activities and/or the palaeoecology of the region. "Micro-vertebrate" includes most of the diminutive fauna such as rats, shrews, snakes, lizards, birds, and bats. However, detailed identifications to the genus and species levels requires a sound understanding of taxonomical identification and taphonomical processes because of the small size of the bones and their often highly fragmented state (for more detail see Stahl 1996).

have been reduced in total land area, the creation of multiple small islands following a sea level rise would have increased the length of coastline available for maritime exploitation; an advantage to humans in view of the limited sources of terrestrial protein on the small Wallacean islands (Shipton et al. Forthcoming). While in areas such as northern Australia and parts of Papua New Guinea and the Bismarck Archipelago, the rarity of pre-LGM sites might be attributable to their submergence by rising seas following the LGM (Swadling and Hope 1992; Ward et al. 2013; Summerhayes et al. 2017), this is less likely to have had an impact on coastal settlements in the Lesser Sundas among which offshore coastal bathymetry is steep (Hawkins et al. 2017; O'Connor et al. 2017) and uplift rates are high (Hantoro et al. 1994; Cox 2009; Kealy, Louys, and O'Connor 2017).

Our study indicates an interesting correlation between prehistoric subsistence-based human occupation intensity at HSE-B on Kisar Island and climate change as recorded on nearby Flores (Figure 4). Kisar was occupied during Heinrich Stadial 1 that is assumed to have been a warmer and wetter period on Flores and the surrounding region (Ayliffe et al. 2013). Yet occupation intensity at HSE increased significantly between 14.5 to 12.8 ka, synchronous with the Bølling-Allerød climactic period and a dryer, colder climate on Kisar (Figure 4). Relatively higher quantities of stone artefacts as well as beads and ochre during Phase 2 also support a peak in site occupancy in this period (O'Connor et al. 2019). Commencing at around 12.7 ka, the warm and wet Younger Dryas corresponds with a sudden fall in occupation intensity at HSE, with a major decline in site use registered between 11.3 to 9.5 ka. By 9 ka the site appears to have been abandoned, contemporaneous with global warming that began to increase dramatically during the early to mid-Holocene. Resumption of low intensity human settlement at HSE occurred after 5 ka (Figure 4).

Further comparisons between the variations in subsistence strategies identified above and the climate record from Liang Luar indicate that global climate fluctuations might have had a role in the changing amplitudes of human occupation at HSE. However, this begs the question of how the early occupants managed to flourish during the colder and drier Bølling-Allerød period, and why there was a sudden drop off in occupation intensity at the beginning of the warm and wet Younger Dryas period, possibly leading to site abandonment in the Early Holocene. Perhaps in the case of HSE occupants, because they lived on a small island with a high dependency on marine and tidal zone fauna, populations were more affected by sea level changes rather than other climactic variations following the LGM.

By preference the occupants of HSE selected those resources that were abundant and easily collected, such as coastal and marine resources and possibly a few terrestrial fauna (snakes and bats), with dietary variation probably occurring as foraging efficiency changed following a shift in climate (Pyke 1984; Burroughs 2005; Lupo 2007; Allen and O'Connell 2008; O'Connell and Allen 2012). High exploitation of tidal zone fauna at HSE, especially urchins, during Phase 1 and 2 (16-9.5 ka) was probably attributable to the ease with which they could be exploited. Burroughs (2005) refers to these tidal communities as "fast foods" because of their abundance and their ease of collection. As suggested by Allen and O'Connell (2008) and O'Connell and Allen (2012), these invertebrate tidal communities provided hunter-gatherer communities (particularly those on small islands) with high optimal foraging opportunities because of a combination of initial high abundance and the low harvesting costs that produced high net returns of protein. As noted above, this heavy dependence on coastal resources, especially in shellfish *(Mollusca),* barnacles *(Maxillopoda)* crabs *(Malacostraca),* and sea urchins *(Echinodermata)* is seen throughout the Wallacean archaeological record at sites such as Golo Cave (Bellwood et al. 1998; Szabó, Brumm, and Bellwood 2007), Tron Bon Lei (Samper Carro et al. 2016; Samper Carro, Louys, and O'Connor 2017), Asitau Kuru (O'Connor 2007), Lene Hara (O'Connor et al. 2010), and Leang Sarru (Tanudirjo 2001, 2007).

