Specialized rainforest hunting by *Homo sapiens* ~45,000 years ago

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Defining the distinctive capacities of *Homo sapiens* relative to other hominins is a major focus for human evolutionary studies. It has been argued that the procurement of small, difficult-to-catch, agile prey is a hallmark of complex behavior unique to our species; however, most research in this regard has been limited to the last 20,000 years in Europe and the Levant. Here, we present detailed faunal assemblage and taphonomic data from Fa-Hien Lena Cave in Sri Lanka that demonstrates specialized, sophisticated hunting of semi-arboreal and arboreal monkey and squirrel populations from ca. 45,000 years ago, in a tropical rainforest environment. Facilitated by complex osseous and microlithic technologies, we argue these data highlight that the early capture of small, elusive mammals was part of the plastic behavior of *Homo sapiens* that allowed it to rapidly colonize a series of extreme environments that were apparently untouched by its hominin relatives.
There is growing evidence that *Homo sapiens* had a unique capacity to adapt to a diversity of extreme environments, both within and beyond Africa, when compared with other members of the genus *Homo*. Nevertheless, studies of migrations of our species into Europe, the Middle East, and Asia have often focused on its increased efficiency in hunting, butchering, and consuming medium-to-large game in open “savanna” settings. Alternatively, coastal settings have been highlighted as providing homogeneous, protein-rich resources that stimulated human evolution as well as migration beyond Africa from the Late Pleistocene. Focus on these environments has meant that small mammals have been neglected in discussions of the human colonization of new environments, despite the fact that a specialization in their procurement is often considered a feature of technological and behavioral “complexity” or “modernity” unique to our species. Concentration on Europe and West Asia in this regard has linked increased usage and capture of agile, but abundant, small mammals to human population growth or climatically driven crises associated with the end of the last glacial period. Nevertheless, the onset and behavioral context of small mammal hunting in other parts of the world, and beyond temperate environments, has remained poorly studied.

From the Late Pleistocene onwards, our species inhabited a number of diverse environments as it dispersed beyond Africa. One of these environments, tropical rainforests, has been considered a barrier to human dispersal. This was mainly due to the fact that mammalian megafauna (> 44 kg), thought to have been attractive to Late Pleistocene humans, and even driven to extinction as a result of our species’ expansion, are lacking in these settings. Nevertheless, in Sri Lanka, Southeast Asia, and Melanesia, as well as other parts of the world, the earliest evidence for human occupation is often associated with rainforest environments. In Sri Lanka, stable isotope evidence has demonstrated that humans relied on rainforest resources for over 30,000 years, perhaps aided by the complex microlith and bone toolkits found at Late Pleistocene and early Holocene sites in the region. However, owing to a lack of detailed faunal analyses, it has remained unknown which foodstuffs sustained human populations during this time, as well as the hunting strategies employed to obtain them.

We apply new chronometric, taphonomic, archaeozoological, and artifactual analyses to the earliest dated archeological site in Sri Lanka, Fa-Hien Lena (Fig. 1), previously dated to 38,000 years ago. Fa-Hien Lena documents the earliest fossil appearance of *H. sapiens* in Sri Lanka, and indeed South Asia, alongside small, quartz microlith technology, and a variety of pointed bone technologies. Rainforest mammals, reptiles, molluscs, and plant remains have been identified at the site. However, human exploitation of specific resources has yet to be directly demonstrated owing to a lack of systematic taphonomic study. Similarly, the early, enigmatic microlith and bone technologies discovered here and elsewhere in South Asia have undergone limited analysis, and their use and adaptive function have remained obscure. The results of our new multidisciplinary analyses document specialized, sophisticated hunting of semi-arboreal and arboreal prey taxa from ca. 45,000 years ago, in the tropical rainforest environments of Sri Lanka.
Results

Stratigraphy and chronology. We divide the dates available for the site into four distinct phases based on our new, and previous, excavations. The phases correspond to concentrations of charcoal, faunal remains, and artifacts, including osseous tools, shell beads, and quartz flakes (Supplementary Figure 1), and represent the major periods of human occupation of the cave. Phase D contains evidence for Late Pleistocene occupation of the cave from c. 48,000 to 34,000 cal. BP and probably included several episodes of occupation, each of which may have been relatively short-lived. Phase C spans the Terminal Pleistocene, with a relatively short-lived episode of human presence in the cave. These phases also align with major lithostratigraphic changes (Fig. 2). The fill of Fa-Hien Lena consists of c. 170 cm of detrital sediment deposited above heavily weathered and karstified gneiss blocks. Phase D consists of pebbly loams and clayey and sandy silt deposits with laminated ash representing intermittent/episodic human occupation and colluvial inwash. The deposits yielded a variety of evidence for human activity, including heavily burned/calced faunal remains, shell beads, bone tools, and other fragments, in addition to micromorphological analyses of sediments evidencing in situ burning (Supplementary Note 1). A roof fall episode appears to have contributed to the exceptional preservation of these deposits by sealing large parts of Phase D from later disturbance. Phase C, which contains the heaviest concentration of artifacts and human occupation debris in the stratigraphy, comprises of a rapidly deposited, heterogeneous mixture of dark colored, organic-rich sandy silty loams. Phases B and A are made up of light colored sandy silts and ash accumulations. For further detailed description, see Supplementary Note 1, Supplementary Tables 1–4, and Supplementary Figures 1–4.

