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Preservation of Mammalian Teeth and Bones Influences Identification of Terminal Pleistocene to Middle Holocene Hunter-Gatherer Subsistence at Ban Rai Rockshelter, Northwest Thailand

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Abstract: Ban Rai Rockshelter in northwest Thailand, dating to the Terminal Pleistocene and Middle Holocene, includes evidence for hunter-gatherer exploitation of mammals, birds, reptiles, fish, and arthropods. Abundant faunal remains, identified throughout site deposits, include macaques (*Macaca* sp.) and Sambar deer (*Rusa unicolor*), but these identifications are influenced by an assemblage largely comprised of preserved tooth elements and fragmented bone. Area 3 at Ban Rai has the largest abundance and diversity of faunal remains recovered and identified in this study. Here, we examine the zooarchaeological assemblage from Ban Rai Rockshelter, to understand long-term hunter-gatherer subsistence change, influenced by site preservation, during and after the Pleistocene–Holocene transition. Our results support the presence of the exploitation of arboreal taxa during the Early and Middle Holocene in northwest Thailand.

Keywords: Pleistocene; Holocene; zooarchaeology; mainland Southeast Asia; Thailand; subsistence; hunter-gatherer; primate

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1. Introduction

During the Terminal Pleistocene and Holocene, hunter-gatherer groups inhabited and foraged within the highland regions of northwest Thailand. Several sites (see Figure 1) support this record, including Tham Lod Rockshelter, Ban Rai Rockshelter, Spirit Cave, Steep Cliff Cave, and Banyan Valley Cave, suggesting that this region was a significant location for the development of human adaptations in the tropics of mainland Southeast Asia [1–10]. Zooarchaeological analyses in the 1960s suggested that during this prehistoric period, hunter-gatherers exploited a wide diversity of plant and animal taxa (see [11]), but recent studies have challenged this record. There was likely a more complex relationship between human population densities, subsistence, and paleoenvironmental change in this region [1,2,8,12–14]. For example, northwest Thailand experienced known faunal change. One of the major changes in ecological communities was the loss of the Sumatran serow (*Capricornis sumatraensis*)—a species which occurs in several archaeological sites within this region, and which was locally extirpated sometime during the Holocene [8,12,14]. Based on this evidence, we investigated the zooarchaeological assemblage from a Terminal Pleistocene–Middle Holocene archaeological site, Ban Rai Rockshelter, to understand shifts in hunter-gatherer subsistence over time, and the taphonomic processes that have influenced this assemblage. A record of broad-scale

faunal and environmental change within Sundaland (an area encompassing portions of mainland and island Southeast Asia during the Last Glacial Maximum) during the Terminal Pleistocene–Middle Holocene [2,8] suggests that there was a shift from large mammal to small mammal exploitation during the period of human occupation at Ban Rai Rockshelter.

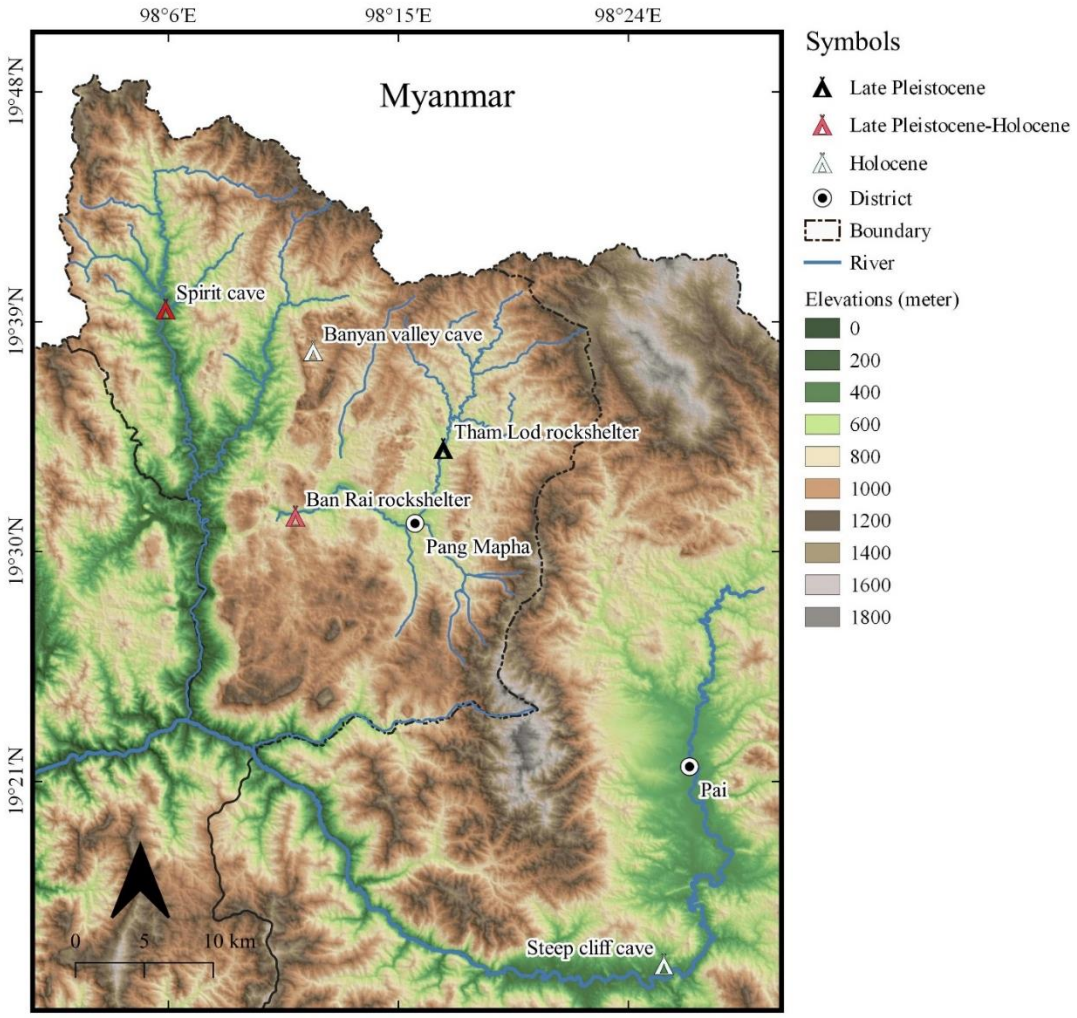


Figure 1. The location of archaeological sites within northwest Thailand discussed in the text, including Ban Rai Rockshelter in Pang Mapha District, Mae Hong Son Province.

In terms of paleoenvironmental change in Southeast Asia, evidence from hunter-gatherer archaeological sites and associated paleontological sites indicates that Sundaland (Figure 2) was likely a large, open grassland savannah corridor environment during the Last Glacial Maximum [12,13,15–19]. As deglaciation occurred during the Terminal Pleistocene, climates shifted to more 'modern' or recent conditions, and a corresponding shift occurred in Southeast Asian faunas and environments. Open grasslands transitioned towards tropical, monsoon-fed forests [19–22]. Holocene environments in mainland Southeast Asia became patchy and increasingly heterogeneous between regions that received different quantities of rainfall. These changes corresponded to changes in faunal assemblages.

For example, faunal change included a shift from the *Ailuropoda-Stegodon* complex (established by [23–25]), which recognized the co-occurrence of the giant panda (*Ailuropoda*) and the now-extinct Proboscideans (*Stegodon*), to 'modern' faunal communities [17,26,27]. There is evidence from this period for a larger biogeographic

dispersal of certain faunas (e.g., *Naemorhedus goral*, *Rhinoceros unicornis*, *Sus barbatus*), strongly suggesting animal mobility within the Indochinese and Sundaic subregions bounded by the Kra Isthmus. Carnivore activity within this area suggests the co-importance of large herbivorous mammals and large carnivorous predators within this past habitat [28].

As these changes occurred in past environments and within animal communities, hunter-gatherers continued to forage and adapt to shifting conditions throughout this region. Ban Rai Rockshelter, situated in a highland location of mainland Southeast Asia, and spanning the critical period of the Terminal Pleistocene to Middle Holocene, thus provides an important opportunity to investigate the dynamics of this process, as it relates to human subsistence strategies, palaeoecologies, and taphonomic processes.