The most intense human occupation at HSE occurs during Phase 2 and coincides with a decline in sea urchin exploitation, and significant increases in crab remains. The decline in the exploitation of sea urchin could be linked with an increase in local crab populations in the wake of sea-level change, resulting in crab over-predation of sea urchins and/or resource competition between sea urchins and crabs (Parker and Shulman 1986; Siddon and Witman 2004). However, other scenarios are also possible. The phenomenal rate of sea level rise during the Meltwater Pulse (MWP)[6] 1A between 14.6 ka and 14.3 ka, might have disrupted urchin communities or the algal communities that formed their primary food sources, making crab exploitation more viable for the human population using HSE. Alternatively, it might simply be that the initial heavy predation of sea urchin habitats near the HSE shelter led to the overexploitation of this resource. Deciding between these scenarios is not possible at this time but might be able to be addressed in the future by finer scaled taxonomic identification of the sea urchin and crab assemblages.

Fish exploitation at HSE is the highest among all other vertebrate fauna. Higher concentrations of *Actinopterygii* (bony fishes) remains coupled to a greater abundance of *Carcharhinidae* (requiem sharks) in Phase 2 compared to other occupation phases and indicates the intensiveness of the fishing activities by HSE inhabitants during this period. The south coast of Kisar has a steep drop off (Major et al. 2013), coupled with the presence of a considerable sea channel between Kisar and Timor, presumably makes for rich near-shore fishing conditions. Intensive fishing activities at HSE are also supported by the presence of shell fish-hooks that have been recovered from most phases of occupation, with largest numbers recovered in Phases 2 and 3 (O'Connor et al. 2019). Interestingly, while fish exploitation peaks in Phase 2, it remains comparatively high during Phase 3, corresponding to this abundance of

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[6] A Meltwater Pulse (MWP) is a rapid deglaciation period causing a corresponding rapid rise in sea levels. MWP phase 1A (MWP 1A) led to the rises in sea levels of approximately 20 m over less than 500 years (Weaver et al. 2003). MWP 1A is contemporaneous with the onset of Bølling-Allerød period.

fish-hooks and perhaps indicating continued and increasing reliance on this marine resource as other tidal and terrestrial options declined. An abundance of sharks, that often operate along the reef edge, during Phase 2 could be related to the lower, but rising sea levels of the terminal Pleistocence when reef edge habitats were closer, compared to the higher sea levels and more extensive reef platforms of the Holocene period (Leavesley 2007).

Analysis of the terrestrial faunal assemblage suggests minor foraging in this zone at HSE compared to the marine and tidal ecosystems. This is understandable given Kisar's small size that strongly limits terrestrial faunal diversity and abundance (Natus 2005; Maryanto and Higashi 2011). However, the avians, herpetofauna, and small mammals could provide scientists with important information for reconstructing Kisar's palaeoenvironment and climate (Gleed-Owen 1998). While the species make-up of small island ecosystems is often attributed to dispersals from neighbouring islands and continents, their long-term survival and adaptations can provide details on the island's palaeoecology (Koch et al. 2009; MacArthur and Wilson 1967).

We recognize that certain small- to medium-sized terrestrial animals can be deposited in cave sediments by non-anthropogenic causes, such as avian predation (Hawkins et al. 2018). However, it cannot be ignored that in certain places small mammals, amphibians, and reptiles are also consumed with regularity by humans (White 1972; Leavesley 2004; Hawkins, O'Connor, and Kealy), especially in regions with limited terrestrial resources. In line with the zooarchaeological findings of Tron Bon Lei (Samper Carro et al. 2016), bone remains at HSE also have variations in colour between brown, black, grey, and white. Although there is a possibility that discoloration is attributable to natural oxidation, the alternative hypothesis that the majority are the direct result of either cooking or incidental burning, is favoured here; suggesting an anthropogenic origin for much of the bone.

During the Pleistocene (Phases 1 and 2), snake and bat remains dominate the terrestrial faunal assemblage followed by birds and lizards (Figure 7). Snakes and lizards are known for their adaptability that allows them to survive in harsh environmental conditions (Shine and Bull 1979). This adaptability could have resulted in greater populations of these reptiles during periods of climatic disturbance. Rodents are completely absent from the Pleistocene record at HSE, with the notable exception of spit 17, coinciding with the peak of occupation, and later in very small proportions from spits 13 and 12 (Phase 2; Figure 7). The appearance of rodent remains in spit 17 could indicate increased diet breadth in relation to increased occupation intensity. Although there has not yet been a detailed taxonomic identification of the rodent remains at HSE, the gradual increase in rodents in the terminal Pleistocene to early Holocene levels likely reflects an increase in forested environments proximal to the shelter in the wake of increased temperatures and rainfall of the Younger Dryas in the region (Ayliffe et al. 2013).

