Paleoenvironment in East Java during the Last 25,000 years as Inferred from Bovid and Cervid Dental Wear Analyses

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Abstract

This paper reports the results of dental mesowear and microwear analyses of bovid and cervid specimens recovered from Late Pleistocene to Middle Holocene deposits of Braholo Cave and Song Terus in Eastern Java. The aim is to infer ungulate dietary traits from dental wear signatures and gain insights regarding the paleoenvironment of the region during the last 25,000 years, a period of drastic climatic fluctuations. We considered three cervid (*Rusa, Axis* and *Muntiacus muntjak*) and two bovid (*Bubalus* and *Bos javanicus*) taxa in the analyses. Results from both cave sites suggest that the Pleistocene-Holocene transition was accompanied by expansion of rainforests as evidenced by the predominance of species that had a browsing or browse-dominated mixed diet. However some of the taxa examined exhibited strong grazing signatures indicative of the continued presence of patches of grasslands up to the Mid-Holocene. Dental wear signatures of specimens from layers dating to the Last Glacial Maximum (LGM) suggest a mosaic environment dominated by grasslands. In Braholo Cave, we observed discrepancies between the mesowear and microwear signatures in specimens dating to the LGM and we take this as evidence of seasonality during this period. The results of the study provide important information on the environments encountered by the hunter-gatherer communities that lived in East Java in periods of climatic change.

Keywords: Microwear, Mesowear, Diet, Southeast Asia, Seasonality

Highlights

- Dental wear analyses of bovid and cervid specimens from two cave sites in Eastern Java.
- Pleistocene-Holocene transition was accompanied by rainforest expansion.
- There was continuous presence of patches of grasslands up to the Mid-Holocene.
- A grassland-dominated mosaic environment during the Last Glacial Maximum (LGM).
- Evidence for the presence of seasonality during the LGM.

1. Introduction

The end of the Pleistocene in Southeast Asia saw pronounced climatic fluctuations, including significant shifts in temperature and precipitation patterns. It also saw rapid sea level rise and drastic inundation of coastal margins resulting in the current configuration of Island Southeast Asia (ISEA). At the height of the LGM, Java, Sumatra, Bali and Borneo were connected to mainland Southeast Asia forming a massive equatorial continent that covered an area of 1.8 x 10^6 km^2 (Verstappen, 1975; Fairbanks, 1989; Hanebuth et al. 2000; Voris, 2000). Computer simulations (Bush and Fairbanks, 2003; Cannon et al. 2009) suggest that such a massive exposed landmass, approximately 75% larger than what exists today, would have had greatly impacted prevailing rainfall, sea currents and wind patterns giving rise to drier and cooler climatic conditions and in turn the predominance of seasonal forests and/or savannah type vegetation (Heaney, 1991; Bird et al. 2005; Wurster et al. 2010; Rabett, 2012). Direct evidence, however, varies from site to site. In some areas, palynological and sedimentological analyses suggest the dominance of grasslands (van der Kaars and Dam, 1995; van der Kaars et al. 2001; Morley,

2000; Sun et al. 2003, Wurster et al. 2010) whereas in other areas evidence indicates the presence of vast stretches of rainforests (Kershaw et al. 2001; Sun et al. 2002; Hu et al. 2003; Kershaw et al. 2007; Wang et al. 2009).

The end of the Pleistocene was also characterized by notable shifts in the lifeways of people that inhabited the region, including significant technological innovations and changes in their subsistence economies. Analyses of faunal remains from numerous archaeological sites in ISEA revealed that the people that inhabited the sites developed a wide range of hunting and foraging techniques to take full advantage of the resources available in the environment (e.g. Barker et al. 2007; Piper et al. 2008; Piper and Rabett, 2009; Rabett, 2012; Amano et al. *in press*). Interestingly, there is an abundance of archaeological evidence in ISEA dating to the Pleistocene-Holocene transition, perhaps indicative of increase in human population size or intensification in the occupation of the sites (Simanjuntak, 2002,2004; Sémah et al. 2004b; Barker, 2005; Barker et al. 2007; Lewis et al. 2008; Rabett, 2012; Pawlik et al. 2014).

Knowledge of the vegetation and environment of ISEA during the Pleistocene-Holocene transition is important in understanding patterns of human behavior. Several paleoenvironmental proxies provide important information on vegetation changes from the LGM to the start of the Holocene, although the coverage of these datasets is still comparatively fragmentary. For example, in the island of Java only four pollen sequences dating to the period have been reported so far. Pollen cores from the Ambarawa basin of Central Java showed a change from a mosaic of submontane forests and open grasslands during the LGM to the dominance of rainforests during the Pleistocene-Holocene boundary (Sémah et al. 2004a). In Western Java, the pollen records from Rawa Danau (100 mASL, van der Kaars et al. 2000) and Bandung (665 mASL, van der Kaars and Dam, 1995; van der Kaars, 1998) suggested cool, dry climatic conditions and the presence of an open environment dominated by grasses and sedges from the LGM through the Terminal Pleistocene. In Rawa Danau the onset of the Holocene coincided with the development of fern-rich closed forest vegetation type (van der Kaars et al. 2000). The pollen record of Situ Bayongbong in the highlands of West Java 1300 mASL, also provided evidence for a much colder climatic condition and the predominance of montane forests dominated by conifers from the LGM through the Terminal Pleistocene. However there was no observed change in rainfall pattern as the taxa consistently represented in the pollen cores, such as *Schima* and *Altingia*, indicate an ever-wet climate (Stuijts, 1993). Studies looking at modern biogeography (e.g. Gathorne-Hardy, 2002; Meijaard, 2003) have also provided clues to the past environment and landscape configuration in Java. Recent investigations have considered other proxy evidence to reconstruct past vegetation in the region, including biomolecules (Tareq et al., 2004) and carbon isotopes (Dubois et al., 2014).

The results of these studies highlight the importance of looking at more sites and using other proxies to gain a more complete picture of the paleoenvironment of Java at this period. Methods looking at diet reconstruction of ungulates through dental wear analyses could supplement available paleoenvironmental data and provide important information on the vegetation of the region during this key period of human history. Dental wear analyses (microwear and mesowear) allow for the reconstruction of the vegetation encountered by animals immediately before their death (e.g. Grine, 1986; Mainland, 1998; Rivals et al. 2009). Because these ungulate remains are from archaeological sites, they can also provide insights on human subsistence economies. Specifically they could give information on the range of habitat types exploited by prehistoric human populations for hunting and foraging.

In this paper we looked at mesowear and microwear patterns in cervid and bovid dental specimens from Braholo and Song Terus, two cave sites in East Java. The specimens were from stratigraphic layers dated from the LGM through Mid-Holocene. Mesowear is based on the physical properties of foods as reflected in the amount of attritive and abrasive wears on the occlusal surface of ungulate molars. First introduced by Fortelius and Solounias (2000), mesowear is recorded by characterizing the sharpness (whether sharp, rounded or blunt) and relief (high or low) of the buccal apices of molar tooth cusps. Numerous studies considering both modern and extinct species have demonstrated the utility of mesowear analysis in testing hypotheses related to paleodiet and paleoenvironment reconstruction (Kaiser et al. 2000; Kaiser and Solounias, 2003; Rivals et al. 2007; 2008; 2009; Semprebon and Rivals, 2007; 2010; Mihlbachler et al. 2011; Rivals and Semprebon, 2012).

Dental wear in browsers, which have low abrasion diets, is generally attritional and is characterized by sharp buccal cusp apices. Grazers, in contrast, have more rounded and blunted molar apices resulting from abrasive diets (siliceous grass) and grit ingestion (feeding near the ground).