Previous excavation in Fa-Hien Lena produced the oldest human fossils so far in Sri Lanka. Remains of a 5.5–6.5 years old child, mixed with remains of at least two infants as well as a young adult female, were dated based on associated charcoal to 30,600 ± 360 BP. These remains were found in layer 4 at the rear of the cave during the 1986 excavations (approximately represented by context 179 during our 2010 excavations) (Fig. 2). Overall, our new data confirm Fa-Hien Lena as the oldest site with \textit{H. sapiens} fossils in Sri Lanka, and wider South Asia. They also indicate that Fa-Hien Lena now represents one of the earliest appearances of microlith toolkits and bone tool technocomplexes outside of Africa.

Zooarchaeology and taphonomy. Our detailed taphonomic and zooarchaeological study of faunal remains at Fa-Hien Lena examined the adaptive context of the first humans on the island. We analyzed a total of 14,485 bone and tooth fragments from the site, 52.6% of which were identified to taxon (number of identified specimens, NISP = 7622). The full dataset can be found in Supplementary Note 2 (see also Supplementary Figures 5–16; Supplementary Tables 5–42). Small mammals (i.e., weighing less than 25 kg) overwhelmingly dominate the faunal assemblage starting from the earliest phase of occupation (c. 48,000–34,000 cal. BP). These animals, including carnivores such as the civet cat, account for more than 90% of the NISP, suggesting deliberate hunting from the Late Pleistocene until the Mid-Holocene (Fig. 3) (Supplementary Note 2). Reptiles, including pythons, colubrid snakes, and water monitors, and fish (mostly catfish and carp) are also present in all phases of site occupation. Several of the specimens identified could represent fauna from natural accumulations (e.g., murids and amphibians accumulated by raptors, 1.9% of the total NISP, see Supplementary Note 2). Other specimens, including birds such as swifts and squamates such as snakes and varanids, could represent the cave’s natural faunal communities. However, the high percentage of burning (> 50% in Phase D) in squamate remains suggests that they were most likely utilized by the people that occupied the site (Supplementary Note 2).

There is no significant difference in the distribution of mammals based on body size from the Late Pleistocene to the Mid-Holocene (Supplementary Note 2). Large ungulates, including cervid, suid, and bovid are present throughout the...
stratigraphy but at very low frequencies (~4%). Monkeys and tree squirrels overwhelmingly dominate the faunal assemblage in all phases of site occupation, accounting for more than 70% of the identified remains (or 82.4% of the total NISP discounting fauna most likely accumulated by non-human cave dwelling species). They represent 84.7% and 76.3% of the total number of identified specimens in the Terminal and Late Pleistocene layers, respectively (72.3% and 66.7% of the minimum number of individuals, MNI). Of the taxa identified in the Late Pleistocene layers, 48.7% are cercopithecoid monkeys. Deliberate targeting of monkeys continued until the Mid-Holocene, where cercopithecoids represent 61.1% of the number of identified bone and tooth fragments. Three cercopithecoid species are currently present in Sri Lanka: the cuscus Macaca sinica (toque macaque), the colobe monkeys Trachypithecus vetulus (purple-faced langur), and Semnopithecus priam (tufted gray langur). These species occur sympatrically and all were identified in the site. Macaques slightly outnumber the leaf monkeys in the faunal assemblage (Supplementary Note 2).

Mortality profiles based on dental eruption and wear suggest that prime-aged adults were deliberately targeted. This, and the fact that the identified monkey species are today mostly arboreal and rarely venture to the ground[24,25], suggests that they were most likely captured by targeted hunting. Trapping usually results in mortality profiles similar to those found in natural populations[26–28]. The presence of bone points and microliths from the outset of site occupation hints at the possible use of projectile technology to hunt arboreal prey (see below, and Supplementary Note 3, Supplementary Figures 17–19, and Supplementary Tables 43 and 44). Modern Southeast Asian hunter-gatherer communities still rely on the use of projectile weapons, including darts and blowpipes, to target arboreal and semi-arboreal taxa[29–31]. The archaeological bone points are consistent in size and breakage patterns with such uses. Regardless of method of capture, entire monkey carcasses were brought and processed in the site as revealed by the pattern of skeletal part abundance (Supplementary Note 2).