The sudden fall in occupation intensity in Phase 3 at HSE (12.7-9.5 ka) occurs at relatively the same time as the Younger Dryas and follows a sudden fall in delta Oxygen-18 isotopes ($\delta^{18}O$) recorded on Flores (Ayliffe et al. 2013). While a marked decline in weights is recorded for all faunal groups, the proportions of fish bones remains high compared to the other faunal groups. Instead, non-fish coastal and terrestrial faunal abundances show very low levels of deposition.

The warmer, wetter conditions recorded during the Younger Dryas climactic period (Ayliffe et al. 2013) could have impacted on faunal abundance, favouring some groups over others (Hewitt 2000), besides changing non-faunal elements of the ecosystem (Russell et al. 2014). Alternatively, overexploitation of particular resources during the previous, intense occupation period, could also have stressed this insular and depauperate ecosystem beyond its ability to recover, particularly in the face of climate change. The human community at HSE might have therefore been forced to rely on alternative resources, possibly encouraging a simultaneous decline in occupation intensity. Alternatively, changing food preferences and improvements in animal capture technologies such as developments in traps and nets, could have precipitated this shift in subsistence focus. While changing patterns in land-use could have reduced occupation, and hence deposition, at HSE.

Interestingly, the Flores climate record shows a sudden spike in $\delta^{18}O$ levels towards the end of the Younger Dryas, suggesting a short, abrupt climate shift towards cooler, dryer weather (Ayliffe et al. 2013). This peak in $\delta^{18}O$ is quickly followed by a rapid and continuous decline until about 7 ka when the warmer, wetter conditions of the Holocene begin to stabilise (Ayliffe et al. 2013). These sudden shifts between climactic extremes during Phase 3 of occupation at HSE could have forced a declining population, already struggling with less favourable conditions, to abandon the site completely. The fall in occupation intensity at HSE during this period can also be related to a scarcity of water that is more critical than temperature to organism survival (De Monocal 2001). The dominance of limestone geology on Kisar (Major et al. 2013) makes freshwater hard to find even today (personal observation Kaharudin), however climactic extremes and drier conditions probably exacerbated the situation.

The inhabitants of HSE could have moved to other locations on Kisar or neighbouring islands such as Timor, Wetar, Romang, or Leti in order to have access to more reliable water and food resources. The maintenance of the relationship between Kisar and Timor can be found in the rock art, oral history, language, and place names that are used together (O'Connor and Ono 2013; O'Connor et al. 2018). Considering their developed seafaring culture (O'Connor, Ono, and Clarkson 2011) and indisputable evidence of the maritime transportation of obsidian between islands in the Lesser Sunda found by Reepmeyer et al. (2016, 2019), early and continuous cultural linkages between the two islands have been demonstrated. Such an abandonment scenario would account for the hiatus in the record, with reoccupation only occurring after climate stabilisation in the Mid- to Late Holocene and supported by the later arrival of Neolithic cultures. Despite likely increases in periodicity during the late Holocene (Gagan et al. 2004), the more massive extremes in climate change experienced globally during the last thousand years of the Pleistocene are largely absent during the Holocene, indicating that sea levels and perhaps climate was comparatively more stable during this time (Richerson, Boyd, and Bettinger 2001).

The final occupation phase at HSE (4) records reoccupation at 5 ka as the climate stabilised after the Younger Dryas and post-Dryas peak (Ayliffe et al. 2013). The level of exploitation of coastal fauna is fairly similar to the initial occupation phase with high sea urchin exploitation. The increase in sea urchin immediately after the hiatus could reflect the re-establishment of this resource on the rocky platforms in proximity to the site after a long period when no exploitation occurred. With the exception of turtle, all marine resources decline in the last phase of occupation at HSE, coinciding with the densest deposits of pottery. The fishing intensity declined continuously with skeletal elements found only occasionally. The lower relative abundance of *Actinopterygii* remains recovered from Phase 4 is probably the result of less intensive human settlement at the site, reflected in a decline in fishing during the late Holocene after reoccupation in the mid-Holocene.