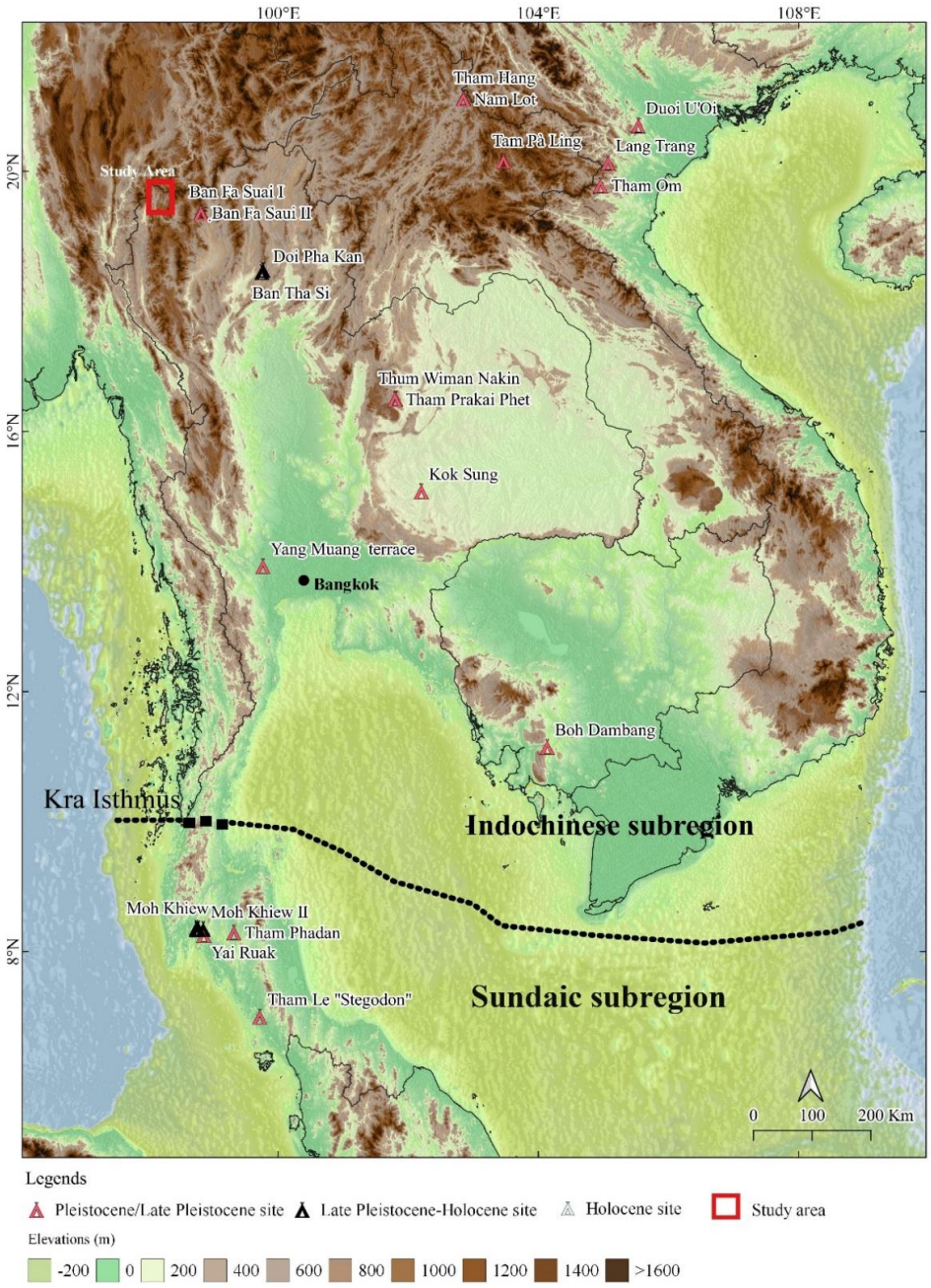


Figure 2. Prominent Pleistocene and Holocene sites in the zoogeographic subregions of mainland and island Southeast Asia (Sundaland) during the Last Glacial Maximum (~21,000 years ago). Sea level depicted at -116 m compared to modern levels [29].

2. Site Excavation, Chronology, and Stratigraphy

Ban Rai Rockshelter (Figure 3) is located on the southern edge of the Lang River Valley, approximately 2–3 km from the nearby village of Ban Rai in Pang Mapha District, Mae Hong Son Province, northwest Thailand. The rockshelter is positioned on the top of a steeply sided valley, approximately 740–760 m above sea level, or approximately 200 m above the Lang River, which flows westward into a sinkhole [7,9]. The lithology of the valley is comprised of Lower Carboniferous limestone, and is thus karstic [30]. Six forest types occur within the vicinity of the site (mixed deciduous, dry dipterocarp forest, hill evergreen forest, dry evergreen forest, bamboo forest, and limestone forest [6]). Except for the roof of the rockshelter (top of the karst) where dry dipterocarp forest occurs, mixed deciduous forest is present throughout the valley [7].



Figure 3. Ban Rai Rockshelter: view from the northeast wing of the rockshelter.

The rockshelter is semicircular in shape, measuring 105 × 142 m and 30 m high from the surface to the hanging wall edge at the center of the shelter. Large limestone debris on the rockshelter floor, especially on the western side of the site, is a component of rock fall from prior geologic events. There are large wooden posts and log coffins throughout the rockshelter, representing the local Log Coffin Culture, dating to the Late Holocene [31]. The Log Coffin Culture occurred throughout northwest Thailand during the past several millennia, and likely represented mixed forager–farmer groups exploiting the upland regions throughout Pang Mapha, using this specific type of interment (see below). A series of prehistoric, realistic, and idealistic rock paintings on the eastern hanging wall of the site currently remains undated [7,9].

The Highland Archaeology Project in Pang Mapha District surveyed and selected the rockshelter for excavation in 2001. Excavation occurred in three areas beneath the log coffins unearthed immediately below the surface, after clearing the rockshelter floor. Each area included two types of units—trenches (4 × 4 m) and baulks (1 × 4 m)—oriented north–south (Figure 4; [7,9]). The excavations included:

Area 1: a ~28 m^2 trench at the center of the rockshelter, with five pits (including S1E4, S2E12, Baulk S2E12, S3E19, and Baulk S3E19) and eight primary layers, totaling ~0.7–2 m in depth.

Area 2: a ~24 m^2 trench about 5 m east of Area 1, with three pits (including S1E6, S2E14, and Baulk S2E14) and five primary layers, totaling ~1.5–1.8 m in depth.

Area 3: a ~16 m² trench at the eastern edge of the rockshelter, with one pit (N5E39) and seven primary layers, totaling 3 m in depth.