Microwear analysis, on the other hand, looks at microscopic scratches and pits produced on the surface of the tooth enamel resulting from the abrasive actions of particles present in the food, including phytoliths that are inherent in plants and exogenous materials such as dirt or grit. The exact mechanisms by which these materials affect microwear patterns, and how they relate to other factors such as tooth morphology, enamel hardness and masticatory biomechanics, are recently beginning to be understood (Semprebon et al., 2004; 2015). Studies have pointed out the importance of exogenous particles, such as quartz dust and enamel chips, in producing microwear scars (Lucas et al., 2013; Schulz et al., 2013; Müller et al., 2014; Hoffman et al., 2015). Controlled animal feeding experiments have provided insights on the factors that cause dental microwear (Schulz et al., 2013; Hoffman et al., 2015). For example Hoffman et al. (2015) performed controlled feeding experiments with domesticated sheep to assess the abrasive effects of exogenous silica particles and found an increase in the number of pits correlated with exogenous grain particle size. They noted that "that microwear can be affected by environment as well as diet" and that following Solounias and Semprebon's (2002) observation, "increased rates of pitting observed in ungulates from semi-arid and arid environments reflect grit consumption. (Hoffman et al., 2015: 1544)." Consideration of these factors is relevant to all microwear approaches.

We performed both mesowear and microwear analyses which allowed for the reconstruction of ancient bovid and cervid diets over very different time scales. Mesowear analysis looks at general tooth occlusal morphology resulting from attrition and abrasion over long periods, usually years or several months, of an ungulate's life (Fortelius and Solounias, 2000). Microwear patterns, in contrast, have a high turnover from hours to several days, usually reflecting an ungulate's last few meals (Grine, 1986; Teaford and Tylenda, 1991; Solounias and Semprebon, 2002). Together these two approaches provide a detailed picture of the environments encountered by human populations present in East Java from the LGM to the Mid-Holocene.

2. The Cave Sites

Braholo Cave and Song Terus are located in the karstic Gunung Sewu ('Thousand Hills') region of East Java, approximately 40 km away from each other (Figure 1A). The Gunung Sewu region is known for more than 135 surveyed archaeological sites some of which produced evidence of human occupation from the last 150,000 years (Simanjuntak, 2002; Simanjuntak and Asikin, 2004; Sémah et al. 2004b; Hameau et al. 2007; Westaway et al, 2007; Morwood et al. 2008). Because of its location along the southern Javanese coast, the current climatic conditions in the Gunung Sewu region are strongly influenced by the Northeast and Southwest Monsoons, producing a distinct dry season, which could be very arid, between May and September and a wet season from October to April (Haryono and Day, 2004). Braholo Cave is located on the westernmost part of Gunung Sewu whereas Song Terus is in the eastern region. Currently, there is a significant difference in terms of vegetation cover between the western and eastern regions of Gunung Sewu, with the eastern region characterized by open, dry vegetation type with some clusters of dry forests whereas the western region is dominated by secondary monsoon forests. Whether such difference in vegetation cover existed in the past and in what extent remains to be seen, but it raises interesting questions especially with regard to human subsistence economies. Ongoing analysis (see also Amano et al. *in press*) reveal the presence of some animal taxa present in great numbers in Braholo Cave that are rare or absent in Song Terus (and vice versa) such as muntjak, slow loris, flying lemur and softshell turtles.

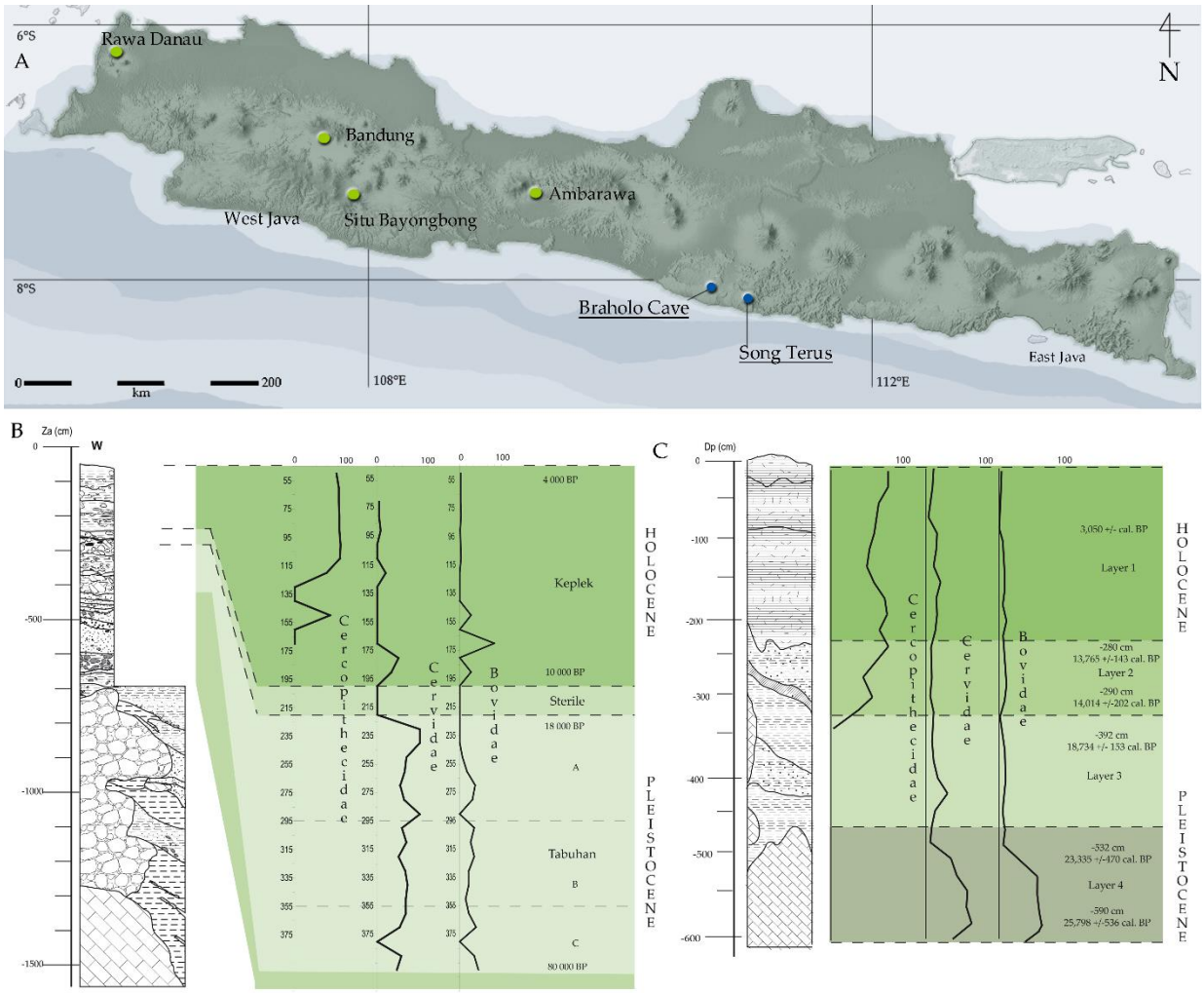

Figure 1. Location (A) and stratigraphy of Song Terus (B) and Braholo Cave (C). The figure also shows the distribution of selected animal taxa across the stratigraphic layers (after Simanjuntak, 2002; Sémah and Sémah, 2012; Amano et al. *in press*) and the location of pollen sites mentioned in the text.

