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# Human Palaeoecological Interactions and Owl Roosting at Tron Bon Lei, Alor Island, Eastern Indonesia

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## ABSTRACT

*We report on tetrapod (Reptilia, Amphibia, Mammalia, Aves) vertebrates recovered during excavations at Tron Bon Lei rockshelter on the south coast of Alor Island, eastern Indonesia. These include both archaeological specimens recovered from a 1 m<sup>2</sup> test pit dating from ~21 kya cal BP to the late Holocene, and a modern eastern barn owl deposit recovered nearby. To discern between the depositional processes that accumulated the small numbers of micro- and macrovertebrate remains from the archaeological deposits, the taphonomic signature of the natural assemblage was quantified and compared to the archaeological record. The taphonomic data indicates that the tetrapod archaeofaunal remains are a combination of barn owl predation of microfauna and human predation of larger fauna. This approach*

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Color versions of one or more of the figures in the article can be found online at <http://www.tandfonline.com/uica>.

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*provides new information on human-tetrapod interactions on Alor in Wallacea during the late Quaternary, including an apparent increase in cave site use and hunting intensity during the Pleistocene-Holocene transition, sea turtle butchery and probable transport, and extinctions of previously unknown giant to large rat species.*

**Keywords** Pleistocene-Holocene transition, vertebrates, taphonomy, Alor Island, Wallacea

## INTRODUCTION

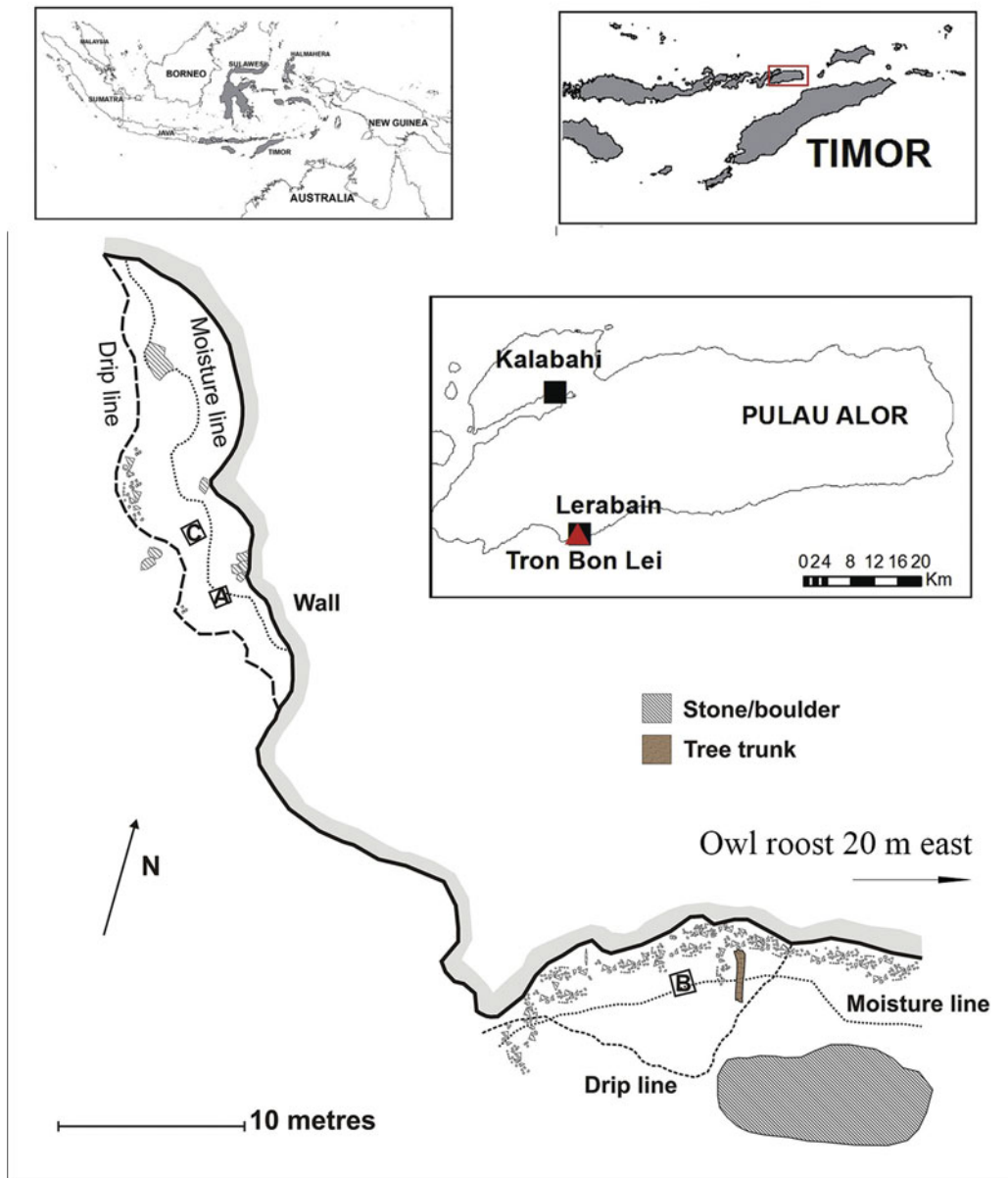
Archaeofaunal sequences from caves and rockshelters have been used as proxies for palaeoecological conditions during hominin settlement of Island Southeast Asia (ISEA) (e.g., Barton et al. 2013; Morwood et al. 2008; O'Connor and Aplin 2007; Piper and Due 2006; Stimpson 2012, 2013; van den Bergh et al. 2009). Such environmental reconstructions also provide data pertinent to hominin occupation sequences in relation to site formation processes and subsistence. Despite some attention in Asia, few reconstructions from long archaeological sequences are available for much of the insular Wallacean region (Timor, Lesser Sunda Islands, Sulawesi, and Halmahera). This region, through which hominins traversed by conducting water crossings since at least ca. 900 kya (Brumm et al. 2010), has never been connected to a continental land mass. Many of the islands are relatively poor in terrestrial native fauna because water crossings act as barriers, limiting movements of terrestrial taxa (MacArthur and Wilson 1967; O'Connor and Aplin 2007).