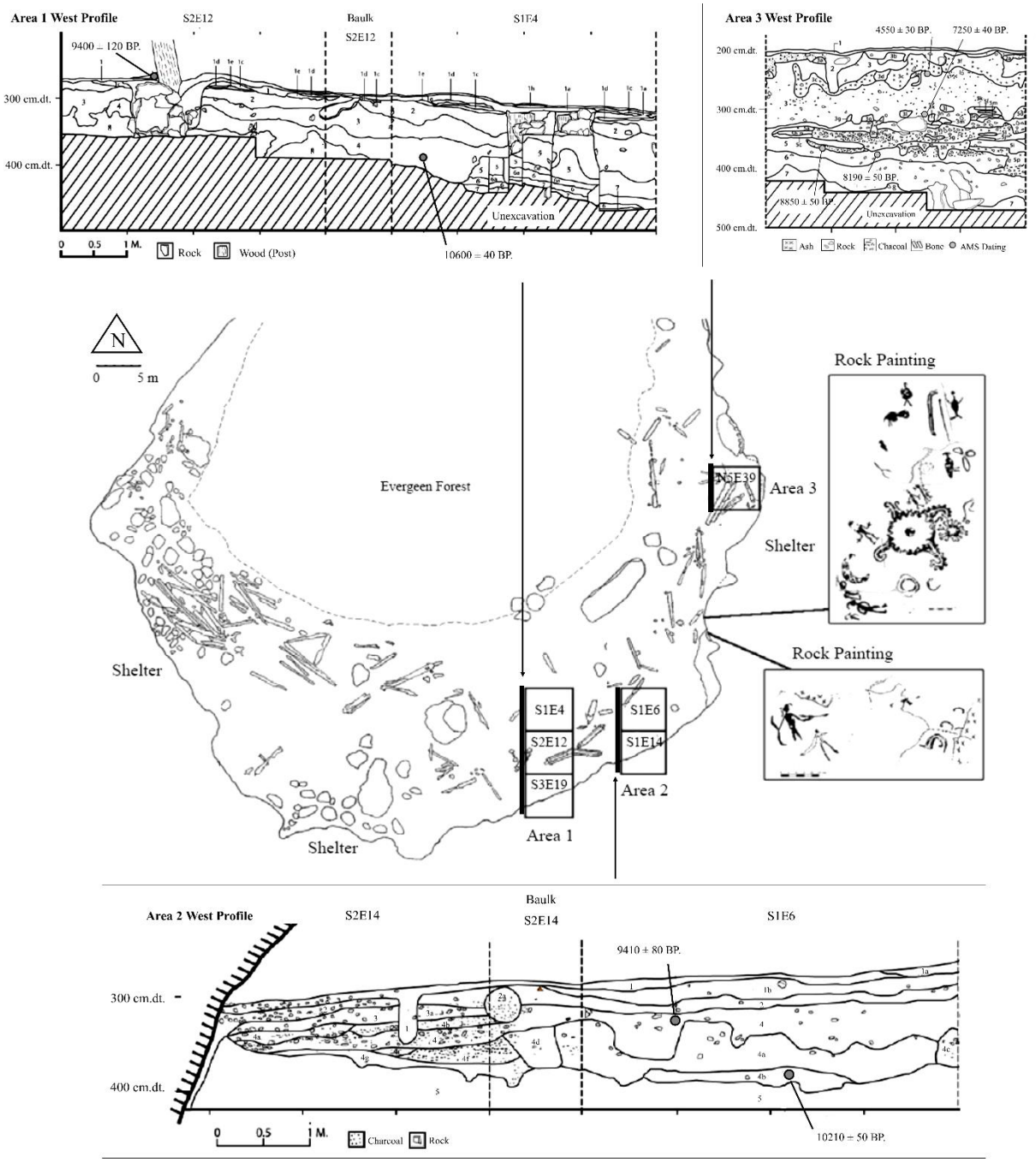


Figure 4. Ban Rai Rockshelter, showing the location of excavation units, radiocarbon determinations, and the west wall profiles from each area (Area 1, 2, and 3) (drawn by Pipad Krajaejun).

Excavations recovered 11,600 lithic items (including 801 items from Area 1, 999 items from Area 2, and 9800 items from Area 3). These stone artifacts included sumatraliths, short axes, wasted cores and flakes, and utilized cores and flakes: they represented a stone tool assemblage, with hunter-gatherers exploiting material far distant from Ban Rai, within patchy and diverse ecological resource zones [7,9,32].

Two standard radiocarbon and seven Accelerator Mass Spectrometry (AMS) radiocarbon conventional dates established a chronological sequence in successive layers, from 10,600 ± 40 radiocarbon (^{14}C) years BP (Beta-168216) in Area 1-S1E4 to 4550 ± 30 ^{14}C years BP (Beta-538749) in Area 3-N5E39 (Table 1). The profile of each area straddled sequential cultural phases, resulting in a two-phased contextual chronological framework from the Terminal Pleistocene to the Middle Holocene [7,9,33].

Table 1. Radiocarbon determinations from Ban Rai Rockshelter [7,9,33].

Laboratory Code	Area	Layer	Material	δ^{13}C	Radiocarbon Years BP	±SD	Calibrated Year BP	Context
Beta-168215	1	2	Charcoal	−25.0	9400	120	11,110–10,250	Hunter-Gatherer
Beta-168216	1	4	Charcoal	−28.8	10,600	40	12,910–12,610, 12,490–12,350	Hunter-Gatherer
Beta-168218	2	4	Charcoal	−25.0	9410	80	11,060–10,950, 10,780–10,420	Hunter-Gatherer
Beta-168217	2	4	Charcoal	−30.8	9720	50	11,210–11,090, 10,920–10,890	Hunter-Gatherer
Beta-168219	2	4	Charcoal	−28.4	10,210	50	12,340–11,670	Hunter-Gatherer
Beta-534121	3	-	Wood	−24.6	1770	30	1744–1605	Log Coffin
Beta-534122	3	-	Wood	−24.4	1840	30	1864–1708	Log Coffin
Beta-534118	3	-	Wood	−24.3	1880	30	1884–1728	Log Coffin
Beta-534119	3	-	Wood	−25.9	1920	30	1947–1812	Log Coffin
Beta-534120	3	-	Wood	−25.5	2040	30	2067–1924	Log Coffin
Beta-538749	3	-	Sediment	-	4550	30	5189–5053, 5318–5257	Hunter-Gatherer
Beta-168220	3	3	Charcoal	−28.0	7250	40	8340–8140	Hunter-Gatherer
Beta-168222	3	5	Charcoal	−29.7	8190	50	9290–9120	Hunter-Gatherer
Beta-168221	3	5	Charcoal	−27.7	8850	50	10,170–9720	Hunter-Gatherer

2.1. The First Cultural Phase

The first cultural phase was located in the lowest portion of each unit in all excavation areas, specifically spanning Layers 5–8 in Area 1, Layer 5 and 4b in Area 2, and Layer 7 in Area 3. These contexts included the oldest directly dated materials, and suggested a Terminal Pleistocene human occupation of nearly 10,600 ^{14}C years BP [7,9]. Based on lenses of charcoal and ash identified throughout each layer and area, hunter-gatherers likely first settled at Ban Rai Rockshelter during this time; however, there were no faunal remains or stone tools from these excavated contexts, only charcoal and ash stains [7].

2.2. The Second Cultural Phase

The second cultural phase consisted of Layers 2–4 in Area 1, Layer 4 and 4a in Area 2, and Layers 3–6 in Area 3. The successive dating of these layers suggested an occupation between 9400 ^{14}C years BP and 4550 ^{14}C years BP (the Terminal Pleistocene to Late-Middle Holocene). Evidence for human occupation included abundant faunal remains and lithic artifacts associated with charcoal and ash. There was also a human skeleton in a primary flexed burial position within a roughly circular pit (64 cm in diameter), buried approximately 90–110 cm deep in Area 2, dating to this period: this was the fragile skeleton of an adult male.

Considering the chronological dating of this burial—from charcoal in sediments near the skeleton—the individual died around 9800 ^{14}C years BP (Beta-168217). According to the sequence of occupation correlated to this absolute chronology, hunter-gatherers likely occupied the center of the rockshelter (Areas 1 and 2) during this initial period. The latest and terminal occupation of the rockshelter shifted to areas near the left wall (in Area 3), based on radiocarbon dating (see Table 1). The second cultural phase consisted of spatially diverse forager activities [7,9], including Late Holocene activity. Regardless, there was a clear Terminal Pleistocene and Early Holocene occupation in Area 1–2, while Area 3 was extensively used from the Early to Middle Holocene. As a result, all areas included evidence of ancient occupations. Simultaneously, the consistency between the dates assigned to the earliest cultural levels identified in Area 3, as well as the latest dates

retrieved from Areas 1 and 2, may indicate a spatial movement across the site, with the main habitation area shifting from the site's center to its eastern side (see [9]).

The uppermost layers of this area (and Areas 1 and 2) suggest the presence of the Log Coffin Culture in the Late Holocene (see [31]). In Highland Pang Mapha, the Log Coffin Culture is an ancient mortuary practice dating to around 2120–1250 B.P. (see [33]). In dry limestone caves and rockshelters, coffins were purposefully placed on wooden posts and beams. The majority of the coffins were made from hollowed-out teak wood trunks; the exterior surface included carvings of bodies and heads, of various shapes and sizes. Human remains are often found in log coffins used for funerals. Log Coffin burials also include faunal remains, earthenware, glass beads, bronze ornaments, iron implements, wooden objects, and textiles (see [33]).

3. Materials and Methods

3.1. Study Materials

During excavations in 2001, archaeologists collected a large assemblage of faunal remains from Ban Rai Rockshelter [7,9,34]. Between 2003 and 2006, an initial analysis of this assemblage identified 55,929 specimens, weighing 71,334.15 g [35]. Subsequent analysis suggested that only 5816 specimens (2409.9 g) were taxonomically unidentifiable—these were extremely fragmented and degraded specimens. A preliminary analysis of the Area 3 specimens identified 21 taxa present in this context at the site [34] (see also [8]).

A recent publication that included analysis of the Ban Rai faunal assemblage [8] has a slightly different taxonomic composition (including counts) than reported here: this is due to the presence of updated identifications and counts of the assemblage for the purposes of this paper (see below). Our results reflect the most recent and up-to-date analysis of the assemblage [33,34].

All the specimens identified and analyzed here (by A.W.) derived from six pits throughout the site: Pit S1E4 and S2E12 in Area 1; Pit S1E6, S2E14, and Baulk S2E14 in Area 2; and Pit N5E39 in Area 3. Compared to pits, baulk samples from the site typically included a smaller number of faunal specimens: for example, 1364, 140, and 83 specimens derived from Baulks S2E12, S3E19, and S3E19, respectively, [34].