2.1 Song Terus

Song Terus is located in Pacitan, East Java near the village of Punung at 8°7'11" S, 111°1'57"E. The cave is approximately 100 m long, 20 m wide and its entrance is at 333 mASL (Sémah et al. 2004b). Systematic excavations in the cave began in 1994 and have yielded well stratified archaeological deposits of more than 15 m deep and thousands of archaeological materials including lithic artifacts and faunal remains (Figure 1B). The stratigraphy of the site is divided into three general phases (Sémah et al. 2002; 2004b; Hameau et al. 2007; Sémah and Sémah, 2012):

Terus layers: The lowermost and chronologically oldest layers which are remnants of fluvial terraces have yielded animal remains as well as numerous patinated stone tools. Coupled ESR/U-Series dating of rhinoceros and tapir teeth associated with lithic artifacts from these layers provided consistent ages of 254,000 $\pm$ 38 000 BP and 341,000 $\pm$ 51 000 BP (Hameau et al. 2007).

Tabuhan layers: Extending from 2.1 to 4 m below the surface, the layers were dated to 80,000-18,000 BP and yielded evidence of human occupation in forms of hearths and animal bones with traces of butchery (Hameau,

2004; Kusno, 2009; Sémah and Sémah, 2012). The upper part of the Tabuhan layers (designated as Tabuhan A) was dated to 30,000 - 18,000 BP. It had a distinct faunal composition characterized by the predominance of cervids, bovids and suids.

Keplek layers: The upper occupational level yielded numerous faunal remains, bone and shell tools, and large amounts of stone flakes. It has been dated to 11,200 ± 600 - 5770 ± 60 years BP (Sémah et al. 2004b). A human burial dated to 9000 BP was recorded in these layers and morphometric analyses of the individual suggested Australo-Melanesian affinity (Détroit, 2002; 2006; Sémah and Sémah, 2012).

A phase of occupational hiatus notably devoid of any artifacts and corresponding to an intensification in karst formation separates the Keplek from the Tabuhan layers. This hiatus marks the Pleistocene-Holocene boundary in the cave stratigraphy (Sémah et al. 2004a; Sémah and Sémah, 2012). Deposits from this phase yielded pollen and spores from lowland rainforest taxa (Podocarpaceae, Dipterocarpaceae, Fagaceae and Pteridophytes) which is in stark contrast from the open environment pollen taxa recorded in the Terus Layer (Poaceae, Asteraceae and Casuarinaceae). The faunal remains from the Pleistocene-Holocene layers of Song Terus are markedly different from those recorded in older layers, with the appearance of new suids, *Elephas* sp. and cercopithecids (*Macaca fascicularis* and *Trachypithecus auratus*) suggestive of forest expansion at the onset of the Holocene (Sémah et al. 2004a; Ingicco, 2012; Sémah and Sémah, 2012).

2.2 Braholo Cave

Braholo Cave is located on the edge of Central Java's Wonosari plateau, around 13 km away from the present-day southern Javanese coast, close to the village of Semugih at 8° 4' 52.1" S, 110° 45' 18.5" E. It is on the slope of a ca. 45 m high limestone hill and has a 15 m high northwest entrance, a domed ceiling reaching ca. 12 m and a floor area of ca. 600 m². Braholo Cave was excavated between 1997 and 2007 by the Indonesian Center for Archaeological Research. The cave has well stratified archaeological deposits dated between 25,798 ± 536 and 3050 ± 100 cal. BP (Simanjuntak 2002). Excavations yielded numerous archaeological materials including those usually associated with the Neolithic of Southeast Asia such as pottery, shell ornaments and polished stone adzes, as well as numerous artifacts typical of the pre-Neolithic of Java such as stone and osseous tools and modified animal bones and teeth. But most notable is the amount of faunal remains recovered from the site, with more than 400,000 animal bone fragments collected. A series of human burials were also recorded in Braholo, including a primary flexed inhumation dated to 9780 ± 230 BP and a secondary burial with associated charcoals yielding a date of 8760 ± 170 BP (Simanjuntak, 2002; Detroit, 2006). Akin to the remains found in Song Terus, analyses suggested that the morphologies of the individuals in the burials were within the Australo-Melanesian range (Widianto, 2002; Detroit, 2002).

The stratigraphy of Braholo Cave was characterized by a series of two distinct sedimentary deposits: dark brown silty clay deposits that extended from around 200 to 700 cm and dated from 33,100 ± 1260 BP to 11,940 ± 160 BP overlain by loose reddish brown sandy clay layers which extended from 40 to around 200 cm below the surface and which yielded dates between 8,500 ± 230 BP and 3,050 ± 100 BP. Within the upper sandy clay layers were notable concentrations of burnt animal bone fragments and hearths. In contrast, several white to dark gray ash layers presumed to be of volcanic origin were sandwiched by the dark brown silty clay deposits. Four chronological phases/layers were identified in Braholo based on site stratigraphy and chronology and the sorting of the faunal remains across stratigraphic layers, as well as taxon distribution and taphonomy (see Amano et al. *in press*). The layers are (dates from Simanjuntak, 2002):

Layer 4- dated to around the LGM, 33,100 ± 1260 BP to 21,210 ± 730 BP
Layer 3- post-LGM layer with dates of 19,570 ± 350 BP- 15,520 ± 520 BP
Layer 2- from the Pleistocene-Holocene boundary with dates of 12,200 ± 160 BP to 11,940 ± 160 BP
Layer 1- Early-Mid Holocene layers with the youngest date obtained at 3,050 ± 100 BP

A total of 17 radiocarbon dates mostly from charcoal anchor the stratigraphy of the site to consistent chronology (i.e. no inversions) from the LGM to the Holocene. For the purpose of this paper, we will rely on these dates, albeit we are in the process of confirming/obtaining a series of new dates for the site. Akin to Song Terus, a

clear biostratigraphical boundary between the Pleistocene and the Holocene was recorded in Braholo Cave. Analyses of faunal remains from reveal a clear trend: the high proportion of taxa adapted to an open environment around the LGM and the subsequent predominance of arboreal and semi -arboreal species during the onset of the Holocene. The presence of forest-adapted species, such as macaques and tree squirrels, in the LGM layers as well as species that usually occur in disturbed environments, forest edges and grasslands in the Early-Mid Holocene suggest the presence of a mosaic of environments in the region surrounding the cave throughout site occupation (Amano et al. *in press*).

3. Materials and Methods

The materials analyzed for this study came from all the archaeological layers of Braholo Cave and the Tabuhan A and Keplek layers of Song Terus. The sample was comprised of upper and lower second molars from different bovid and cervid taxa. Two bovid taxa were identified in both cave sites, *Bubalus* sp. and *Bos javanicus*, differentiated from each other by tooth size and morphology. Cervid remains from the sites, on the other hand, were grouped into three taxa, *Muntiacus muntjak*, *Rusa* and *Axis*, with the large non-muntjak cervids assigned to *Rusa* and the smaller specimens to *Axis* (Sémah and Sémah, 2012; Amano et al. *in press*). For mesowear analysis, a total of 164 samples (107 from Braholo Cave and 57 from Song Terus) were included. On the other hand, a total of 159 dental specimens were sampled for microwear analysis, including 107 from Braholo Cave and 57 from Song Terus (summarized in Table 1, including number of samples per taxa and per layer). The study also included comparative reference samples of Southeast Asian bovid and cervid species from the Comparative Anatomy laboratory of the *Muséum national d'Histoire naturelle*, University of the Philippines Archaeological Studies Program and the field collection of the *Mission Quaternaire et Préhistoire en Indonésie*/Indonesian National Research Centre of Archaeology (summarized in Table 2). The specimens were carefully screened and those that were in good conditions (i.e. without taphonomic alterations or damage in the enamel resulting from recovery or storage) and with visible wear facets in the occlusal surface were included in the study.