Despite these limitations, fossil and archaeological sites in Wallacea indicate that a greater diversity of larger bodied native terrestrial fauna were once coeval with hominins (e.g., Brumm et al. 2010; Dennell et al. 2014; Glover 1986; van den Bergh et al. 2016). For example, *Homo floresiensis* inhabited a grassland environment around Liang Bua ca. 100–60 kya, potentially exploiting megafauna such as stegodon, Komodo dragons, and giant storks as well as a number of giant rat species (Sutikna et al. 2016; van den Bergh et al. 2009). Declines in terrestrial faunal diversity are reported from Wallacea from before the time *Homo sapiens* first arrived in the

region (e.g., Louys et al. 2016; van den Bergh et al. 2009), such that by the time of their arrival the only terrestrial resources available to first *H. sapiens* appears to have been rodents, medium to small reptiles, birds, and amphibians. Thus, with the exception of a few inland sites on Timor (Aplin and Helgen 2010; Glover 1986; O'Connor and Aplin 2007) and Sulawesi (Simons and Bulbeck 2004), subsistence behaviors of early modern humans in Wallacea appear to have focused on marine resources, even in the earliest occupation levels sampled (O'Connor et al. 2011; Samper Carro et al. 2016; Sazbó and Amesbury 2010).

Microvertebrates are by far the most common component of the terrestrial faunal record recovered from most archaeological sites in the ISEA region. For example, Niah Cave on Borneo (Sarawak) has preserved thousands of bat, bird, and small murid remains in association with human settlement dating back 50 kya (Stimpson 2012, 2013). The dominance of microvertebrates in archaeological deposits should be particularly pronounced on islands which lack large- or medium-bodied native terrestrial faunas, such as the many isolated oceanic islands of Wallacea (Figure 1). Indeed, cave sites such as Liang Bua on Flores (Indonesia) (Piper and Due 2006; van den Bergh et al. 2009), Uai Bobo 1 & 2 in Timor-Leste (Glover 1986), Sulawesi sites (Simons and Bulbeck 2004) and Tron Bon Lei on Alor (Samper Carro et al. 2016) all have tetrapod assemblages dominated by microfauna.

Ethnographic accounts indicate that historic communities in some parts of Indonesia utilized small fauna for food (e.g., Wadley and Colfer 2004), and this likely occurred throughout the past. However, difficulties in recognizing and excluding



**Figure 1.** Map of Island Southeast Asia and Wallacea (upper left), showing Wallacea and the lesser Sunda Islands in eastern Indonesia (upper right), the location of Tron Bon Lei in Lerabain village on Alor island (center), and Tron Bon Lei rockshelter site plan (below).

natural processes in microfaunal accumulations in cave and rockshelter archaeological sites are well documented, particularly through taphonomic studies from other parts of the world (e.g., Fernández et al. 2012; Nel and Henshilwood 2016). Nevertheless, very few such studies have been conducted in the faunally depauperate Wallacean islands. Important exceptions are the studies of small murid and swiftlet remains from Liang Bua on Flores, which were found to be digested by avian predators (Meijer et al. 2013; Piper and Due 2006).

Recent research of archaeofaunal deposits from the Tron Bon Lei (TBL) rockshelter on Alor Island, in the Lesser Sunda islands of eastern Indonesia (Figure 1), recovered a predominantly marine record (Samper Carro et al. 2016), with fishing for carnivorous and herbivorous reef fish fluctuating over time and in response to changing marine ecologies and/or cultural practices during the Pleistocene-Holocene transition (Samper Carro et al. 2016). Only small quantities of marine turtle, human remains, and terrestrial microvertebrates were reported from the TBL assemblage, including small rodents (Muridae), lizards (Lacertilia), snakes (Serpentes), frogs/toads (Anura), fruit bats (Pteropodidae), microbats (Yangochiroptera), and several species of bird (Samper Carro et al. 2016).

Here we examine the tetrapod vertebrate remains from TBL to inform on site formation processes, prehistoric human rockshelter use, and palaeoecological interactions during the late Quaternary. This was facilitated by the discovery of a modern eastern barn owl (*Tyto alba delicatula*) roost deposit in the TBL rockshelter, which provided us with the unique opportunity to quantify natural taphonomic processes occurring in the very same locality as the archaeological deposit. We predict that the archaeologically deposited fauna will differ from the natural deposit. We assess taxonomic identity, skeletal element survivorship, bone breakage, and bone surface modifications from these two assemblages in an effort to establish criteria to distinguish human from a naturally accumulated baseline of terrestrial tetrapod remains. In

the natural assemblage, taxonomic composition is expected to be more specialized on the most abundant small taxa within the barn owl predation range, bone breakage and loss to be much less pronounced, and light digestion patterns to be present in low frequencies on skeletal specimens. Conversely, human predation is likely to be focused on larger taxa that fall outside the size range of barn owl predation, have increased rates of burning, butchery marks, and display no signs of digestion.

## GEOGRAPHIC SETTINGS

Alor is a small island ( $82 \times 30$  km) on the eastern end of the outer Bunda volcanic arc of the Lesser Sunda Chain (Figure 1). It is largely comprised of deeply incised, mountainous volcanic breccias, agglomerates and tuffs, with the only significant limestone terraces restricted to the north of the island (Heering 1941). TBL comprises a series of small rockshelters and shallow but high caves on the southern and western aspects of an agglomerate outcrop. The local environment is comprised of almost completely open schlerophyll woodlands and grasslands.

## MATERIALS

### Test Pit B Tetrapod Archaeofauna

Three 1 m<sup>2</sup> test pits were excavated in TBL, with Test Pit B yielding the larger amount of archaeological material. Archaeological deposits of Test Pit B had been excavated in 5 cm (approximately) levels down to the bedrock base at a depth of c. 3.2 meters. All material from the deposit was wet sieved through a 1.5 mm mesh ensuring fine grained recovery of small vertebrate skeletal elements. Thirteen stratigraphic layers, containing features such as hearths, shell accumulations, white ashy lenses, and a secondary burial, were recorded in Test Pit B, from which 24 radiocarbon dates were obtained (Samper Carro et al. 2016). The chronostratigraphic sequence defined three



major occupation phases: the youngest phase, comprising layers 1 to 5 and dated to the late Holocene (3010–4090 cal BP); an intermediate phase, with layers 6 to 11 covering the early Holocene to the late Pleistocene (7440–12,545 cal BP); and an older occupation, consisting of layers 12 and 13, dated to 18,890–21,000 cal BP. Detailed analysis of the vertebrate material from Test Pit B revealed that the assemblage was dominated by fish remains (Samper Carro et al. 2016), with the small component of terrestrial fauna and marine turtle fauna presented in this article.