A.W. identified specimens, using a combination of comparative skeletal material and reference guides [27,36–43]. Comparative skeletons provided the final identification criteria, whenever possible, due to known inconsistencies within published reference guides. Comparative specimens included skeletons from the Chulalongkorn University Museum of Natural History, the Natural History Museum, National Science Museum Thailand in Bangkok, and the Palaeontological Research and Education Centre in Mahasarakham University, Mahasarakham Province.

3.2. Zooarchaeological Methods

Measuring taxonomic abundance included quantification of both the number of identified specimens (NISP) and the minimum number of individuals (MNI) [44,45]. NISP is the counting of the abundance of all skeletal elements, including fragments of specimens which are identifiable to the smallest possible taxonomic levels (species and subspecies). MNI quantification involved identifying individual taxonomic abundance, based on the number of diagnostic skeletal elements of particular taxa, using overlapping features (e.g., element side and age) and other contextual data from the archaeological units, areas, and cultural layers.

Given zooarchaeological evidence from nearby hunter-gatherer sites in northwest Thailand suggesting the presence of various taphonomic influences affecting faunal assemblages [1,2], we examined a linear model of Ban Rai's faunal data between taxonomic abundance and the number of taxa identified or taxonomic richness (NTAXA) (see [44,46–48]): this provided the examination of the relationship between NISP and

NTAXA or NISP–NTAXA, as well as between MNI and NTAXA or MNI–NTAXA, that enabled us to understand how sample size biases impacted the assemblage. We did not log-transform zooarchaeological count data for this analysis, due to known issues with this technique (see [49]). We also explored the relationship between identified tooth and bone skeletal elements in Area 3, to evaluate the role and influence of tooth enamel preservation on our identifications and analysis. Finally, we examined the diachronic relationships between abundances of specific faunas, to evaluate hunter-gatherer subsistence patterns at Ban Rai Rockshelter during the Pleistocene and Holocene, given these taphonomic constraints. These analyses allowed for an interpretation of long-term hunting strategies during periods of environmental change.

In addition, A.W. also recorded evidence of weathering, butchery marks, root etching, burning, and rodent/carnivore gnawing on the surface of all bone and tooth specimens [35]. We analyzed all data, and created visualizations in R (v.4.0.4) and RStudio (v.1.4.1717; see [50] for source code) (see: https://github.com/cylerc/BanRai) (accessed on 1 November 2022).

4. Results

4.1. Taxonomic Composition

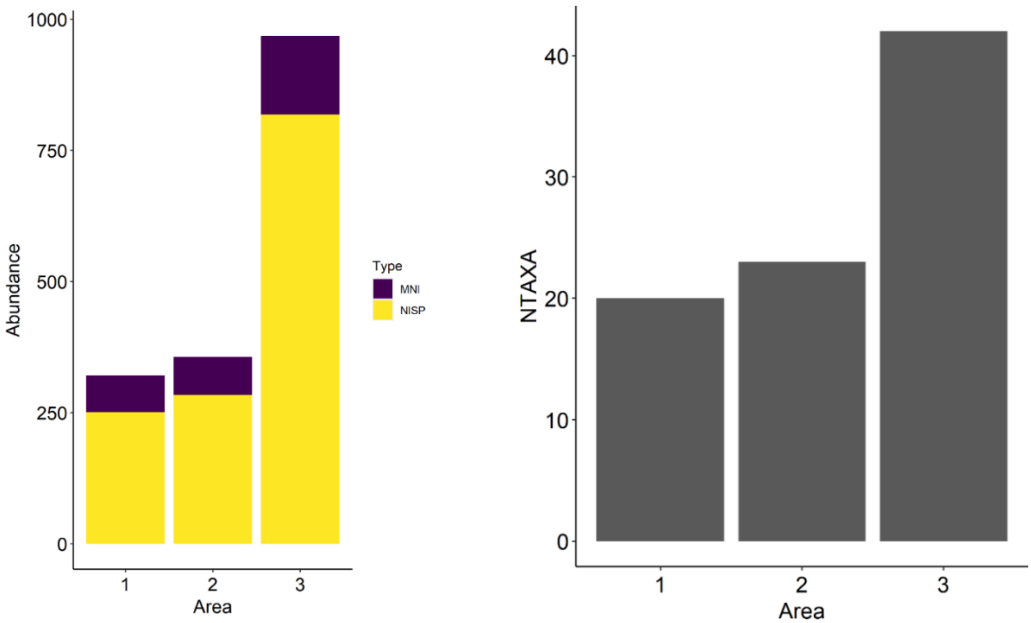
Zooarchaeological analysis of the Ban Rai Rockshelter assemblage resulted in the identification of over 1000 mammalian, avian, reptilian, fish, and arthropod specimens throughout Areas 1, 2, and 3 (Table 2, Tables S1–S3). Our analysis does not currently include molluscan taxa. In total, A.W. identified 1353 specimens (NISP), representing 292 individuals (MNI). Bone specimens were highly fragmented at the site and, thus, identification often occurred through the presence of morphologically distinguishing features on mammalian tooth fragments (see [8]). Examination of faunal remains from Ban Rai Rockshelter included identification of surface modifications (e.g., cut marks, bone breaks, burning), but are not further reported here.

Considering taxa identified to the genus and species level, Ban Rai was comprised of a large number of primates and artiodactyls. Macaques (*Macaca* sp.) and Sambar deer (*Rusa unicolor*) were abundant throughout site contexts, particularly in Area 3. Unidentified turtles, tortoises, and Cyprinidae fishes (carps and minnows) also occurred relatively abundantly throughout each area.

Taxonomic diversity and abundance within each excavation area at Ban Rai differed, but Area 3 was especially distinct in terms of its zooarchaeological assemblage (Figure 5). Areas 1 and 2 at Ban Rai had relatively small abundances of taxa (Table 2 and Supplemental Tables S1–S3). Primate diversity and abundance—with three taxa in only two Families and one genus identified (*Macaca* sp., Cercopithecidae, Colobinae)—were almost identical between these two areas: Area 1, NISP = 7 and MNI = 3; Area 2, NISP = 11 and MNI = 5. Only NISP = 3 or MNI = 2 of Macaque (*Macaca* sp.) occurred in Area 1, and NISP = 7 in Area 2; likewise, there were NISP = 4 (or MNI = 2) Cercopithecidae specimens in Area 1, and only NISP = 2 (or MNI = 2) in Area 2. Additionally, NISP = 2 (or MNI = 1) Colobinae primate specimens were present in Area 2. In contrast, Area 3—represented by a single unit, N5E39—included specimens from four families of primates, two genera, and three species (*Nycticebus* sp., *Macaca mulatta*, *Macaca arctoides*, *Macaca* sp., Cercopithecidae, *Trachypithecus* cf. *phayrei*, Colobinae, and Hylobatidae) with a total of NISP = 354 or MNI = 47. The proportion of primate specimens varied from 2.8% of the total NISP (NISP = 7/251) or 5.5% of the total MNI (MNI = 4/72) in Area 1 to 6.7% of the total NISP (NIS*P* = 19/283) or 12.5% of the total MNI (MNI = 9/72) in Area 2; however, Area 3 had a higher proportion of primates than the other Areas: 43.3% of the total NISP (NISP = 354/818) or 31.3% of the total MNI (MNI = 47/150).

While Areas 1 and 2 included carnivores, they occurred in relatively minor abundance (Area 1: NISP = 3, MNI = 3; Area 2: NISP = 4, MNI = 3) compared to Area 3 (NISP = 49, MNI = 16): for example, identification included one Asian black bear (*Ursus*

thibetanus) within Area 1, and only one unidentified Carnivora specimen in Area 2; yet, Asian black bear, unidentified bears (*Ursus* sp.), hog badger (*Arctonyx collaris*), binturong (*Arctictis binturong*), possibly dog (*Canis* sp.?), tiger or leopard (*Panthera* sp.), and unidentified Felids all occurred within Area 3. Area 3's analysis identified several elephant (*Elephas* sp.: NISP = 4, MNI = 1) and rhinoceros (Rhinocerotidae) specimens (NISP = 10, MNI = 2)—the only such elements within the site.



(**A**) (**B**)

Figure 5. Abundance of fauna and number of identified taxa identified in each area at Ban Rai Rockshelter: (**A**) abundance (NISP, number of identified specimens and MNI, minimum number of individuals) of faunas; (**B**) number of identified taxa (NTAXA).