3.1 Microwear

We followed the protocol for microwear analysis outlined by Solounias and Semprebon (2002) and Semprebon et al. (2004a; 2004b). The specimen's occlusal surfaces were molded using high-resolution polyvinyl siloxane (Heraeus Provil® Novo) and transparent epoxy resin (CTS® EPO 150) casts were made from the molds. The casts were examined using a Zeiss Stemi 2000c stereomicroscope under incident light at 35x magnification. We looked for microwear features, including scratches and pits, in unaltered enamel surfaces on the protoconid of lower second molars and paracone of upper second molars. Following Solounias and Semprebon (2002) and Semprebon et al. (2004a), we identified pits as microwear scars that have more or less similar widths and lengths giving them a circular appearance while scratches as elongated scars with straight parallel sides. The number of pits and scratches were counted in a 0.4 mm x 0.4 mm square area using an eyepiece reticle as guide. Scratch and pit counts were obtained from two distinct areas of the enamel band and were averaged for each specimen. We then calculated the average number of scratches and pits for each species in an archaeological layer.

By counting the number of pits and scratches, and using a reference database constructed from extant taxa (Solounias and Semprebon, 2002), it is possible to differentiate between grazers (ungulates that feed on grass), browsers (those that feed on dicotyledonous plants) and mixed feeders (ungulates that feed on grass, forb and browse). Grazers, because of their reliance on highly siliceous plants, usually show a higher number of scratches than browsers. Browsers, on the other hand, have larger variations in the number of pits than scratches in contrast to grazers. Mixed feeders have microwear signals that overlap with those of browsers and grazers and are classified as either seasonal/regional mixed feeders or meal-by-meal mixed feeders. To separate the

mixed feeders from browsers and grazers, we calculated the percentage of individuals in a sample with a number scratches between 0 and 17 (% LSR, based on Solounias and Semprebon, 2002; Semprebon and Rivals, 2007; Rivals and Semprebon, 2012). Browsers have a higher percentage of individuals with a lower number of scratches (72.7-100%) than grazers (0-22.2%). In contrast, 20.9- 70% of mixed feeding populations have individuals with low scratch numbers (no overlap between browsers and mixed feeders and very small overlap between grazers and mixed feeders).

In addition to counting the number of pits and scratches, we noted and scored the relative size of pits (large vs small) and texture of scratches (fine, coarse, mixed) as well as the presence of cross scratches and gouges. Scoring of these parameters allows the identification of habitat differences and niche partitioning, thereby refining the categorization of ungulate samples beyond the broad trophic groups of grazer/browser/mixed feeder (Solounias and Semprebon 2002; Semprebon et al. 2004a; Semprebon and Rivals, 2007; Rivals et al. 2009; Rivals and Semprebon, 2012). Large pits are easily differentiated as they have at least twice the diameter of smaller pits. They are also deeper, less refractive and characterized by less regular outlines. Coarse scratches are deeper and wider and have higher refractivity than do fine scratches. Samples in the 'mixed' category have high proportion of both fine and coarse scratches in the same enamel band (Solounias and Semprebon 2002). Following Rivals et al. (2007a), scratch textures were converted to scratch width score (SWS) with samples having only fine scratches given a score of '0', those with only coarse scratches '2' and a score of '1' for samples in the mixed category. Individual scores were averaged to obtain the SWS. Cross scratches are defined as those that were oriented perpendicular to the majority of the scratches in the observation field and the presence or absence of more than four cross scratches in the 0.16 mm^2 observation field was recorded. Gouges are large pit-like scars with distinctive, irregular edges and their presence or absence was also recorded (Figure 2).

3.2 Mesowear

In this paper, we followed the standardized mesowear method by Mihlbachler et al. (2011) wherein specimens are given scores ranging from 0 to 6 based on shape and relief of molar cusp apices. Specimens with high and sharp cusps were given a score of 0, those with rounded cusps and high relief a score of 2. Teeth with rounded cusps and low relief were assigned a score of 4 and molars with cusps that were completely blunt and without relief were given a score of 6 (see also Fortelius and Solounias, 2000; Rivals et al. 2009; Rivals and Semprebon 2012; Sánchez-Hernández et al. *in press*). Because mesowear is affected by the age of an individual (Rivals et al. 2007b), heavily worn (or worn nearly to the dentinoenamel junction, from old individuals) and unworn (from young individuals) specimens were excluded from the analysis. We also omitted from the study specimens with taphonomic alterations (i.e. severe $CaCo_3$ concretion) as well as those with broken or damaged cusp apices.

4. Results

Throughout the stratigraphic sequence, the microwear scores (MWSs) for cervid specimens in Braholo Cave ranged from 0.6 to 2, indicative of mixed feeding and browsing habits (Table 1). This was in contrast to the MWSs for the bovid specimens, which ranged from 1.8 to 3.2, suggesting habits that varied from browse-dominated mixed feeding to grazing. Generally we observed a trend of decreasing MWS, from older to younger stratigraphic layers, in all specimens examined except for *Axis* and *Bubalus*. *Muntiacus* from Layer 3 (post-LGM) had an MWS of 1.3 and an MWS of 0.6 in Layer 1 (Early-Mid Holocene). Similarly, *Bos* had MWSs that ranged from 3.2 in Layer 4 (LGM) to 1.8 in Layer 1. In contrast, *Bubalus* specimens had little variation across time (MWS: 2.67-3). *Axis* from the Holocene layer had an MWS of 0.8 suggestive of a browse-dominated diet. From Layer 2 (Pleistocene-Holocene boundary) to Layer 4 however, the mesowear scores of *Axis* indicated a mixed feeding habit that more or less stayed the same (MWS: 1.83-2). *Rusa*, the other large cervid present in the zooarchaeological assemblage of Braholo Cave, also exhibited MWSs (1.67-2) typical of a low-abrasive diet. This is interesting especially considering that the bovids in the assemblage showed higher MWSs (2.8-3.2) in the same period.

In Song Terus, where there is a notable absence of *Muntiacus* specimens, the cervids had MWSs that varied from 1.5 to 2.7 (mixed feeders). Bovids on the other hand had MWSs that ranged from 2.5 to 3.2 or mixed to grazing feeding habits (Table 1, Figure 3B). Akin to those in Braholo Cave, *Axis* specimens from Song Terus for both the Keplek and Tabuhan A layers had mesowear signatures indicative of a browse-dominated mixed feeding diet (MWS: 1.5-2.08). *Rusa* specimens from Keplek and Tabuhan A had more or less the same MWS (2.67-2.4), which are very similar to those obtained for *Bos* (MWS: 2.5). These mesowear scores indicate grass dominated mixed feeding. We also observed signatures for grass dominated mixed feeding in the *Bubalus* teeth we examined from the Keplek layers (MWS= 2.6). *Bubalus* specimens from Tabuhan A had a higher mesowear score suggestive of a more abrasive diet.

In terms of microwear, we found that *Muntiacus* specimens from the first two layers of Braholo Cave exhibited evidence of browsing (LSR= 81.3% and 80 % respectively). On the other hand, *Muntiacus* from Layer 3 had a lower scratch range (LSR= 66.7%) placing them within the range of mixed feeders. *Rusa* specimens from Layer 3 also had a microwear score that placed them within the range of mixed feeders (LSR= 33.3%). In contrast, all the *Rusa* specimens from Layer 4 had a high number of scratches (LSR = 0%), indicative of a grazing feeding habit. The microwear scores for *Axis* specimens showed little variation throughout the cave's archaeological layers, with all values falling within the range of mixed feeders. The lower score recorded in Layer 4 (LSR= 25%) indicates a grass dominated mixed feeding habit whereas the score for Layer 1 (LSR= 60%) suggests a less abrasive mixed diet dominated by browse (Figure 3B).

The microwear scores of the bovid specimens from Braholo Cave showed interesting patterns across the stratigraphy. All of the *Bubalus* specimens analyzed had scratch numbers averaging to more than 17 (LSR= 0%). This points to *Bubalus* having a strict grazing dietary trait in all archaeological layers. *Bos* specimens on the other hand, had a microwear score that ranged from 0% in Layer 4 to 40% in Layer 1, indicative of a shift in feeding traits from strict grazing in the lower layers to mixed feeding in the upper layers. *Bos* specimens from Layer 2 showed an intermediate, grass dominated mixed feeding habit (LSR= 25%).