### Owl Roost Surface Accumulation

A faunal assemblage was recovered from a modern owl roost deposit from a surface area measuring approximately 180 × 120 cm in size approximately 20 m east of Test Pit B (Figure 2). All pellets had broken up and decomposed to their constituent components. All material was collected from the surface of the floor with a brush and pan and sieved through a 1.5 mm sieve in an identical fashion to the archaeological material. A barn owl was observed in residence above the deposit but flew away before it could be pho-

tographed. Trainor et al. (2012) identified the eastern barn owl (*Tyto alba delicatula*) as present on Alor, and it is likely that this subspecies was responsible for the TBL microvertebrate surface deposit.

## METHODS

Standard taphonomic practices developed for the analysis of small mammal deposits in caves were employed (Andrews 1990). Taxonomic identifications of archaeological and modern owl deposits were based on morphological comparisons with reference specimens housed at The Australian National University Archaeology and Natural History Osteology Laboratory. The assemblages were quantified using number of identified specimens (NISP), minimum number of elements (MNE) and minimum number of individuals (MNI) (Lyman 2008). MNE was calculated by manual overlap of the most frequent skeletal portion and diagnostic zone, while MNI was calculated based on the most frequent sided skeletal element. Vertebrae were identified to atlas, axis, cervicals 3–7, thoracic, lumbar, sacral, and caudal vertebrae to give more resolution on skeletal vertebra loss along the



**Figure 2.** The owl roost deposit in situ on the surface of Tron Bon Lei.

axial skeleton. Taxonomic diversity was assessed by considering richness (the number of taxa present; NTAXA) and quantifying evenness of the relative abundance (NISP) of quantified taxa using the Shannon-Wiener diversity index (Keylock 2005). Evenness values close to zero indicate faunal abundance was concentrated on few taxa (specialized predation) whereas values closer to 1 indicate a more even spread over a wider range of taxa (generalist predation).

Skeletal element loss was assessed by the percentage of bone survivorship using the following formula:  $MNEi / (Ei \times MNI) \times 100$ , where MNEi is the minimum number of skeletal elements recorded for each skeletal element and Ei is the expected number of each element per individual (MNI). Murid postcranial and cranial proportions were investigated using three indices after Andrews (1990):

Index 1:  $[(\text{femur} + \text{tibia} + \text{humerus} + \text{radius} + \text{ulna}) / (\text{mandible} + \text{maxilla} \times 0.625)] \times 100$

Index 2:  $[(\text{humerus} + \text{femur}) / (\text{mandible} + \text{maxilla})] \times 100$

Index 3:  $[(\text{femur} + \text{humerus}) / (\text{tibia} + \text{radius})] \times 100$

Index 1 indicates the proportions of long bones to cranial material, Index 2 the ratio of upper limb bones, femora, and humeri to cranial material, and Index 3 was used to show the relative proportions of upper and lower murid long bone elements.

Skeletal element breakages were examined by proportions of complete, proximal, shaft and distal long bones as well as skull breakage, after Andrews (1990), where complete skulls, maxillae with and without zygomatic arches, and mandibles with or without ascending ramus were all recorded, as was maxillary and mandibular molar and incisor loss.

Bone modifications were recorded after observing each individual specimen under a binocular microscope (Zeiss Stemi 2000-C W-PI, 10×/23 magnification) for signs of digestion, burning, color, and predation (tooth punctures). Digestion was recorded based on distinctive pitting morphology

and patterning that differs from weathering and burning. Digested pitting appears as localized rounded pitting and fissures on articular surfaces of long bones, rather than evenly spread as seen in natural pitting, as limb bone shaft surfaces are resistant to digestion, while rectangular cracking and pitting on occlusal edges of tooth enamel is obvious (Andrews 1990). Degree of pitting and bone penetration was recorded on a scale of 0–4, ranging from 0 (*absent*) to 4 (*extreme*) for long bones and teeth based on the stages set out by Andrews (1990). This is important for determining specifically the avian predator, all of which have different feeding behaviors and digestive tracts with varying degrees of enzyme strength. However, most of the bones had some degree of carbonate coating of the outer surface making observation of these modifications difficult. Carbonate encrustation was especially thick and prevalent on the bone from Layer 12, and less concentrated for Layers 8–9.

Methods of recording signs of burning, cut marks, and color were conducted in accordance with those used on the adjacent archaeological material (Samper Carro et al. 2016). Burning was investigated based on hexagonal pitting, cracking, and shrinkage morphology on bone surfaces, as well as color whereby blackened bones imply carbonization from lower temperatures while calcined white blue/grey indicates bones burnt at higher temperatures (Nicholson 1993; Shipman et al. 1984).

Finally, to investigate changes in prehistoric human hunting behavior at TBL relative to owl roosting during the Pleistocene and Holocene, we created a hunting abundance index:

$$\{(\text{marine turtle} + \text{giant rat} + \text{Pteropodidae NISP}) / (\text{Owl roost NISP} + \text{marine turtle} + \text{giant rat} + \text{Pteropodidae NISP}) \times 100\}.$$

This was calculated for each archaeological layer, allowing us to examine any trends in hunting behavior relative to owl predation over time. Change was quantified statistically using Cochran's test of linear trends (Zar 2010).