Although there were turtles and tortoises found throughout each area (Area 1: NISP = 52, MNI = 9; Area 2: NISP = 61, MNI = 11; Area 3: NISP = 53, MNI = 4), the unidentified bird (NISP = 1, MNI = 1) and lizard (NISP = 3, MNI = 2) elements appeared only within Area 3. This was largely true for all identified rodent taxa as well, including the variable squirrel (*Callosciurus finlaysonii*; NISP = 1, MNI = 1), the flying squirrel (Petauristinae; NISP = 1, MNI = 1), the squirrel (Sciuridae; NISP = 5, MNI = 2), the long-tailed giant rat (*Leopoldamys sabanus*; NISP = 1, MNI = 1), the bandicoot rat (*Bandicota* sp.; NISP = 1; MNI = 1), the bamboo rat (Rhizomyidae; NISP = 6, MNI = 2), the Old World porcupine (Hystricidae; NISP = 19, MNI = 3), and unidentified rodents (NISP = 29, MNI = 6). Only unidentified rodent specimens occurred within Area 1 (NISP = 29, MNI = 6), as well as bamboo rats (Rhizomyidae) in Area 2 (NISP = 6, MNI = 4). In similar form to primates, there was a large abundance of Cyprinidae within Area 3 (NISP = 61, MNI = 15), with few specimens from Areas 1 (NISP = 2, MNI = 2) and 2 (NISP = 3, MNI = 2). A single crab (NISP = 2, MNI = 1) occurred in Area 2.

Identification and analysis of artiodactyls suggested a more complex pattern within the site. In general, the largest NISP of all identified artiodactyls occurred within Area 3 (NISP = 131, MNI = 39), compared to the largest MNI in Area 1 (NISP = 99, MNI = 42) and Area 2 (NISP = 100, MNI = 31). There were large abundances of Sambar deer (*Rusa unicolor*) in each area (Area 1: NISP = 50, MNI = 12; Area 2: NISP = 52, MNI = 8; Area 3: NISP = 33, MNI = 7), as well as the smaller hog deer (*Axis* sp.) (Area 1: NISP = 13, MNI = 7; Area 2: NISP = 20, MNI = 4; Area 3: NISP = 19, MNI = 6). The ecologically significant—due to their extirpated and threatened status [13,15]—Caprinae from Ban Rai included the Sumatran serow (*Capricornis sumataensis*) and the Chinese goral (*Naemorhedus griseus*). The latter

taxon only occurred in Area 1 (NISP = 1, MNI = 1), while the serow was present in all areas (Area 1: NISP = 2, MNI = 2; Area 2: NISP = 6, MNI = 4; Area 3: NISP = 8, MNI = 2).

Within each area, there was also a diachronic change in taxonomic presence and abundance. Area 1, with relatively large abundances of artiodactyls and turtles/tortoises, experienced accumulation of large numbers of artiodactyls in Pit S1E4, from the deeper layers to the surface (Figure 6). In Area 1 Pit S2E12, accumulation of artiodactyls and turtles/tortoises increased from the deeper layers up to Layer 3, where abundance peaked, then decreased towards the surface layers.

In contrast, Area 2, with lower taxonomic abundances overall, had experienced minimal change over time in the accumulation of faunas (Figure 7). Pit S2E14 and Pit S2E14 Baulk both had small faunal abundances, with a decrease in the relative abundance of artiodactyls from the deeper layers to the surface levels. This trend was also present in Pit S1E6, where artiodactyls decreased over time, while turtle and tortoise abundance tended to increase over time.

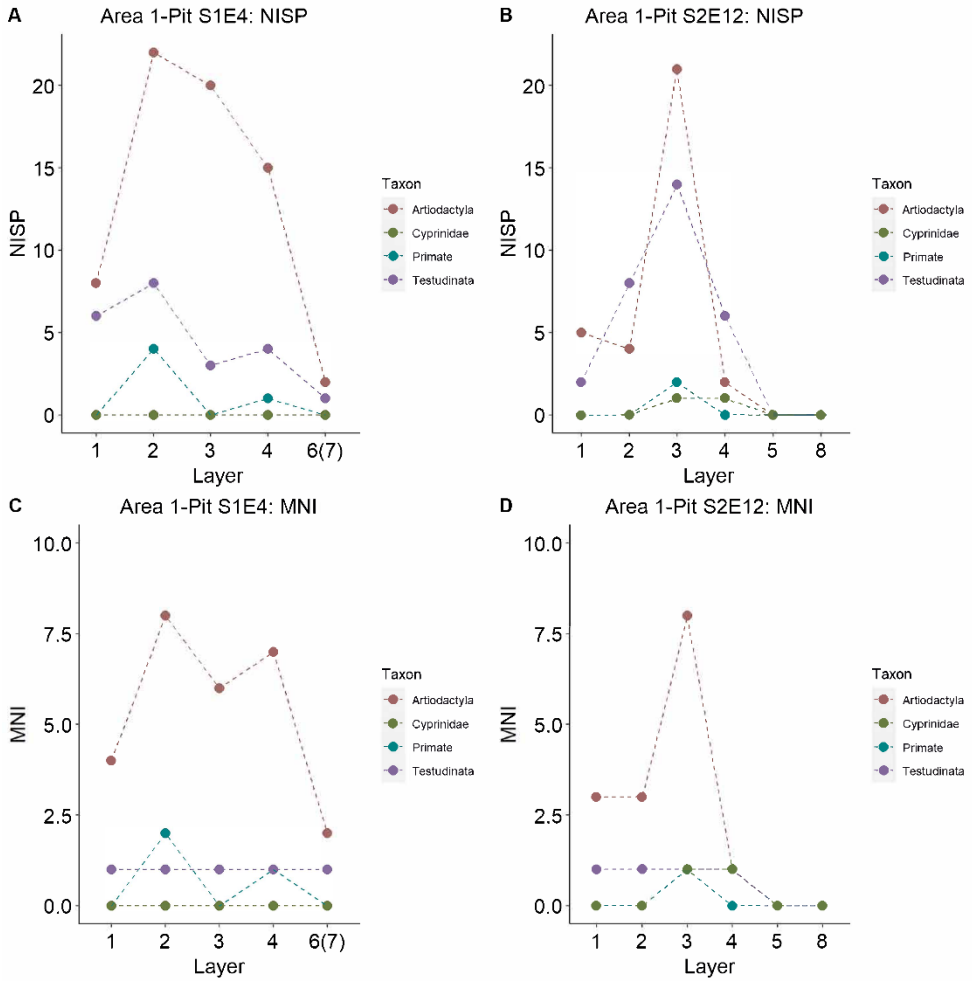


Figure 6. Diachronic change in taxonomic abundance (NISP, number of identified specimens and MNI, minimum number of individuals) within Area 1: (**A**,**C**) S1E4; and (**B**,**D**) S2E12.

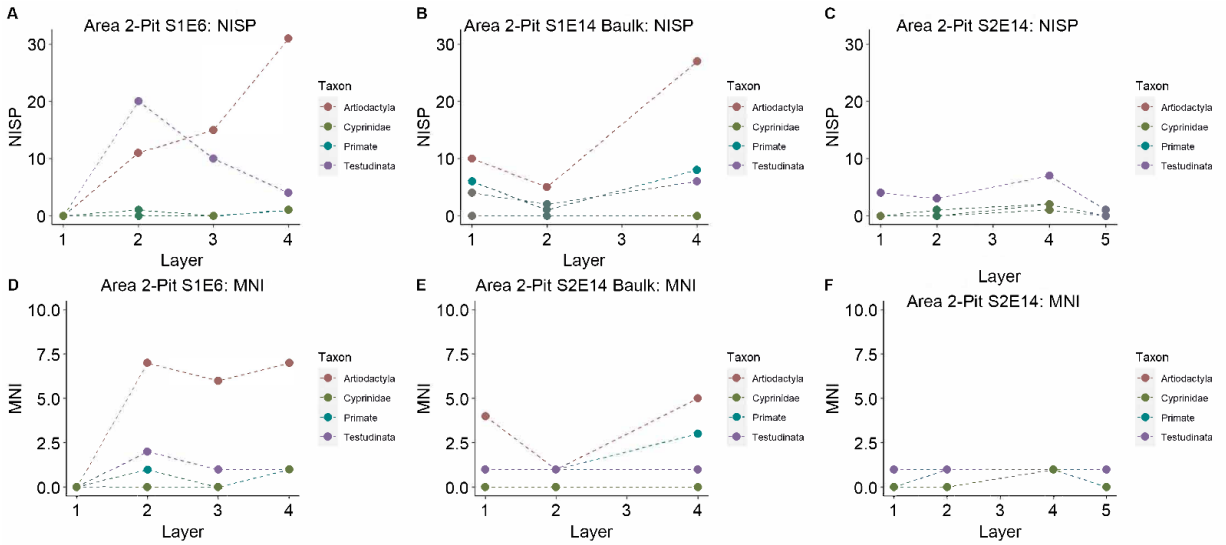


Figure 7. Diachronic change in taxonomic abundance (NISP, number of identified specimens and MNI, minimum number of individuals) within Area 2: (**A**,**D**) S1E6; (**B**,**E**) S2E14 Baulk; and (**C**,**F**) S2E14.