Figure 4 shows the bivariate plot of the microwear signatures of the archaeological specimens from Braholo Cave in comparison with those of extant ungulate taxa (Solounias and Semprebon, 2002). The plot displays the predominance of specimens with grazing or grass-dominated mixed diet from layers dated to the LGM/Terminal Pleistocene (Figure 4C and D). This is in contrast to the prevalence of specimens with browse-dominated mixed diet in the Holocene layers (Figure 4A). All taxa showed a change in diet except for *Bubalus* which was a strict grazer all throughout the stratigraphy.

In Braholo Cave, several ash layers were found within Layers 3 and 4. Further studies are needed to ascertain the source of these ash deposits, but they are presumably volcanic in origin (Simanjuntak 2002). Since microwear patterns could be affected by abiotic silica (i.e. present in volcanic ash; Hoffman, 2013), it is important to address this issue, especially with regards to the interpretation of microwear signatures. We are confident that the presence of ash in the cave does not invalidate our interpretation. The ash layers in Braholo Cave are sterile and yielded no faunal remains. We also did not find any bone with pathologies that would indicate volcanic ash ingestion.

In Song Terus, we observed a general increase in microwear scores from the older Tabuhan A layers to the younger Keplek layers similar to the trend observed in Braholo Cave. *Axis* specimens from Tabuhan A had a microwear score (LSR= 30.8%) indicative of a mixed feeding habit whereas specimens from the Keplek layers exhibited evidence of a browse-dominated diet (LSR= 75%). *Rusa* specimens from both the Tabuhan A and Keplek layers had microwear scores that suggest a grass-dominated mixed feeding dietary trait (LSR= 25%-33.3%). *Bos* specimens from Tabuhan A had a microwear score that provided evidence for a grass-dominated diet (LSR= 14.3%). This is much lower compared to the microwear score (LSR= 50%) obtained for specimens from the Keplek layers which suggests a less abrasive, mixed diet. In contrast to the *Bubalus* teeth from the Early-Mid Holocene layers of Braholo Cave, which showed high numbers of scratches suggestive of a strict

grazing diet, the *Bubalus* specimens from the Keplek layers of Song Terus fell within the range of grazing and grass-dominated mixed feeding habits (Figure 3D).

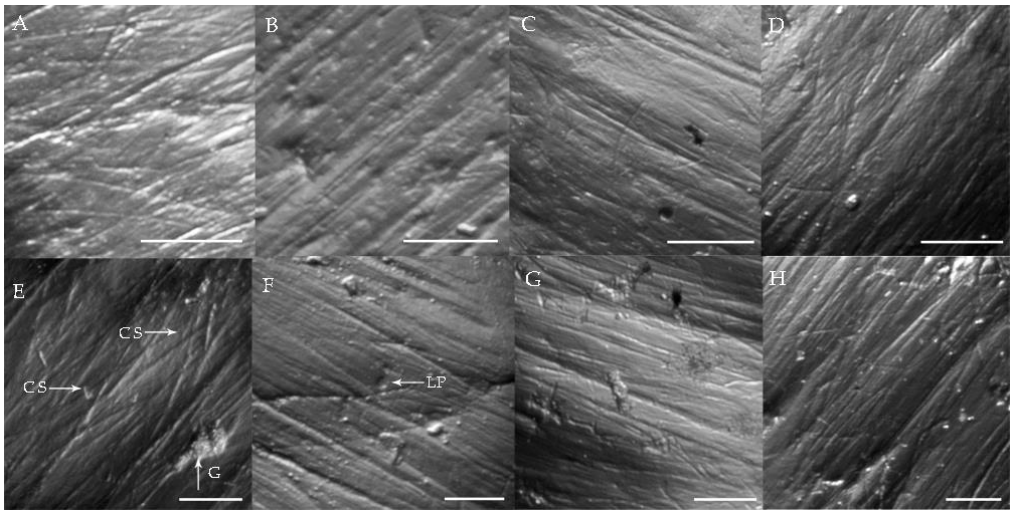

Figure 2. Photomicrographs of microwear marks on *Axis* and *Bos javanicus* molars from Braholo Cave at 35 x. (A) *Axis* Level 1; N8-001 (B) *Axis* Level 2; J9-005 (C) *Axis* Level 3; I8-006 (D) *Axis* Level 4; D5-016 (E) *Bos* Level 1; G7-006 (F) *Bos* Level 2; O8-007 (G) *Bos* Level 3; D5-014 (H) *Bos* Level 4; G7-013 (scale bars = 0.2 mm, CS- cross scratch, G- gouge, LP- large pit).

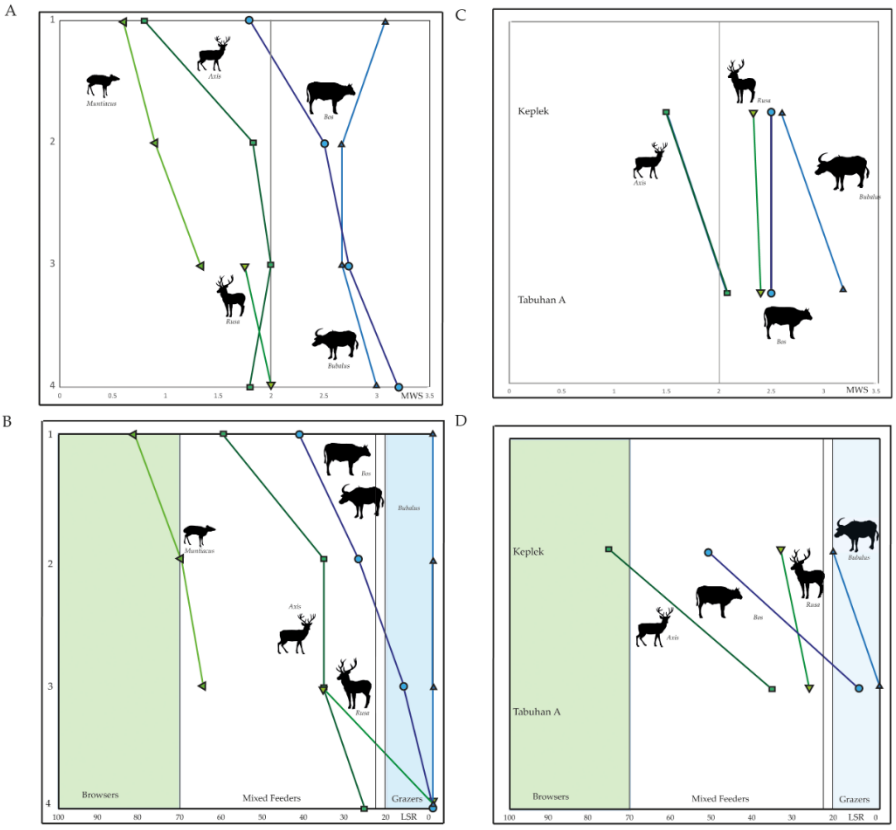

Figure 3. Comparison of the mesowear (MWS) and microwear (%LSR) scores of cervid and bovid specimens in Braholo Cave (A and B) and Song Terus (C and D) in different stratigraphic levels.

Table 1. Mesowear (MWS- mesowear score) and microwear values (LSR- percent with scratches between 0-17; NP- average number of pits; NS- average number of scratches; %CS- percent with cross scratches; %G- percent with gouges, SWS- scratch width score) for bovid and cervid specimens from Braholo Cave (Layers 1-4) and Song Terus (Keplek and Tabuhan A). There were more archaeological specimens considered for mesowear analysis (N=164) than microwear analysis (N=159) because of taphonomic alterations in the enamel surface in some samples.