## RESULTS

### Test Pit B Tetrapod Archaeofauna

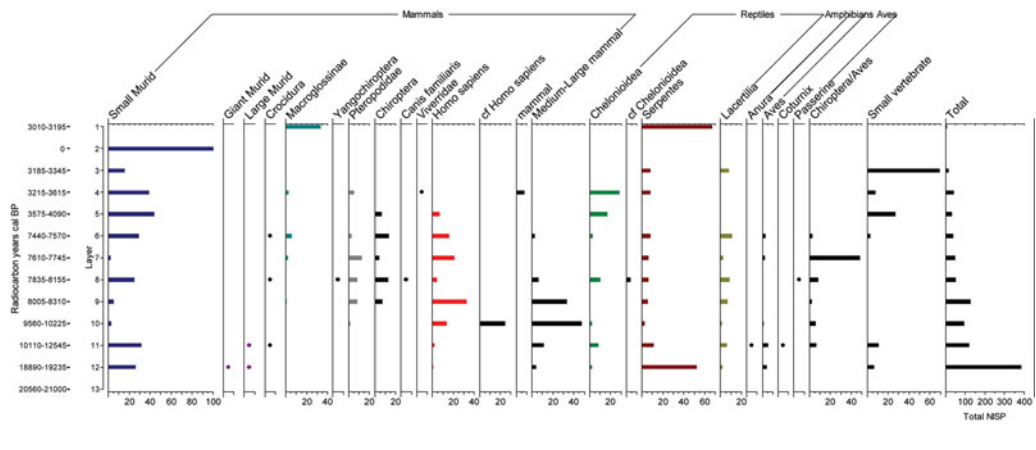
**Taxonomic Composition.** A total of 939 tetrapod remains weighing 220.73 grams were recorded from the archaeological deposits in Test Pit B (supplemental [SI] Table 1, available online). Most of the vertebrate material was concentrated in Layer 12 (NISP = 384) a ~45 cm thick Pleistocene deposit dated between 18,890 and 19,925 cal BP (Figure 3). Abundance appears to decline quite dramatically for the succeeding layers (11–1). Tetrapod vertebrate material was not identified from the basal Layer 13.

At least sixteen distinct taxa (10 mammalian, 3 reptilian, 1 amphibian, 2 Aves) were identified (Figure 3, SI Table 1, available online). Mammal taxa include at least three species of rat based on size (small, large, and giant). Large rat (Layers 11–12) and giant rat specimens (Layer 12) were few and most likely represent species that have gone extinct sometime during the terminal Pleistocene to Holocene. Formal taxonomic treatment of these species will be published elsewhere. Small quantities of shrew (*Crocidura* sp.), a dog (*Canis familiaris*) incisor from Layer 8, and a civet (Viverridae) cervical vertebrae from Layer 4 were also present. At least three bat taxa were recorded based on small quantities of chiropteran remains, including those of a large fruit bat (Pteropodidae), a smaller blossom fruit bat (Macroglossinae), and a microbat (Yangochiroptera). Human remains were also recovered from sieved material from Layers 5–12. Most of these include neonatal human skeletal material present in Layers 9–10. Reptilian taxa include marine turtle, present in small numbers from Layers 4–12, and small lizards (Lacertilia) and snakes (Serpentes) were also present throughout the deposit. Amphibians include anuran remains present only in very small numbers in Layer 11. Avian remains were only present in very small quantities and include only two identified taxa, quail (*Coturnix* sp.) and song bird (Passerine).

While the number of taxa per layer does not significantly change over time ( $r_s = 0.35$ ,  $p = 0.22$ ), there were some significant changes in taxonomic diversity (SI Table 2, available online). The evenness values of each taxon showed a strong negative correlation by layer indicating that there was a significant decline in evenness (e), or generalized foraging, with increasing age ( $r_s = -0.90$ ,  $p = 0.00002$ ) (SI Figure 1, available online).

**Skeletal Element Survivorship.** The small murid skeletal elements appear to have suffered from significant post-depositional bone destruction, judging by the high proportion of element loss (SI Figure 2 and SI Table 3, available online). Mandibles, tibiae, and incisors dominate the assemblage, but 20% of maxillae, humeri, femora were also present. Vertebrae, ribs, scapulae, ulnae, radii, and pelves were all under-represented while tarsals/carpals and metapodia were mostly absent. The proportion of postcranial to cranial skeletal elements indicates that postcranial elements survived in greater proportions, although the upper limb/crania index indicates that maxillae and mandibles survived in greater proportions than upper long bones (humeri, femora), while the upper limb/lower limb index indicates that upper limbs survived in greater proportions to lower limbs (SI Table 4, available online). Snakes were represented by vertebrae and ribs only. Marine turtle elements were dominated by shell (carapace, plastron) fragments and phalanges, with very few long bones, skull, and vertebrae fragments (SI Table 5, available online). The few giant rat skeletal elements are incisors and molars with no long bone fragments. Large pteropids were represented mostly by wing long bone elements (clavicles, humeri, radii, metacarpals, phalanges) and mandibles, with lower limb bones, crania, and vertebrae absent (SI Table 6, available online). The few smaller Macroglossinae elements were represented by mandibles and a single humerus only. Human neonate skeletal material from Layers 9–10 consists mostly of vertebrae and long bones





**Figure 3.** Tilia diagram showing the distribution of relative taxonomic abundance (%NISP) by Layer and time period (years cal BP), Tron Bon Lei Test Pit B.

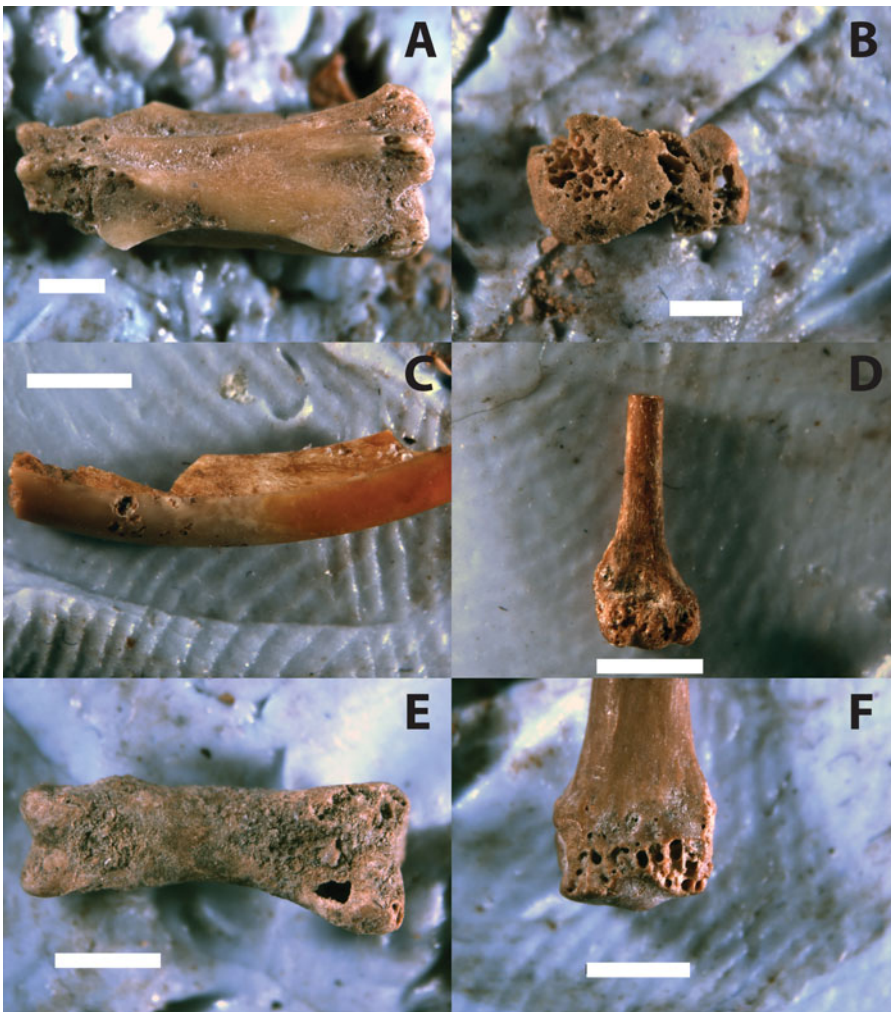
(humerus, radius, phalanges) as well as a carpal/tarsal, rib and teeth.