Area 3, with the largest taxonomic richness and abundance of fauna, experienced a relatively consistent pattern of change over time, with artiodactyls, primates, turtles/tortoises, and fishes increasing, up to surface Layers 1–2 (Figures 8 and 9). Primates dominated the taxonomic abundance of this unit in Area 3, suggesting significant exploitation and/or accumulation of these taxa within Middle Holocene contexts at Ban Rai Rockshelter.

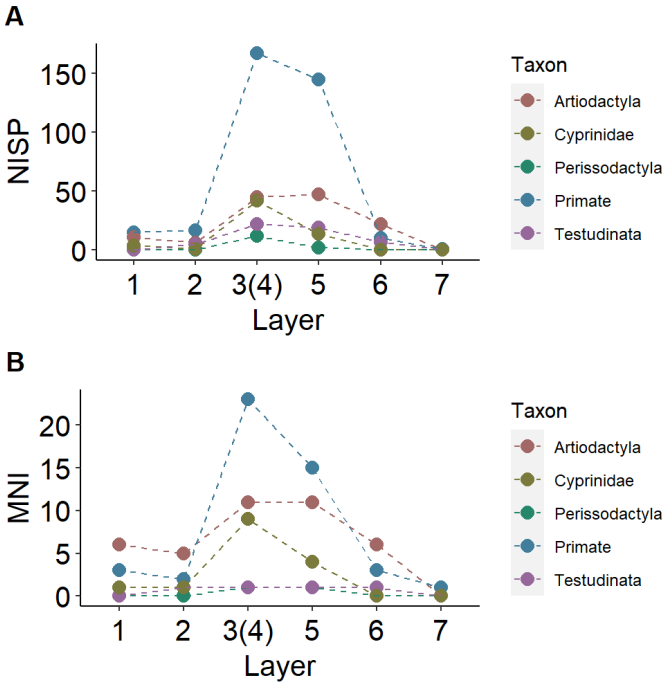


Figure 8. Diachronic change in taxonomic abundance within Area 3 N5E39: (**A**) NISP, number of identified specimens; and (**B**) MNI, minimum number of individuals.

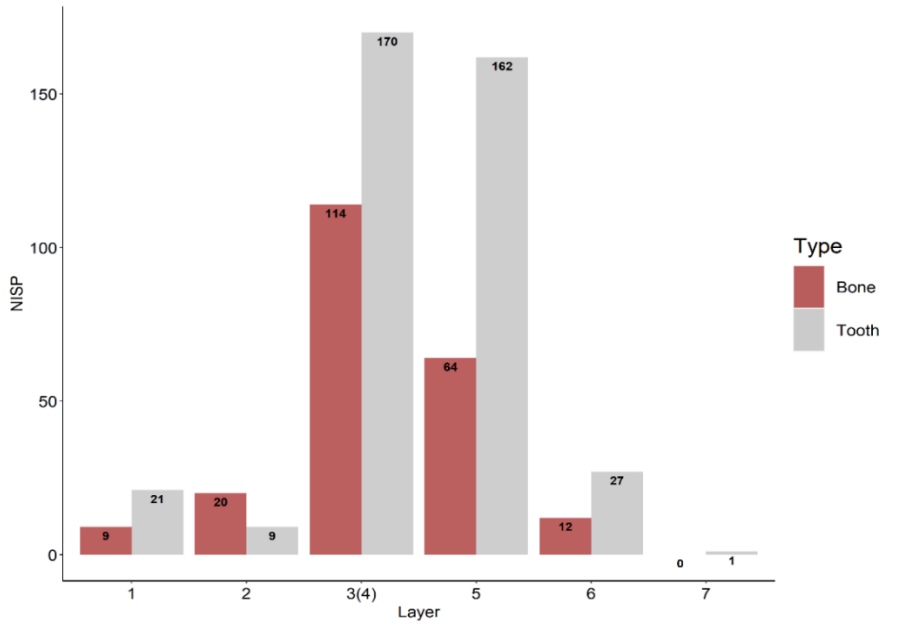


Figure 9. Relationship between identified bone and tooth for Artiodactyla, Perissodactyla, Testudinata, Primates, and Cyprinidae within Area 3 at Ban Rai Rockshelter, listed as the number of identified specimens (NISP).

Table 2. Summary of identified taxa in the Ban Rai Rockshelter zooarchaeological assemblage. Area 1 includes Layers 2–4 of both S1E4 and S2E12. Area 2 includes only Layer 4 of pit S1E6, S2E14, and Baulk S2E14. Finally, Area 3 includes Layers 3, 4, 5, and 6 of pit N5E39. Taxonomic abundance listed as the number of identified specimens (NISP) followed by the minimum number of individuals (MNI); additional data in Supplementary Tables S1–S3.

Taxon	Common Name	Area 1 S1E4		Area 1 S2E12		Area 2 S1E6		Area 2 S2E14		Area 2 Baulk S2E14		Area 3 N5E39	
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Mammalia	Mammal	51	4	29	6	21	4	17	3	51	4	88	5
Manis sp.	Pangolin											1	1
Nycticebus sp.	Loris											1	1
Macaca mulatta	Rhesus macaque											13	6
Macaca arctoides	Stump-tailed macaque											11	7
Macaca sp.	Macaque	1	1	2	1			5	1	2	1	243	19
Cercopithecidae	Old World monkeys	4	2			1	1	8	3			1	1
Trachypithecus cf. *phayrei*	Phayre's langur											2	2
Colobinae	Langur					1	1	2	1	1	1	73	9
Hylobatidae	Gibbon											10	2
Ursus thibetanus	Asia black bear											1	1
Ursus spp.	Bear	1	1									4	2
Arctonyx collaris	Hog badger											1	1
Arctictis binturong	Binturong											1	1
Canis sp.?	Dog											8	2
Panthera sp.	Tiger or leopard											2	1
Felidae	Felids											6	3
Carnivora	Carnivors	1	1	1	1	1	1	3	2			26	5
Elephas sp.	Elephant											4	1
Rhinocerotidae	Rhinoceros											10	2
Sus scrofa	Eurasian wild pig			1	1	3	3					8	4
Muntiacus sp.	Muntjac	8	3	2	2							13	4
Muntiacus feae?	Fea's muntjac							4	2				
Panolia eldii	Eld's deer	10	3	2	2	3	1						

Rusa unicolor	Sambar deer	30	7	20	5	30	4	22	4			33	7
Panolia/Rusa sp.	Sambar/Eld's deer											18	4
Axis sp.	Hog deer	9	5	4	2	8	3	12	1			19	6
Cervidae	Cervids	3	2			1	1					19	4
Bubalus arnee	Wild water buffalo	1	1	1	1							5	3
Bos gaurus	Gaur							1	1			2	2
Bos javanicus	Banteng					1	1						
Bos sp.	Wild cattle	2	2			4	2					6	3
Bovinae	Bovid					1	1	1	1				
Capricornis sumatraensis	Sumatran serow	2	2			5	3			1	1	8	2
Naemorhedus griseus	Chinese goral	1	1										
Artiodactyla	Even-toed ungulates			1	1								
Callosciurus finlaysonii	Variable squirrel											1	1
Petauristinae	Flying squirrel											1	1
Sciuridae	Squirrel											5	2
Leopoldamys sabanus	Long-tailed giant rat											1	1
Bandicota sp.	Bandicoot rat											1	1
Rhizomyidae	Bamboo rat					3	1	1	1	2	2	6	2
Hystricidae	Old World porcupine											19	3
Rodentia	Rodent											29	6
Aves	Bird											1	1
Lacertilia	Lizards											3	2
Testudinata	Turtle	22	5	30	6	2	2	12	3	15	4	53	4
Indotestudo elongata	Elongated tortoise					28	2						
Cyprinidae	Carp or minnow			2	2	1	1			2	1	61	15
Eumalacostraca	Crab									1	1		
	Total	**155**	**43**	**96**	**29**	**119**	**33**	**90**	**24**	**74**	**15**	**818**	**150**

4.2. Taphonomic Insights

Preservation of tooth enamel clearly influenced the composition and identification of faunal remains within Area 3, and was representative of the faunal assemblage as a whole from Ban Rai (Figure 5). In each area and unit, there tended to be larger assemblages of identified teeth in comparison to bone, and in some layers within Area 3 this difference was considerable. For example, in Layer 5, ~72% of the identified zooarchaeological assemblage derived from tooth fragments.