		Mesowear		Microwear							
		N	**MWS**	**N**	**LSR**	**NS**	**SD**	**NP**	**SD**	**%CS**	**% G**	**SWS**
Braholo Cave												
1	*Axis*	7	0.8	5	60	18.3	4.5	16.9	3.9	80	40	0.8
	Muntiacus	16	0.6	16	81.3	16.61	4.1	15.88	2.9	61.9	19.04	0.86
	Bos	5	1.8	5	40	20.6	4.1	15.3	1.9	40	40	1
	Bubalus	5	3	4	0	28	0.6	1.5	0.9	0	0	0
2	*Axis*	6	1.83	6	33.3	21	4.3	9.5	5.4	33.3	33.3	0.83
	Muntiacus	10	0.9	10	80	17.9	3.8	17.4	3.7	60	30	0.9
	Bos	5	2.5	4	25	23.13	7.4	11.25	8.3	50	25	1.5
	Bubalus	5	2.67	4	0	23.65	6.8	4.67	3.7	33.3	33.3	1.67
3	*Axis*	6	2	6	33.3	20.83	4.4	8	4.1	66.67	0	0.67
	Rusa	6	1.67	6	33.3	21.75	6.7	9.83	5.0	0	0	1
	Muntiacus	3	1.33	3	66.7	16.33	3.2	8.17	2.5	33.3	33.3	1
	Bos	7	2.86	7	14.3	22.43	3.1	7.14	4.2	0	14.29	0.71
	Bubalus	5	2.8	6	0	25.67	4.2	3.83	1.4	33.3	0	1.33
4	*Axis*	5	1.8	4	25	23.62	5.1	3.75	1.0	25	0	0.5
	Rusa	7	2	7	0	25	2.5	5	3.1	0	0	1
	Bos	5	3.2	5	0	26.1	2.5	2.2	1.0	20	20	1
	Bubalus	4	3	5	0	25.25	2.2	6.5	2.5	0	0	1.25
Song Terus												
Keplek	*Axis*	4	1.5	4	75	17.25	4.2	16.63	2.7	75	50	1
	Rusa	6	2.67	6	33.3	22.5	5.2	10.67	5.5	33.3	0	1
	Bos	4	2.5	4	50	19.63	5.8	15.38	2.1	75	25	1
	Bubalus	6	2.6	5	20	23.3	5.2	7.8	6.3	20	20	1.4
Tabuhan A	*Axis*	13	2.08	13	30.8	20.33	5.9	14.25	5.8	30.76	7.69	1
	Rusa	12	2.4	12	25	22.13	4.8	5.83	3.4	16.67	0	0.92
	Bos	7	2.5	7	14.3	23.29	4.9	9.86	5.5	8.33	0	1.14
	Bubalus	5	3.2	5	0	26.4	1.7	7	3.2	2.8	0	0.4

Table 2. Mesowear (MWS- mesowear score) and microwear values (LSR- percent with scratches between 0-17; NP- number of pits; NS- number of scratches; %CS- percent with cross scratches; %G- percent with gouges, SWS- scratch width score) for modern Southeast Asian bovid and cervid specimens from museum comparative collections.

	N	MWS	LSR	NS	SD	NP	SD	% C	% G	SWS
Cervids										
Axis axis (ax)	15	2.21	40	21.2	4.4	10.4	3.0	26.67	13.33	1
Axis porcinus (ap)	8	2.36	12.5	23.43	5.3	10	2.2	12.5	0	1.13
Muntiacus muntjak (mm)	22	1.14	40.9	18.86	4.4	17.09	2.3	54.5	0	0.95
Rusa alfredi (ra)	4	0.75	100	12.16	3.4	9.87	3.6	50	50	0.75
Rusa marianna (rm)	3	1.67	66.67	15.67	2.1	5.83	3.3	33.3	0	1.33
Rusa timorensis (rt)	9	2	22.2	21.83	3.3	13.39	6.1	33.3	0	1
Rusa unicolor (cu)	6	2.2	20.75	16.67	3.4	7.5	4.1	16.67	0	1
Bovids										
Bos javanicus (bj)	8	3.13	0	26.62	2.2	7.12	2.5	25	0	1
Bubalus arnee (bb)	6	3.5	0	24.42	2.9	7.5	3.6	0	0	1.5