**Bone Breakage.** The archaeological tetrapod vertebrate assemblage suffered extensive breakage over the course of the sequence. Although many of the tetrapod skeletal elements were complete (21.41% of NISP), the high survivorship of dense, compact snake vertebrae inflates this number, which had by far the highest proportion of complete skeletal elements (SI Table 7, available online). Small murid crania and long bones are characterized by few complete elements and extremely high rates of fragmentation (SI Table 8, available online).

**Bone Modifications.** Signs of butchery were not present on any specimens. However, digestion of small murid, snake, lizard, bird, and blossom fruit bat skeletal material was consistent throughout most of the layers in varying proportions (Figure 4, and SI Tables 7 and 9–10, available online). There were no cases of extreme digestion and fewer cases of heavy digestion, and the mostly absent to light-moderate digestion patterns (SI Table 10) indicates a predator with weak digestive acid consistent with that of the barn owl (see Andrews 1990). Digestion was not observed on any

of the turtle, giant rat, or large fruit bat remains.

Many of the bones appear black or grey/white/blue (approximately 15.6% of total non-fish NISP) suggesting that they were potentially burnt either before or after deposition (SI Table 7). Discoloration appeared visible on most taxa but was higher for unidentified chiropteran and bird fragments, large fruit bats, giant rat, and turtle remains, but was also consistently observed on snake, small murids, and other microvertebrate remains. Microvertebrate material showed no obvious signs of shrinkage and cracking consistent with burning. This includes some microvertebrate material that also showed signs of discoloration and digestion, indicating either post deposition burning or chemical staining. A single human bone fragment from Layer 9 appeared blackened, but otherwise all other human remains appear unaffected by heating. The sea turtle remains, on the other hand, appeared to have suffered a degree of shrinkage and cracking in addition to being carbonized and calcined consistent with burning, especially on the shell and phalanx fragments and a cervical vertebra.



**Figure 4.** Examples of digestion on microfaunal remains from Tron Bon Lei Test Pit B: A) spit 2, layer 2, murid caudal vertebra; B) spit 4, layer 4, murid femur; C) spit 4, layer 4, murid incisor; D) spit 13, layer 6, lizard humerus; E) spit 41, layer 11/12, bird phalanx; F) spit 17, layer 7, bat metacarpal. Scale bar equals 2 mm.

#### TBL Modern Eastern Barn Owl Surface Deposit

**Taxonomic Composition.** A total of 2994 microvertebrate specimens weighing 150.72 grams were identified from the owl roost, of which over 80% were small murids (SI Table 11, available online). This equates to 63.5% of the total MNI composed of

this taxonomic group. We record a greater species diversity of small mammals and reptiles on Alor, where previously only one rodent had been recorded. We also extend ranges on the island for at least three species of rat (*Halomaberrmmys* sp., *Rattus exulans*, *Rattus rattus*), and at least one species of mouse (*Mus* sp.). Small quantities of other mammal taxa were also present in-

cluding two shrew species (*Crocidura* spp.; 2.64%), and several unidentified species of small blossom fruit bats (Macroglossinae; 5.65%). Small amounts of frogs/toads (Amphibia; 2.2%), were recovered, as were reptilian microfauna including at least three species of small lizard (skinks and geckos) based on size and morphology (Lacertilia; 7.09%). Six species of bird (Aves; 1.78%) were identified to genus or order including quail (*Coturnix* sp.), coucal (*Centropus* sp.), at least three species of song bird based on size (Passerines), and finally one unidentified yet distinctive species. These avian taxa are all small-bodied and well within the barn owl's predatory capability and can be found in open grassland to woodland habitats. Only one species each from *Coturnix* and *Centropus* are recorded on Alor; the Brown Quail *Coturnix ypsilophora* and the Lesser Coucal *Centropus bengalensis*, while a wide range of song birds are extant on Alor (Trainor et al. 2012).

These data reveal a diverse diet for the barn owl at TBL, with at least 19 taxa (9 mammals, 3 reptiles, 1 amphibian, 6 Aves) represented, albeit focused mostly on small murids. Quantifying biodiversity abundance based on NISP evenness values,  $E = 0.27$  (Shannon  $H = 1.365$ ), confirms that while the owl diet at TBL was opportunistically diverse, it was specialized mostly on just a few taxa (SI Table 2).

**Skeletal Element Survivorship.** The most frequent murid skeletal elements that survived in the owl roost are mandibles, maxillae, humeri, atli, tibiae, and femora, with significant loss of the other skeletal elements, particularly the smaller phalanges, metapodials, carpals, tarsals, ribs, molars, and thoracic to caudal vertebrae (SI Figure 2 and SI Table 12, available online). This loss is likely attributed to raptor consumption and post-depositional processes with some loss of smaller elements during recovery. This pattern is comparable to typical small mammal element representation reported from barn owl pellet studies from elsewhere (e.g., Andrews 1990; Lyman et al. 2003; Saavedra and Simonetti 1998). The proportion of postcranial to cranial skeletal elements indicates that postcranial el-

ements survived in greater proportions to crania, although the upper limb/crania index indicates that maxillae and mandibles (being denser) survived in greater proportions than dense upper long bones, while the upper limb/lower limb index indicates that upper limbs survived in greater proportions to lower limbs (SI Table 4).