There was also clear sample size influence occurring within the Ban Rai Rockshelter faunal assemblage—largely driven by the abundance and diversity of the Area 3 assemblage, compared to Areas 1 and 2. When including Area 3 (Figure 10), a positive correlation existed between NISP–NTAXA ($r^2 = 0.94$, $p \leq 0.01$) and MNI–NTAXA ($r^2 = 0.97$, $p \leq 0.01$). The inclusion of Area 3 contributed significant leverage to this correlation: when Area 3 was removed from this model, its influence became clear for both NISP ($r^2 = 0.46$, $p = 0.12$) and MNI ($r^2 = 0.63$, $p = 0.07$).

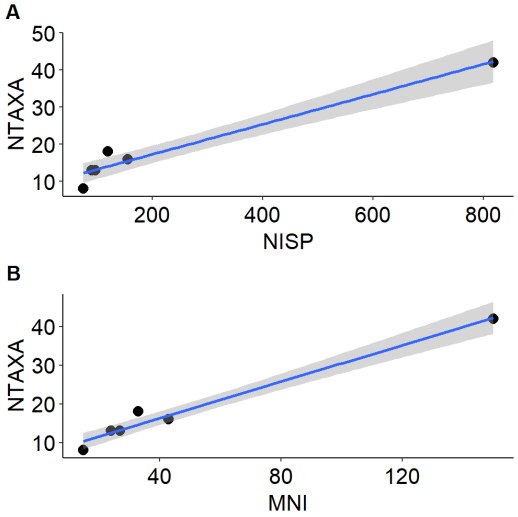


Figure 10. The linear model between taxonomic abundance (NISP and MNI) and taxonomic richness (NTAXA) at Ban Rai Rockshelter (the points represent values per unit in each Area): (**A**) NISP–NTAXA and (**B**) MNI–NTAXA. NISP: the number of identified specimens, MNI: the minimum number of individuals, and NTAXA: the number of taxa identified.

Previous zooarchaeological research at Ban Rai suggests that differential preservation influenced the assemblage [35]. A subset of the assemblage was examined here, and it was discovered that the specimens from Ban Rai contained evidence for bone and tooth weathering, root etching, and rodent/carnivore gnawing [35]. Chemical processes also occurred in specimens, such as calcium carbonate concretions covering the surface of the bones. The nearby and related site of Tham Lod Rockshelter also showed evidence of calcium carbonate formation on bones [7,35] (see Tables 3–6).

For aspects of taphonomic information in Area 1 (Table 3), there was a lack of clear evidence in the lower layers (Layers 5–8), with only one burned specimen observed in Layer 8. The upper layers of Area 1 (Layers 1–4) contained the bulk of the evidence for specimens exhibiting taphonomic processes. In Layer 4, the first evidence of ancient human activity on faunal elements (including butchering, tool marks, and burning) occurred, but the greatest abundance appeared in Layer 3. The upper layers contained several bones with butchering marks, and bones worked into tools. This layer also included a moderate amount of evidence for bone burning. There was a general lack of evidence for chemical alteration in bones from Layers 1–4, or for plant root etching. Little evidence existed from these layers for carnivore and rodent scavenging.

Area 2 exhibited a taphonomic pattern which was similar to Area 1 (see Table 4). Only burned elements occurred consistently in Area 2. From Layer 4 to Layer 1, there were small pieces of possibly worked bone tools, with a small number in each layer. Layer 4 contained the oldest evidence from Ban Rai for human modification of bone, including five butchering marks, 27 bone tools, and a burned element. Butchering evidence only occurred in Layers 1 and 4 with a small number of elements, and there was no evidence for bone weathering. Calcium carbonate concretions occurred on a specimen in Layer 3, and there was root etching evidence in Layer 2. Layers 1–4 also showed moderate evidence of carnivore/rodent gnawing.

Table 5 shows that the trend in Area 3 differed from the trends in Areas 1 and 2. Layer 5 in Area 3 had the most butchered specimens (12 specimens) and the most bone tool specimens (24 specimens) combined. Layers 3 and 4 had the most burnt specimens (72 specimens). There was no weathering and root etching evidence for non-ancient human activity in Area 3. There was some evidence of calcium carbonate concretions in almost all layers, except Layer 5. Consistent evidence for carnivore/rodent gnawing also occurred in all layers.

Consequently, according to taphonomic evidence [35], ancient human activity at Ban Rai Rockshelter was clearly different in Area 3, which corresponded to the area with the largest abundance of faunal specimens and the highest density of charcoal and ash. Root etching and calcium carbonate concretions were generally rare at the site, but carnivore/rodent gnawing and disturbance likely occurred over time. It is important to note that during excavations, porcupines would visit Ban Rai Rockshelter, and there was evidence of areas being disrupted by recent scavengers.

Table 3. Taphonomic evidence in Area 1 of the Ban Rai Rockshelter, in numbers of specimens.

Layer	Butchery Mark [1]	Bone Tool [1]	Burning	Weathering [1]	Chemical Process [1]	Gnawing Damage [1]	Root Etching [1]	Total
1	1	3	15	0	1	5	0	**25**
2	6	7	25	0	0	5	1	**44**
3	8	14	21	1	3	6	0	**53**
4	7	8	10	0	2	4	0	**31**
5	0	0	0	0	0	0	0	**0**
6	0	0	0	0	0	0	0	**0**
7	0	0	0	0	0	0	0	**0**
8	0	0	1	0	0	0	0	**1**
Total	**22**	**32**	**72**	**1**	**6**	**20**	**1**	**154**

[1] Previous data [35].

Table 4. Taphonomic evidence in Area 2 of the Ban Rai Rockshelter, in numbers of specimens.

Layer	Butchery Mark [1]	Bone Tool [1]	Burning	Weathering [1]	Chemical Process [1]	Gnawing Damage [1]	Root Etching [1]	Total
1	3	12	11	0	0	6	0	**32**
2	0	9	21	0	0	4	1	**35**
3	0	4	13	0	1	3	0	**21**
4	5	27	37	0	0	7	0	**76**
5	0	0	3	0	0	0	0	**3**
Total	**8**	**52**	**85**	**0**	**1**	**20**	**1**	**167**

[1] Previous data [35].

Table 5. Taphonomic evidence in Area 3 of the Ban Rai Rockshelter, in numbers of specimens.

Layer	Butchery Mark [1]	Bone Tool [1]	Burning	Weathering [1]	Chemical Process [1]	Gnawing Damage [1]	Root Etching [1]	Total
1	2	2	14	0	1	4	0	**23**
2	1	2	21	0	1	5	0	**30**
3,4	7	12	72	0	4	11	0	**106**
5	12	24	38	0	0	3	0	**77**
6	1	2	13	0	1	1	0	**18**
Total	**23**	**42**	**158**	**0**	**7**	**24**	**0**	**254**

[1] Previous data [35].

5. Discussion

Zooarchaeological analysis of specimens recovered from excavations in Areas 1–3 at Ban Rai Rockshelter provides insights into the patterns of human subsistence within highland, mainland Southeast Asia during the Terminal Pleistocene to Middle Holocene. Our discussion of the results focuses on: (1) the composition of the assemblage, (2) diachronic patterns in faunal exploitation, and (3) overall changes in paleoenvironments and faunas in mainland Southeast Asia.

5.1. Sample Size Influence, Tooth Preservation, and Area 3

Our examination of sample size in the Ban Rai Rockshelter zooarchaeological assemblage clearly indicated that Area 3 was distinct from Areas 1 and 2. When Area 3 was included in the regression model, there was a significant relationship between increasing numbers of identified specimens and increasing numbers of taxa, and this was also true for minimum numbers of individuals; however, the removal of Area 3 from the model also removed the significant statistical relationship between these same variables.

An examination of the taxa of interest (Primate, Artiodactyla, Perissodactyla, Testudinata, and Cyprinidae) indicated that tooth preservation likely influenced the underlying presence or absence of faunal remains. Within Area 3, tooth preservation drove the identification of the majority of taxa, especially taxa identified at species level. Turtles and tortoises were all identified based on bone elements, and thus were identified broadly. When species were identified to genus and/or species level (e.g., *Bos gaurus*), this was typically due to the presence of tooth elements.

While our data did not allow for a further examination of additional taphonomic and fragmentation metrics (e.g., [44,51]; see other examples at Spirit Cave [2]), they did indicate that understanding the spatial context and preservation of the faunal remains at Ban Rai was significant. Areas 1 and 2 included smaller total abundances of specimens and species richness. In contrast, Area 3 was abundant in both species richness and specimens, but the presence of a large number of preserved tooth specimens influenced these counts. The influence of Area 3 on these regression models thus suggested that the unique characteristics of this area's faunal assemblage was meaningful for understanding human subsistence activities at the site.