In this final occupation phase at HSE, we also see an increase in rodents and the arrival of shrews and dogs, indicating a major change in site use with the arrival of pottery technology and exotic fauna. While at present we do not have complete taxa identifications for the rodents, their increase in Phase 4 likely reflects the introduction of exotic species and an increase in diversity as well as abundance. Preliminary identifications of this late Holocene occupation level (Phase 4) indicates the presence of *Rattus exulans* and *R. rattus* (O'Connor et al. 2019; personal observation Hawkins), both exotic to the island and probably incidental translocations arriving with new migrants in the last 2.5 ka. These rats have been shown to thrive in close relationships with humans and disturbed/agricultural habitats (Kirch et al. 2015). The distribution of rats is also often associated with the movement of people (Mahirta et al. 2004; Aplin et al. 2011). This is further supported by the presence of shrew, a mainland Southeast Asia species thought to be translocated by people, also in the last three spits of Phase 4. Dogs also appear for the first time alongside the shrews, probably introduced as a commensal domesticate during the Late Holocene. The earliest dog specimen in the region is from nearby Timor-Leste, dated at around 3 ka cal BP (Gonzalez et al. 2013).

CONCLUSION

Here we investigated how human prehistoric settlements developed on small islands during the profound changes in climate during the Pleistocene-Holocene transition and into the Holocene. We have done so by examining the archaeological record from Here Sorot Entapa rockshelter on Kisar Island in combination with the palaeo-environmental data from Flores, in the Lesser Sunda Islands of Eastern Indonesia. Our findings follow and complement the story of initial human migration and subsistence adaptations within this insular region as early modern humans migrated east of Sunda, penetrating the water barriers of Wallacea.

The necessity of having maritime technologies for prehistoric travel and resource collection on small islands is clear. Marine and coastal ecosystems are profuse in the Wallacean Archipelago, making these resources more favourable for exploitation than the more limited and less reliable terrestrial options. While there is no significant correlation between specific climatic conditions and human settlement intensity at HSE, the fluctuations in global climate clearly influenced the selection and development of subsistence strategies. Climate change is seen to precipitate strategy change.

HSE is one of many sites at which occupation either began or increased following the LGM. Changes in the intensity of occupation and diet could be linked to environmental factors that were notably unstable during the terminal Pleistocene to mid-Holocene. The peak in occupational intensity at HSE (14.5-12.8 ka), coincided with a dryer, cooling Bølling-Allerød climactic period and pronounced sea level rise. Conversely, decreasing intensity of occupation (11.3 ka) followed by site abandonment (9.5 ka) could have been the result of climactic upheavals that probably led to the instability of reef habitats during and immediately following the Younger Dryas. Fishing was the prime subsistence activity both before site abandonment and again following reoccupation, with the exploitation of sharks decreasing as the reef stabilised and the edge moved farther from the focal point of fishing activity.

Changes in the terrestrial faunal composition indicate that island terrestrial habitats could also have been in a state of flux during the Younger Dryas. Snakes dominated the terrestrial faunal assemblage during the terminal Pleistocene to early Holocene, but once settlement was re-established at HSE, rodents and shrews dominate. This could have been the result of a combination of factors including increased forest habitat in the early Holocene as wetter and warmer conditions prevailed. In the final phase of occupation at HSE exotic rodents, shrews and domestic species were probably introduced either deliberately or accidentally by Neolithic human migrants, as indicated by the appearance of pottery at HSE during the late Holocene.

List of abbreviations

AISM	: Australian-Indonesian Summer Monsoon
B-A	: Bølling-Allerød
CI	: Confidence Interval
EASM	: East Asian Summer Monsoon
g	: gram
HS1	: Heinrich Stadial 1
HSE	: Here Sorot Entapa
ISEA	: Island Southeast Asia
ka	: kilo annum, or ‘thousand years’ signifies “thousand calendar years ago”
LGM	: Last Glacial Maximum
MNI	: Minimum Number of Individuals
MWP	: Meltwater Pulse

NISP : Number of Identified Specimens
Sp. : spits
YD : Younger Dryas

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APPENDIX

Table A1. Zooarchaeological material recovered from HSE-B. Weights adjusted according to corresponding spit weight. All values are in grams (g). For raw data see O'Connor et al. (2019).