Other taxa had various patterns of skeletal element survivorship and loss. Amphibians (Anura) were missing crania (SI Figure 3 and SI Table 13, available online), probably due to their small and fragile nature. The urostyle was the most frequent anuran skeletal element, but the tibiae, femora, pelves, and radii/ulnae were also well represented. Vertebrae, humeri, sacral vertebrae, and astragals/calcanei were not so well represented, while scapulae, metapodials, and phalanges were absent. Blossom fruit bat elements (SI Figure 4 and SI Table 14, available online) which survived in the greatest abundance were mandibles, while wing elements, clavicles, scapulae, humeri, and radii were well represented as were tibiae. Metacarpals, phalanges, ribs, ulnae, and crania were not well represented in any great proportions nor were lower limb elements, femora, and pelves. Vertebrae were not present at all. Small lizards (skinks and geckos) are also frequent in the assemblage (SI Figure 5 and SI Table 15, available online). Crania and mandibles were present in the greatest frequency by MNE survivorship. Limb bones are present in more modest frequencies (scapulae, pelves, humeri, tibiae, ulnae, radii) while vertebrae, ribs and phalanges were largely missing.

**Bone Breakage.** Bone breakage of murid cranial and postcranial skeletal elements was common (SI Tables 8 and 12). Some crania were completely intact (22.96%), but usually maxillae with intact zygomatic arches (35.56%) were recovered, or maxillae without zygomatic arches (41.48%). Tooth loss was quite low with about 22% molars missing from tooth rows, and the same for incisors from premaxillae. Mandible breakage was also very low with just over 80% of mandibles complete and low proportions of molars and incisors

missing. Postcranial breakage was moderate with proportions of complete long bone elements ranging between 74% and 53% for humeri, ulnae, femora, and tibiae. The upper limb to lower limb index shows that upper limb femora and humeri elements survived in greater proportions to lower limb elements (tibiae and radii), indicating that they may be denser for small murids.

Bone breakage in amphibian skeletal elements varied (SI Table 13), with pelves and humeri largely broken; however, the other skeletal elements had high proportions of complete skeletal elements. Blossom fruit bat skeletal elements had high rates of breakages for skeletal elements that are more fragile, either because they are less dense or more elongated, including crania, phalanges, radii, ribs, and mandibles, while femora, humeri, ulnae, and tibiae had high proportions of completeness (SI Table 14). Lizard skeletal element completeness was high for compact and possibly denser elements such as vertebrae, humeri, pelves, scapulae, tibiae, and ulnae (SI Table 15). Crania and mandibles were quite fragmented, while femora, ribs, phalanges, and radii were moderately fragmented.

**Bone Modifications.** Bone modifications are recorded in SI Tables 11 and 16–19, available online. No cut marks or cracking and hexagonal bone surface pitting modifications associated with burning was observed on any of the bones. Nor did many of the bones (two appeared white) show any signs of discoloration associated with burning and post-depositional diagenetic processes. The bones appeared uncolored, tan, or very light brown, with a number showing digestive pitting (SI Table 11) associated with owl digestion on all major taxonomic groups including Anura, Muridae, Macroglossinae, Lacertilia, Soricidae, as well as specific bird taxa *Coturnix* sp. and *Centropus* sp. SI Table 16 shows the digestion pattern by skeletal element for murids. None was observed on the molars, where typically digestion is not commonly observed (Andrews 1990), but high rates of light digestion were recorded on the postcranial skeletal elements especially on the distal and proximal femora (44.64%),

the distal and proximal humeri (30.63%), and on the pelves (26.47%) with smaller proportions of ulnae and tibiae showing signs of digestion. Only a few postcranial bones show moderate to heavy signs of digestion, and there were no extreme cases of murid bone digestion.

SI Table 17 shows the proportion of skeletal elements with digestion marks for anurans; upper limb bones present in the assemblage had no signs of digestion. Digestion was more focused in low proportions on the pelvic girdle and lower limb bones, with tibiae showing high rates of light and moderate digestion. In SI Table 18 the blossom fruit bat crania and mandibles have small proportions of light and moderate digestion. Relatively high rates of light and moderate digestion were recorded on wing skeletal elements, possibly because these elements have less flesh to protect the bone from the weak acids in the barn owl's stomach. For the lower limb and pelvic girdle anatomical region, the few pelves present showed signs of light digestion, and the one femur present was observed with moderate digestion. A few of the tibiae showed signs of light and moderate digestion. Lizard skeletal elements showed light digestion on the scapulae, ulnae, radii, pelves, femora, and tibiae (SI Table 19).

## DISCUSSION

Our data indicate that barn owls were the primary accumulator of microvertebrate remains at TBL and suggests that larger fauna, such as fruit bats, giant rats, and marine turtles, were likely the only tetrapods deposited by prehistoric people at the rockshelter (Table 1). Barn owls are one of the most common accumulators of microfauna in caves and rockshelters (Andrews 1990; Kusmer 1990). These mostly nocturnal raptors typically prefer prey smaller than themselves because of the need to kill quickly and reduce the risk of injury. They also prefer to swallow their prey whole so that they can easily digest soft tissue in their stomachs, although they can adapt to different-sized prey and will opportunistically take



**Table 1. Barn owl and human predated tetrapod fauna at Tron Bon Lei; fauna selection criteria based on taxonomic size, presence/absence of digestion, presence/absence burning, bone breakage, and skeletal element survivorship.**

Owl predation	Human predation
Frogs/toads	Large fruit bats
Small to large rats	Giant rats
Small birds (quail, coucal, passerines)	Marine turtles
Snakes	
Small blossom fruit bats	
Microbats	
Small lizards	

larger prey in small numbers, which they must dismember to ingest (Taylor 2004). Their preferred prey tends to be the most abundant small mammal taxa that traverse open habitats inside their territory in a ca. 5 km radius (Taylor 2004). However, this is also dependent on the local environments and small freshwater fish have been known to dominate some North American lake-side cave barn owl roosts (Broughton et al. 2006).

The differences between the archaeological vertebrate assemblage recovered from the Test Pit B, representing an 18,000 year sequence spanning the late Pleistocene to Holocene (Samper Carro et al. 2016), and the modern owl roost surface deposit, both collected at TBL rockshelter, are stark. Both the tetrapod assemblages are dominated by a variety of microfauna. There are, however, differences in their taxonomic composition.