For example, there was little evidence from the faunal assemblage at Ban Rai Rockshelter to suggest that a non-anthropogenic agent accumulated animal bones and teeth within this site—aside from carnivores and rodents gnawing at bones deposited by past forager occupants. The clear human association with these specimens, and the distinct nature of lithic assemblages—including sumatraliths, core tools, and flakes—in Area 3, suggested that humans occupied and inhabited this portion of the site more frequently than other areas. Area 3 was likely a butchering and habitation area, based on used stone tool debris, faunal remains, and thin charcoal layers. This area of the site also received the most sunlight. According to chronological analyses, the main habitat area at Ban Rai shifted from the center of the rockshelter (Areas 1 and 2) to the east wing (Area 3) [7]. This type of selective hunter-gatherer use of space matches known patterns from elsewhere in Southeast Asia: for example, at Niah Cave, where faunal debris in the inside cave area moves away from the entrance [52,53].

Other contemporaneous prehistoric archaeological sites in Thailand also exhibit evidence for this type of spatially distinct occupation within individual sites. Lang Kamnan in west-central Thailand is a useful comparative example of this type of context [54,55]. At this site, hunter-gatherers occupied certain areas, and then discarded lithic materials and faunal remains against a specific portion of the rockshelter wall. It is likely that a similar situation existed at Ban Rai Rockshelter in Area 3; however, further geoarchaeological research is required to understand if a specific taphonomic process facilitated the preferential preservation of tooth enamel within Area 3, in comparison to Areas 1–2.

5.2. Long-Term Subsistence Change

Recent evidence from several sites suggests that at some time during the Holocene, a shift towards the exploitation of primates and other arboreal taxa occurred throughout mainland and island Southeast Asia [2,8,56,57]. Paleoenvironmental research indicates the replacement of open grasslands by forested areas after the Last Glacial Maximum period [12,58,59], and this likely drove a transition away from higher abundances of Artiodactyla in the environment. During this period, arboreal and terrestrial forest taxa appear to have

increased in the environment, and hunter-gatherers appear to have adapted their exploitation strategies to hunt these newly abundant preys. As with other nearby and contemporary sites (e.g., Ban Tha Si and Doi Pha Kan in Lam Pang province [60–62], and Spirit Cave, Steep Cliff Cave, and Banyan Valley Cave in Mae Hong Son province [1–3]), the fauna of Ban Rai Rockshelter is dominated by arboreal taxa, especially primates in Area 3. This differs slightly from sites dominated by artiodactyls during this period (e.g., Doi Pha Kan and Steep Cliff Cave), and suggests that the transition towards arboreal fauna was relatively consistent throughout northwest Thailand during the Early–Middle Holocene.

At Ban Rai Rockshelter Areas 1 and 2, both dating to the Terminal Pleistocene, assemblage data included evidence for the exploitation of artiodactyls and turtles/tortoises; however, there was possible change over time in the abundance of artiodactyls in each area—or, in this case, change in hunter-gatherer exploitation strategies. Sambar deer abundance likely influenced this change, as they were not present in the deepest layers of either area, but increased in abundance through time, before decreasing again in the upper layer of each context. A decrease in artiodactyls during this Terminal Pleistocene period is relevant, as it relates to the faunal assemblage from Area 3.

In Area 3 deposits dating to the Early and Middle Holocene, there was a substantial increase in the abundance of primates, beginning in Layer 5. Artiodactyls, turtles/tortoises and fishes also increased over time, but in lower comparative abundance than primates. In these contexts, within Area 3, primates dominated the total NISP and MNI for the unit: they only decreased in abundance, along with all other taxa, in the upper layers of this area.

In light of the above considerations, we diagnosed the relationship between artiodactyl exploitation in Areas 1–2 and primate exploitation in Area 3, based on the differences in the chronological age of each context. The findings suggest that hunter-gatherers occupying Ban Rai Rockshelter shifted their exploitation of arboreal prey to include primate taxa during the Pleistocene–Holocene transition or shortly thereafter.

Evidence from Late Pleistocene sites, such as Tham Lod Rockshelter [7,35], Ban Tha Si [60,61], and the Late Pleistocene Layers of Niah Cave [52,53] suggest that the subsistence patterns present during the Late Pleistocene focused on ground-dwelling prey, which shifted during the Early Holocene. Increased primate and arboreal exploitation identified throughout Southeast Asia at this transitional period—including Holocene Layers at sites such as Moh Khiew II [63], Niah Cave [52,53], and Song Gupuh [64]—helps support this record.

A relevant example to the pattern of shifting faunas and human exploitation identified at Ban Rai Rockshelter was found at Braholo Cave and Song Terus [56,57], in eastern Java. Braholo Cave and Song Terus, also dating to the Terminal Pleistocene/Early–Middle Holocene, are dominated by non-human primate specimens. Javan langur (*Trachypithecus auratus*) is the most abundant Cercopithecidae present, accompanied by long-tailed macaque (*Macaca fascicularis*) and Javan surili (*Presbytis comata*)—all of which were identified through analysis of dental morphology and metrics. In contrast to Ban Rai Rockshelter, the identified skeletal assemblages from Braholo Cave and Song Terus contained a large number of post-cranial (non-tooth) elements: these specimens were specifically collected by past hunter-gatherers focused on the manufacture of bone tools—especially at Song Terus, where there was dedicated production of bone tools. This suggests that, while our determination of animal exploitation and change identified within the Ban Rai Rockshelter deposits is similar to patterns found throughout Southeast Asia, the exact preservation and taphonomic processes occurring within each site's zooarchaeological assemblage significantly impacts the way in which those determinations are supported. At Ban Rai, preserved tooth elements support a shift towards arboreal taxa during the Holocene.

5.3. Changes in Paleoenvironments and Paleofaunas

During the Terminal Pleistocene to Middle Holocene, the overall paleoenvironment of northern Thailand was a closed-canopy semi-tropical rain forest with more stable humidity and temperature [65], and limited montane forest at higher elevation, separated by a grassland and open-canopy woodland in the inland [12,13,20,21]. Meanwhile, sea level increased and transgressed in Thailand's central plain and south and east coastlines [65–67], as supported by marine environmental proxy data from continental sites far distant from the modern sea level [68,69]: coastal mud, mangrove pollen, marine shell, and corresponding high precipitation, and increased wetland and water resource areas, occurred in Thailand's interior [68,69].

Thus, an increased arboreal faunal diet for hunter-gatherers at Ban Rai Rockshelter is a useful proxy for understanding the highly stratified closed-canopy rainforest change that occurred during the end of the Pleistocene to the Middle Holocene. The remains of ground dwelling fauna—such as gaur, serow, hog deer, sambar deer, elephant, long-tailed giant rat, hog badger, and more (following previous studies [1,8] and an earlier isotope analysis on faunal teeth [12,13])—suggest the presence of a denser rainforest. A few of these ground-dwelling animals appear at Ban Rai Rockshelter, such as Asian black bear, Eld's deer, bamboo rat, goral, and wild water buffalo, which matches the evidence we expect for a transition from a partly open environment (such as an open-canopy woodland/grassland) to a montane forest and swamps (or muddy swamps) around the valley river [1,8,70,71].

Zooarchaeological evidence dating from the Terminal Pleistocene to the Middle Holocene at Ban Rai Rockshelter highlights the importance of arboreal taxa in prehistoric human diets, and supports a pattern that matches broader scale paleoenvironmental and paleoclimate changes in this region.

6. Conclusions

Three excavated areas at Ban Rai Rockshelter in Pang Mapha District, Mae Hong Son Province, northwest Thailand, establishes a zooarchaeological sequence suggesting specific exploitation of artiodactyls, primates, turtles, tortoises, and fishes throughout the Terminal Pleistocene and Holocene. Area 3, with the largest and most diverse faunal assemblage, suggests that hunter-gatherers focused their occupation of the site in this area; however, poor preservation of bone influenced the identification of taxa within this site assemblage. The shifting abundance of primate exploitation over time indicates that arboreal fauna became increasingly important for human subsistence during the Holocene era. These results add to a growing body of research suggesting that paleoenvironmental change, tied with faunal shifts and changing human population densities, led to differing human adaptations throughout the Southeast Asian tropics after the Last Glacial Maximum.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/quat5040051/s1: Table S1—Taxonomy and profile of Pit S1E4 and S2E12 of Area 1; Table S2—Taxonomy and profile of Pit S2E14, Baulk S1E14 and S1E6 of Area 2; Table S3—Taxonomy and profile of Pit N5E39 of Area 3.

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