Phase	Spit	Spit Weight	Mollusca	Maxillopoda	Echinodermata	Malacostraca	Actinopterygii	Chondrichthyes	Testudines	Serpentes	Lacertilia	Aves	Chiroptera	Rodentia	Soricidae	Carnivora	Tetrapod	Unidentified	Human
P 4	1	64840	363.819	95.157	0.278	0.162	0.79	-	-	0.054	0.147	0.1	0.062	0.162	-	0.015	0.362	0.247	-
	2	64245	126.352	46.782	0.397	0.272	1.178	-	-	0.023	0.918	0.521	0.023	1.494	0.047	0.335	0.537	-	-
	3	63960	513.602	150.876	0.407	40.228	17.814	-	4.651	1.102	0.43	1.345	0.031	2.001	0.024	1.313	0.758	0.367	-
	4	46450	727.557	204.521	8.913	54.532	53.91	0.043	1.313	2.045	0.054	0.205	0.032	0.592	-	-	1.303	0.646	-
	5	39980	686.093	206.853	6.141	28.452	74.938	-	3.664	1.563	0.075	0.188	0.025	0.338	-	-	0.325	0.05	-
	6	64230	347.781	183.092	3.285	9.474	24.236	-	2.226	0.311	-	-	-	0.226	-	-	0.101	0.358	-
P 3	7	28885	555.046	194.392	1.679	4.501	77.88	-	1.194	0.173	-	0.225	-	0.641	-	-	0.121	0.19	-
	8	44445	174.148	57.667	0.236	3.206	66.087	-	0.394	0.056	-	0.034	-	0.371	-	-	0.574	-	-
	9	29860	168.336	11.303	0.017	16.544	83.448	-	-	0.167	-	-	-	0.318	-	-	0.117	-	-
	10	49240	436.566	82.89	0.579	46.974	119.463	0.091	0.02	0.305	-	0.538	0.01	0.254	-	-	0.295	-	0.264
P 2	11	42150	817.544	265.561	0.047	32.669	61.205	0.024	0.35	0.593	-	-	-	-	-	-	0.107	-	-
	12	41465	3459.954	1005.909	1.507	60.847	145.446	0.446	3.159	5.547	0.024	0.036	0.084	0.048	-	-	1.23	-	-
	13	43975	3034.497	906.958	1.145	109.653	85.645	0.315	0.159	6.64	0.05	0.057	0.637	0.011	-	-	0.523	1.637	-
	14	41495	1954.537	618.147	0.41	56.814	68.746	0.036	0.398	7.145	0.048	-	0.289	-	-	-	0.313	0.422	-
	15	37565	3000.679	1151.338	2.037	89.951	103.033	0.359	0.146	15.666	0.013	0.04	0.053	-	-	-	0.067	0.652	-
	16	41390	2849.191	996.618	1.136	157.683	139.472	0.471	0.966	10.437	-	0.024	0.012	-	-	-	0.447	-	-
	17	74710	6712.823	2099.632	6.887	338.683	221.312	0.435	9.002	11.183	0.127	0.341	0.375	0.107	-	-	1.807	0.964	0.743
	18	40450	2181.867	1576.02	8.27	220.816	101.012	0.012	-	1.829	0.062	0.556	-	-	-	-	-	0.173	-
	19	50825	1195.514	673.881	4.624	59.912	53.931	0.01	-	0.728	-	0.128	-	-	-	-	-	-	-
P 1	20	32095	859.526	60.57	36.423	8.008	73.736	0.28	-	1.776	0.249	0.374	0.016	-	-	-	0.608	0.374	-
	21	82770	518.6	7.044	15.036	4.023	42.882	0.073	-	0.646	0.024	0.036	0.018	-	-	-	0.024	-	-
	22	68430	752.594	4.998	11.735	0.227	48.531	-	2.309	0.307	0.022	0.073	0.161	-	-	-	0.073	0.351	-
	23	36080	579.282	11.1	8.855	1.968	37.421	-	0.832	0.291	0.042	0.014	0.014	-	-	-	0.152	-	-
Sterile Layer	24	124954	108.78	0.304	-	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer	Sterile Layer
	25	163850	115.96	2.2	0.006														