The high taxonomic diversity of the modern owl roost deposit, combined with the low evenness of taxonomic relative proportions, indicates that while the barn owl diet is varied and opportunistic, it was primarily specialized on small murids. The relative proportions of small murid bones are much lower in the archaeological assemblage and these specimens all appear to belong to the Rattini. Small

murid (NISP = 201) and snake (NISP = 236) remains dominate the archaeological Test Pit B assemblage, but combined with smaller quantities of chiropteran, lizard, anuran, shrew, and bird faunal remains. Through time, taxonomic richness does not significantly change while the evenness increases possibly reflecting increasing human interactions with terrestrial fauna relative to roosting owls at the cave. The assemblage started with very specialized and low evenness values in Layer 12, like the owl roost, suggesting that initially the cave may have been only sporadically used by humans, with owls responsible for most of the tetrapod vertebrate deposit.

Bone breakage of microvertebrates in the modern owl roost deposit is consistent with trampled owl pellets recorded by Andrews (1990), and were probably caused by goats which were visible in the area during fieldwork, and goat scat was observed on the shelter floor. However, microvertebrate bone breakages were much higher for the archaeological assemblage. One explanation for the paucity of microvertebrates at TBL could be that Test Pit B was peripheral to owl roosting activity. Another likely explanation is that cumulative natural and cultural post-depositional taphonomic processes (proximal cooking activities, trampling, diagenetic weathering) resulted in the destruction of a great deal of bone material, and thus in reduced survivorship of skeletal elements compared to the more recent owl roost.

Direct evidence of human consumption on any of the vertebrate remains in the form of cut marks was not observed, but nor were avian predation puncture marks. However, direct evidence of avian consumption, in the form of bone surface digestion pitting, was observed in similar proportions on microfauna from the owl roost and Test Pit B assemblages (SI Table 7 and 11). The regurgitating of pellets (bones and teeth wrapped in skin and hair) of small vertebrates, once the soft tissue has been digested by weak stomach enzymes, results in distinctive taphonomic signatures unique to barn owls, namely small frequencies of lightly pitted skeletal element articular surfaces from digestive en-



zymes and low rates of skeletal breakage and loss (Andrews 1990). Taxa with digested marks also included the large rat remains from the Pleistocene period of Test Pit B. While these large rats may have fallen outside the preferred prey size of barn owls, small proportions of larger mammal taxa are known to be opportunistically preyed (Taylor 2004).

While burnt bones are circumstantial evidence for human consumption as post-deposition incidental burning or bone used as fuel by people complicate the interpretation, bones exposed up to 6 cm from a heat source during cooking do result in similar burnt bone morphologies (Stiner et al. 1995). Compared to the high proportion of bones which appeared black and grey/white in the archaeological deposit, the owl roost bones showed very few signs of discoloration. This discrepancy could be due to longer periods of archaeofauna deposition, providing more time for chemical alteration. It is also likely to represent episodes of prehistoric fire-place use in the archaeological record or incidental fires, as frequent ash and charcoal lens were observed in Test Pit B (Samper Carro et al. 2016). While shrinkage and cracking were observed on the larger fauna, such as marine turtles, these were not observed on any microfauna. This suggests that shrinkage, pitting, and cracking, commonly observed in actualistic taphonomic studies on large mammal fauna (Shipman et al. 1984), may not be applicable to microfauna due to differences in bone microstructure and density or that they were not burnt.

The high density of fish bones recorded by Samper Carro et al. (2016), in combination with the lithic artefacts found throughout the archaeological sequence (Reepmeyer et al. 2016) points to periods of human site use with various subsistence activities. Avian predators are unlikely to inhabit the rock shelter while humans are present. Our data suggests that TBL is likely to have been largely used by humans with barn owls only visiting on an alternating and temporary basis. The lack of tetrapod vertebrate material from basal Layer 13, dated to around 20,560–21,000 cal BP,

suggests that initially avian predators did not occupy the rockshelter.

Prehistoric human subsistence at TBL was predominantly marine and initially focused on large inshore carnivorous fishes, while fishing activity in general appeared to decline with time (Samper Carro et al. 2016). However, three tetrapod taxa (Pteropodidae, giant murid, Cheloniodea) not present in the modern owl roost and displaying indirect burning evidence and lacking digestion marks may also have featured as part of subsistence activities at TBL during the Quaternary. The tiny amount of these taxa relative to fish remains indicates that they never formed a significant component of human diet at TBL.

The marine turtle remains reported here could be an extension of maritime practices that included opportunistic exploitation of turtles either feeding on the reef or seasonal nesting events (Bliege-Bird and Bird 1997). However, only turtle shell, a phalanx, and cervical vertebrae were recovered, many of which were clearly burnt, with shrinkage, cracking, and discoloration observed. This suggests that some sea turtle butchery and processing took place at the rockshelter, butchery waste was deposited, and the meaty limb bone portions may have been transported and consumed elsewhere. This pattern is not likely to reflect post-depositional bone destruction, as dense long bone fragments are completely absent, but it may reflect spatial sampling issues in the cave.

The giant rat specimens represent a significant discovery as giant rats were previously unknown in Alor. While burning on one of the teeth is not direct evidence of human consumption, their association with archaeological material dated between 18,890 and 19,235 cal BP, lack of digestion, their large size outside the usual prey range of the three owl species (*Tyto delicatula*, *Ninox boobook*, *Otus* sp.) known today from Alor (Trainor et al. 2012), and their record of consumption on Timor (Aplin and Helgen, 2010; Glover 1986), is indirect evidence that they were likely consumed by TBL's prehistoric inhabitants.

Another taxon that was likely consumed by the inhabitants of TBL are large

fruit bats, represented by few remains between Layers 4–10, and dating to between 10,225 and 3215 cal BP. Bats were an important component of prehistoric human diet in the tropical Asia-Pacific region, especially on faunally impoverished tropical islands, although direct evidence of human consumption is often not present in the archaeological record (Hawkins et al. 2016). In the case of the large pteropids in Test Pit B, none showed signs of digestion and they are also likely too large for barn owls to prey on. Furthermore, only smaller blossom fruit bats were found in the modern owl roost. The skeletal elements recovered included only wing bones and a mandible. The former are common in archaeological sites due to their high number per individual. Another similarity with archaeological fruit bat deposits are the lack of vertebrae and lower limb bones (Hawkins et al. 2016). These latter skeletal elements represent body parts with the greatest meat, suggesting the processing of non-meaty elements near Test Pit B and consumption of meaty portions elsewhere. However, a similar pattern was found in the modern owl roost blossom fruit bat assemblage and post-depositional processes and archaeological sampling issues cannot be ruled out.