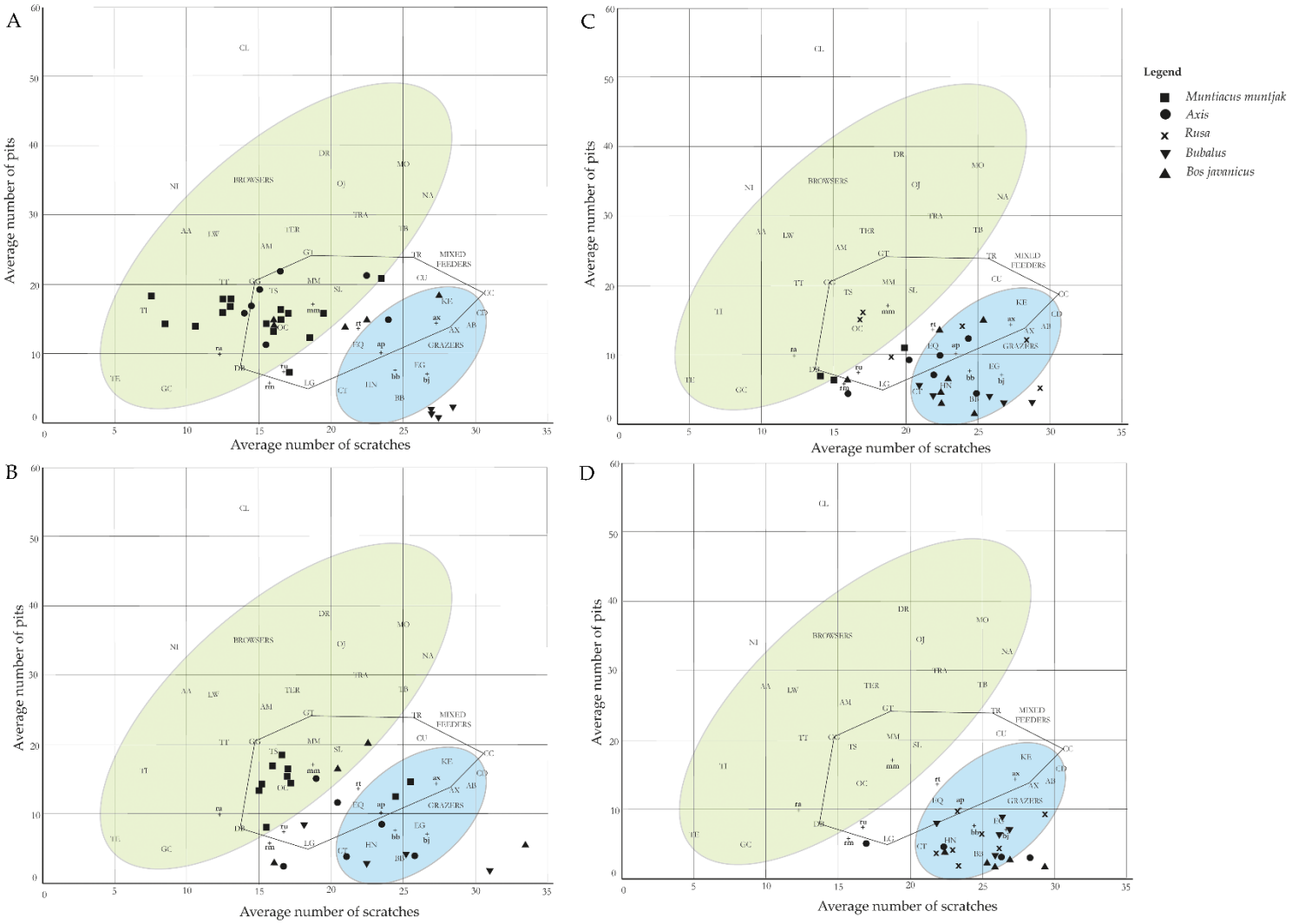

Figure 4. Bivariate diagrams based on microwear signatures of archaeological specimens from Braholo Cave (A. Layer 1; B. Layer 2; C. Layer 3; D. Layer 4), modern museum comparative specimens and extant ungulate taxa from Solounias and Semprebon (2002). Abbreviations: Modern comparative museum specimens (this study): ax- *Axis axis*, ap- *Axis porcinus*, bb- *Bubalus arnee*, bj- *Bos javanicus*, mm- *Muntiacus muntjak*, ra- *Rusa alfredi*, rm- *Rusa marianna*, rt- *Rusa timorensis*, ru- *Rusa unicolor*; **Browsers**: AA- *Alces alces*; AM- *Antilocapra americana*; CL- *Camelus dromedarius*; DB- *Diceros bicornis*; DR- *Cephalophus dorsalis*; GC- *Giraffa camelopardalis*; LW- *Litocranius walleri*; MO- *Moschus moschiferus*; NA- *Cephalophus natalensi*; NI- *Cephalophus niger*; OJ- *Okapia johnstoni*; SL- *Cephalophus silvicultor*; TB- *Tapirus bairdii*; TE- *Tragelaphus euryceros*; TER- *Tapirus terrestris*; TRA- *Tragulus* spp.; TI- *Tragelaphus imberbis*; TT- *Tragelaphus strepsiceros*; **Mixed feeders**: AX- *Axis*; CC- *Cervus canadensis*; CU- *Cervus unicolor*; GG- *Gazella granti*; LG- *Lama glama*; MM- *Muntiacus muntjak*; OC- *Ovis canadensis*; TR- *Boselaphus tragocamelus*; **Grazers**: AB- *Alcelaphus buselaphus*; BB- *Bison*; CD- *Cervus duvauceli*; CT- *Connochaetes taurinus*; EG- *Equus grevyi*; EQ- *Equus quagga*; HN- *Hippotragus niger*; KE- *Kobus ellipsiprymnus*.

With regards to the other microwear parameters, *Axis* (%CS = 25-80, see Figure 2A) and *Muntiacus* (%CS= 33.3-61.9) specimens from Braholo Cave showed high levels of cross scratches typical of mixed feeders. *Bos* specimens from the upper layers also showed high percentage of cross scratches (%CS= 40-50, see Figure 2E). We also observed other traits which provide evidence of a mixed feeding habit (e.g. feeding on fruit/seed,

root and bark as well as ingestion of grit), such as high percentages of gouges and hyper-coarse scratches, in *Axis*, *Muntiacus* and *Bos* samples (Table 1).

Table 2 summarizes the mesowear and microwear scores obtained for modern Southeast Asian bovid and cervid specimens. To our knowledge, this is the first study that looked at the dental wear patterns of wild *Bubalus arnee*, *Bos javanicus*, *Rusa timorensis*, *Rusa marianna* and *Rusa alfredi* specimens. *B. javanicus* and *B. arnee* had dental wear scores indicative of a strict grazing diet. B. *arnee* is a grazer by preference, feeding mainly on grasses when available, but also herbs, fruits, and bark (Daniel and Grubh, 1966; Hedges et al., 2008). B. *javanicus*, in contrast, has a wider dietary range. Although it relies mainly on grasses, it is known to consume a lot of browse and fruits depending on season and local food availability (Hoogerwerf, 1970; Timmins et al., 2008). Most of the modern bovid specimens considered in this study were from mainland Southeast Asia (Vietnam and Cambodia) where they are restricted to open, dry deciduous forests (Wharton, 1968; Hoogerwerf, 1970). *R. unicolor* and *R. marianna* are deer species known for their adaptation to a wide range of environmental conditions, from dense rainforests to open grasslands. In the current study, dental wear signatures of specimens of both species suggest mixed feeding trait, albeit R. *unicolor* exhibited a grass-dominated mixed diet and *R. marianna* a more browse-dominated diet. The only deer species currently present in Java, *R. timorensis* also showed a mixed feeding trait. Like *R. unicolor* and *R. marianna*, *R. timorensis* is highly flexible, with populations recorded in forests, grasslands, shrublands and marshes (Rouys and Theuerkauf 2003, Keith and Pellow 2005; Hedges et al., 2015). The only deer species examined that exhibited a strict browsing trait, *R. alfredi* is known to currently inhabit dense dipterocarp forests. The dental wear signatures observed in *Axis* and *Muntiacus* specimens are consistent with published studies (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). Both had mesowear and microwear scores indicative of a mixed feeding trait.

5. Discussion

Whereas computer simulations and global coupled models suggest that the climate in Sundaland during the last glacial period was cooler and drier than today, little is known about the response of vegetation to these conditions. Attempts at modelling the vegetation cover of the exposed Sunda Shelf provide conflicting results. Simulations by Bird et al. (2005) suggests relatively open environments covering much of Sundaland during the LGM while further modelling by Cannon et al. (2009, see also Cannon, 2012) suggests the predominance of vast undisturbed rainforests. Not surprisingly, direct evidence varies from site to site. A series of sediment cores from the South China Sea has indicated the presence of vast areas of rainforests during the LGM (Kershaw et al. 2001; Sun et al. 2002; Hu et al. 2003; Kershaw et al. 2007; Wang et al. 2009). In other areas, evidence suggested herb and grassland expansion (Morley, 2000; Sun et al. 2003, Wurster et al. 2010). This highlights the importance of looking at more sites and using other proxies to gain a more complete picture of the paleoenvironment of the region at this period.

The mesowear and microwear signatures obtained for the bovid and cervid specimens from Braholo Cave and Song Terus show a clear trend. In most of the taxa analyzed (*Muntiacus*, *Axis* and *Bos*), we observed a change from a grass-dominated mixed diet in specimens dated to the LGM/Terminal Pleistocene to a browse or browse-dominated mixed diet in specimens coming from the Holocene layers. The trend is consistent with the distribution of the faunal remains from both sites, in that archaeological layers dated to the Holocene showed a dominance of small and intermediate sized arboreal and semi-arboreal taxa, most notably cercopithecids (Ingicco, 2010; 2012; Sémah and Sémah, 2012; Amano et al. *in press*). This is in contrast to the preponderance of large sized ungulates in assemblages from before the Pleistocene-Holocene transition. Such a change in distribution reflects a regional trend of rainforest expansion starting in Island Southeast Asia around 14,000 years ago (Sémah et al. 2004a; Lewis et al. 2008; Piper and Rabett, 2009; 2014; Piper et al. 2011) and is in accordance with palynological datasets for the region (van der Kaars and Dam, 1995; Sun and Li, 1999; Sun et al. 2000; Anshari et al. 2001; 2004; van der Kaars et al. 2001; Hope, 2001; Sémah et al. 2004a; 2004b).

From the distribution of faunal remains across the stratigraphy of Braholo Cave, Amano et al. (*in press*) suggested that although the onset of the Holocene was accompanied by expansion of rainforests, it did not result in the complete disappearance of grasslands and open woodlands which were dominant prior to the Pleistocene-Holocene transition. This hypothesis was based on the continued presence up to the mid-Holocene layers of taxa often associated with more open environments, albeit in very small numbers. For example cervids and bovids are present in layers postdating the Pleistocene-Holocene boundary, although they account for only 1.99% and 1.24% respectively of the total number of identified specimens of one excavation unit. The current study provides strong evidence to support this hypothesis. *Bubalus* specimens from Braholo Cave had microwear scores indicative of strict grazing (LSR= 0% in all layers) and mesowear scores suggestive of diets ranging from grazing to grass-dominated mixed feeding. The same observation was made for the Holocene *Bubalus* and *Rusa* specimens from Song Terus where both mesowear and microwear signatures indicated grazing and grass-dominated mixed feeding habits. In other words, the present study provides new evidence to support the notion that the hunter gatherers that lived in this part of Eastern Java subsisted in a complex mosaic of environments which included forests and grasslands from Early to Mid-Holocene.

The previous analysis also noted the presence of forest-obligate species such as *Trachypithecus auratus* and *Ratufa bicolor* in the LGM and pre-Holocene layers of Braholo Cave (Amano et al., *in press*). But because of the very low number of bone fragments attributable to these taxa (N= 13, or 1.63% of the assemblage from layers prior to the Pleistocene-Holocene transition), substantial claims regarding the possible presence of patches of forests or woodlands in the region at this period cannot be made. The current study provides evidence to support the presence of forests in the area, albeit only up to a certain extent. Mesowear and microwear signals for *Axis*, *Rusa* and *Muntiacus* from Layer 3 suggest a mixed feeding trait and in the case of *Muntiacus* the scores indicate a browse-dominated mixed feeding diet. We take this as evidence for the presence of forest/woodland in the region surrounding Braholo Cave from around 19,570 $\pm$ 350 BP to 15,520 $\pm$ 520 BP. However, the current study does not provide strong concrete evidence for the presence of forests in the area around 20,000-30,000 years ago. Instead we recorded discrepancies between the mesowear values and the microwear scores of the specimens examined which could be indicative of seasonality.

The microwear and mesowear methods we used in the study provided consistent results except for *Rusa* and *Axis* specimens from Layer 4 of Braholo Cave. *Rusa* specimens from this layer had mesowear value which indicates a mixed feeding habit whereas the microwear score suggests strict grazing. For *Axis* specimens, the mesowear value is suggestive of a browse-dominated mixed diet while the microwear score indicates a grass-dominated mixed feeding trait. Discrepancies between mesowear and microwear are indicative of seasonality (Rivals and Deniaux, 2003; Rivals et al. 2009a; Sánchez-Hernández et al. *in press*), owing to the fact that these two dietary proxies have different temporal scales. Mesowear is the cumulative result of attrition and abrasion over a long period and is therefore a close approximation of an ungulate's annual diet (Fortelius and Solounias, 2000; Kaiser and Solounias, 2003). Microwear, in contrast, provides a snapshot of the paleoenvironmental conditions weeks or even days within the time of the animal's death (Grine, 1986; Solounias and Semprebon, 2002). In other words microwear signatures contain signals that cannot be resolved by mesowear signatures (Rivals et al. 2009).

The evidence for seasonality in the LGM specimens from Braholo Cave implies seasonality in the vegetation and seasonality in cave occupation at around 20,000- 30,000 years ago. To our knowledge, this is the first evidence for seasonality in the area provided by faunal remains. Several palynological and geomorphological studies have provided evidence for the presence of seasonal vegetation in Sundaland during the LGM, including studies conducted in peninsular Malaysia (de Dapper and Debaveye, 1986), southern Kalimantan (Morley, 1981; Kershaw et al. 2001), Java Sea (Verstappen, 1997) and West Java (van der Kaars and Dam, 1995). A recent study that looked at vegetation response to changes in rainfall seasonality in Indonesia over the last 25,000 years has provided evidence that demonstrated pronounced monsoon-driven dry seasons in southern Indonesia during the LGM (Dubois et al. 2014). So it is no surprise that seasonal vegetation was also present in East Java at the same period. The increased seasonality in the region during the last glaciation resulted from changes in monsoon patterns following sea-level fall (e.g. Verstappen, 1975; Fairbanks, 1989). This is in contrast to evidence from

offshore Northeast Borneo which suggested the absence of a pronounced dry season despite generally drier glacial conditions (Dubois et al. 2014).

This could also imply seasonality in the occupation of Braholo Cave during the last glacial period. Although this is a preliminary hypothesis and more research is needed to support this notion, seasonality in cave use can explain the paucity of evidence for long term occupation in the Braholo Cave's basal levels that that are very common in the cave's Early-Mid Holocene layers, including hearths, sites of stone and osseous tool production and human burials. Intensification in cave occupation, interpreted as long-term cave use, starting with the onset of the Holocene has been recorded in numerous sites in Island Southeast Asia (Sémah et al. 2004b; Simanjuntak and Asikin, 2004; Barker, 2005; Barker et al., 2007; Lewis et al., 2008; Rabett, 2012; Pawlik et al., 2014).

Finally from a methodological standpoint, the current study also provides insights on the effect of chronological divisions or analytical units in the interpretation of dental wear signatures. In the Tabuhan A layers of Song Terus, *Axis* showed mesowear and microwear values typical of a mixed feeder. All other taxa analyzed showed dental wear signatures typical of grazers. The Tabuhan A layers of Song Terus correspond approximately to Layers 3 and 4 of Braholo Cave. If the ungulate specimens from Layer 3 and 4 were analyzed together as a unit, the results are more or less similar to those obtained for Tabuhan A (*Axis*: LSR= 28.57%, MWS= 1.86; *Rusa*: LSR= 20%, MWS: 1.8). The discrepancies between the mesowear and microwear scores observed in the samples from Layer 4 were diluted by the addition of samples from Layer 3 and therefore evidence for seasonality was not recorded.

6. Conclusion

The results of dental wear analyses of cervid and bovid dental specimens from Braholo Cave and Song Terus contribute to the growing body of knowledge of the Late Pleistocene to Mid-Holocene paleoenvironment of ISEA. In East Java, the Pleistocene-Holocene transition was accompanied by expansion of rainforests as evidenced by the predominance of ungulates with browse or browse-dominated mixed diets. This is consistent with other zooarchaeological evidence from the sites, including the massive increase of arboreal and semi-arboreal species in the assemblages following the onset of the Holocene. Nonetheless, rainforest expansion did not result in the complete disappearance of grasslands which were dominant prior to the Pleistocene-Holocene transition. The microwear and mesowear signatures of *Bubalus* and *Rusa* specimens showed evidence for grazing all across the stratigraphic sequence.

The study also supports the hypothesis for the presence of forests or woodland vegetation in the area during the last glacial period. This is in accordance to studies in other parts of Java, Borneo and peninsular Malaysia that noted the continuous presence of forests in Sundaland from the LGM to Mid-Holocene. Results also suggest the presence of seasonality in vegetation and cave occupation in East Java at around 20,000-30,000 years ago. Our results are consistent with those of recent studies looking at other proxy evidence which have shown increased seasonality in southern Indonesia during the LGM, specifically an increase in the duration and intensity of the dry season (Dubois et al., 2014).

The results of the study provided important contexts on hunter-gatherer subsistence strategies and behavior during a key period in human history. The people that inhabited Braholo Cave and Song Terus hunted and foraged in a complex mosaic of environments that included rainforests, open woodlands and grasslands from the last glacial period up to the Mid-Holocene. Their ability to live in the area throughout this time, despite the drastic changes in their surroundings, indicates behavioral flexibility and a complex knowledge of the environment.

Acknowledgement

We would like to thank the interdisciplinary research network, *Pusaka: Human Ecology in Island Southeast Asia*. We would also like to acknowledge Dr. Joséphine Lesur for allowing us access to the bovid and cervid comparative collection of the *Muséum national d'Histoire naturelle*. The study forms part of NA's PhD research under the Erasmus Mundus International Doctorate in Quaternary and Prehistory which is funded by the European Union.

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