The results from the hunting abundance index (SI Figure 6) indicate that there was a significant increase in human hunting of tetrapods (Pteropodidae, giant murid, Cheloniodea) over time relative to avian predation ( $X^2_{trend} = 27.97$ ,  $p < 0.001$ ). Hunting appears to have reached a peak in Layer 4 during the mid to late Holocene before the record of human-tetrapod interactions at TBL disappears sometime after 3300 BP in Layers 1–3.

## CONCLUSIONS

This study provides critical taphonomic data that aids in distinguishing avian predation from cultural deposition at TBL rockshelter, and which can be applied to the wider Wallacea region. Using taxonomic composition, skeletal element representation, bone breakage patterns, and bone modifications, it moves beyond the focus

by microvertebrate taphonomic studies on small rodents (e.g., Fernández et al. 2012), to extend the analysis to taxa commonly found in ISEA vertebrate assemblages (bats, birds, amphibians, snakes, and lizards).

The taphonomic data for the microfauna is to some extent consistent with palaeontological studies conducted on barn owl pellets found elsewhere (Andrews 1990; Fernández et al. 2012; Kusmer 1990). Microfauna in both the natural and archaeological TBL assemblages showed consistent patterns of owl predation. While small murids dominate the owl roost assemblage in terms of relative abundance (with smaller proportions of small lizards, blossom fruit bats, amphibians, and birds), snakes and small murids dominate the Test Pit B archaeological deposits, with smaller quantities of other microfauna (frogs, lizards, bats, birds) and macrofauna (giant to large rats, large fruit bats, marine turtles). Although taxonomic diversity did not change significantly over time, the evenness of relative abundance significantly increased, indicating a rise in general and mixed predation patterns and consistent with a scenario of alternating human and owl roosting activities during the Pleistocene to Holocene transition. While some bone destruction and element loss occurred in the modern owl deposit, post-depositional skeletal element loss in Test Pit B was significantly greater and likely exacerbated by long-term natural processes and prehistoric human activities.

Our data suggest that initially human hunting at TBL rockshelter was more sporadic than during later parts of the sequence, and included processing of giant murids and marine turtles. However, most of the early period tetrapod accumulation at the shelter was conducted by owls. By the beginning of the Holocene, barn owl predation declined relative to human use of the rockshelter. Fireplaces became more ubiquitous and human hunting of marine turtles and large fruit bats significantly increased relative to owl pellet deposition. Domesticates and wild faunal translocations were introduced by the late Holocene, although the exact timing of this remains uncertain.

Owl predation persisted throughout the Holocene sequence, indicating that hu-

mans used the shelter only sporadically. The site appears to have been used not only for fish consumption, but also perhaps to butcher sea turtles for transport of meaty body parts for consumption elsewhere.

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## SUPPLEMENTAL

Supplemental tables and figures for this article are available at the publisher's website at <http://dx.doi.org/10.1080/15564894.2017.1285834>. The following supplemental materials are available:

- **SI Table 1.** Test Pit B taxonomic abundance (NISP) by layer.
- **SI Table 2.** Modern owl roost and Test Pit B Taxonomic diversity and evenness by layer.
- **SI Table 3.** Small murid skeletal element survivorship, Tron Bon Lei Test Pit B archaeological fauna. Ei (expected skeletal elements per individual).
- **SI Table 4.** Tron Bon Lei murid cranial and postcranial indexes.
- **SI Table 5.** Turtle skeletal element fragments (NSIP) by layer at Tron Bon Lei Test Pit B.
- **SI Table 6.** Large Fruit Bat (Pteropodidae) skeletal element fragments (NISP) by layer at Tron Bon Lei Test Pit B.
- **SI Table 7.** Tron Bon Lei Test Pit B skeletal element completeness and bone modifications (% NISP).
- **SI Table 8.** Tron Bon Lei modern owl roost and Test Pit B small murid crania and post-cranial long bone breakage.
- **SI Table 9.** Tron Bon Lei Test Pit B digestion by taxon and layer (%NISP).
- **SI Table 10.** Tron Bon Lei Test Pit B degree of digestion by taxon.
- **SI Table 11.** Tron Bon Lei owl roost taxonomic composition by NISP, MNE, MNI, % NISP, MNE, MNI, and %NISP digested by taxon.
- **SI Table 12.** Tron Bon Lei owl roost, murid skeletal element completeness (co%) and %survivorship data. Ei (skeletal elements per individual), Ni (Number of identified specimens).
- **SI Table 13.** Tron Bon Lei owl roost Anura (Frog/toad) skeletal element completeness (co%) and %survivorship data. Ei (skeletal elements per individual), Ni (Number of identified specimens).
- **SI Table 14.** Tron Bon Lei, Blossom fruit bat skeletal element completeness (co%) and %survivorship data. Ei (skeletal elements per individual), Ni (Number of identified specimens).
- **SI Table 15.** Tron Bon Lei owl roost Lacertilia (squamate lizard) skeletal element completeness (co%) and %survivorship data. Ei (skeletal elements per individual), Ni (Number of identified specimens).
- **SI Table 16.** Proportions of digested small murid skeletal elements, Tron Bon Lei owl roost.

- **SI Table 17.** Proportions of digested Anura skeletal elements, Tron Bon Lei owl roost.
- **SI Table 18.** Proportions of digested Blossom fruit bat skeletal elements, Tron Bon Lei owl roost.
- **SI Table 19.** Proportions of digested lizard skeletal elements, Tron Bon Lei owl roost.
- **SI Figure 1.** Evenness ( $e$ ) values of the tetrapod taxonomy by layer at Tron Bon Lei, Test Pit B. ( $r_s = -0.90$ ,  $p = 0.00002$ ).
- **SI Figure 2.** Small murid skeletal element survivorship from the modern owl roost and Test Pit B, Tron Bon Lei.
- **SI Figure 3.** Anura skeletal element survivorship from the modern owl roost, Tron Bon Lei.
- **SI Figure 4.** Blossom fruit bat skeletal element survivorship from the modern owl roost, Tron Bon Lei.
- **SI Figure 5.** Lizard skeletal element survivorship from the modern owl roost, Tron Bon Lei.
- **SI Figure 6.** Hunting abundance Index, Test Pit B, Tron Bon Lei. ( $\chi^2$  trend = 27.97,  $p < 0.001$ ).

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