Bone fragments with anthropic modification, ranging from burning to butchery marks, were recovered in all phases of site occupation. Butchery marks were recorded on a total of 92 bone fragments (0.64%), the majority of which were from small mammals (92.2%) (Supplementary Note 2). The Late Pleistocene layers yielded a total of nine (0.7% of NISP) bone fragments with clear evidence for butchery, including squirrel, otter, and civet cat long bones from the oldest occupation deposit of the site (Fig. 4). The placement of the cutmarks, both in the shaft surface and the distal epiphyses, is suggestive of a carcass processing sequence that involved disarticulation and defleshing[32]. Burnt and calcined bone fragments represent 19.7% of the total specimens studied (23.9% of the Late Pleistocene assemblage). A high proportion of the small mammal (17.1%) remains identified at the site exhibit evidence for burning, including 16.1% of the monkey remains.

**Bone tool industry.** Primates and giant squirrels appear to have been targeted not just for subsistence, but also for technological production. A total of 36 bone specimens with surface modifications consistent with systematic tool manufacture were recorded in the Late Pleistocene layers (Phase D) of the site (1.3% of the NISP). These consist of 10 fragments of finished implements, including proximally hafted unipoints, mesially hafted bipoints, and small geometric bipoints. The rest are fragments that represent either waste pieces or tool blanks. These specimens are characterized by the presence of heavy surface and/or edge polish and striations or grinding marks. In situ tool production accounts for the high level of fragmentation of cercopithecoid bones in all levels of site occupation, but most notably in the Late Pleistocene layers (Supplementary Note 2).

The osseous tools from the Late Pleistocene layers of the site appear to have been manufactured exclusively from cercopithecoid long bone fragments, save for one worked macaque canine recorded from the earliest phase of site occupation (context 253) (Fig. 4). Tools and artifacts made from large ungulate bone, teeth, and antler only start to appear during the Terminal Pleistocene. Most of the bone points examined exhibited evidence for damage consistent with high velocity impact (four out of the five points recorded in Phase D, e.g., Fig. 4)[33], which, in addition to what appears to be deliberate targeting of prime age adults, further
suggests that projectile hunting, rather than trapping, was utilized in the exploitation of small semi-arboreal and arboreal game.

Discussion
The consistently high percentage of arboreal small mammal taxa in all phases of occupation in Fa-Hien Lena is unheard of even among modern ethnographic groups hunting in tropical rainforest environments, with perhaps one exception. Even with access to rifle technologies and wire cord and snare traps, modern foragers never show such a bias. Late Pleistocene hunting of arboreal primates has also been demonstrated at the Niah Caves, Borneo from 50,000 to 35,000 years BP. However, here, in contrast to Fa-Hien Lena, humans seemingly primarily relied on large ungulates as their main source of protein. This, alongside associated evidence from what is, to our knowledge, one of the earliest bone assemblages in South and Southeast Asia (contemporaneous with the bone tools from Niah Caves dated between 50,000 and 35,000 years BP), and also one of the earliest beyond Africa, implies highly tuned hunting abilities in tropical rainforest settings upon arrival in this part of the world. Moreover, despite targeting prime age adults, these human populations were able to exploit primate and giant squirrel taxa, often considered to be rainforest game types that are among the most vulnerable to overhunting, from ~45,000 to 4,000 years ago. This suggests close knowledge of life cycles, territories, and sustainable hunting strategies.

Discussions of Late Pleistocene dispersals of *H. sapiens* beyond Africa have tended to focus on human reliance on large, mammalian megafauna that are often linked to open grassland or mixed woodland and grassland environments. Alternatively, scholars have focused on reliable coastal resources as providing adaptive corridors for a rapid dispersal around the Indian Ocean, through Southeast Asia, and into Australia, and also into the Americas. Our current data, demonstrate instead that some of the earliest known *H. sapiens* in Sri Lanka, and indeed in the South Asian tropics, focused on the specialized hunting of small semi-arboreal and arboreal mammals in tropical rainforests. Traditionally, the use of such difficult-to-catch resources has been associated with a “broad spectrum” revolution in the face of growing populations and climate change. However, continued emphasis on prime age animals across over 40,000 years, rather than a broadening of capture strategy, implies no such stress in the tropical rainforests of Sri Lanka. Furthermore, while stable isotopic data from human and faunal tooth enamel in the Wet Zone of Sri Lanka highlights subtle environmental changes from the Late Pleistocene to the Holocene, the persistence of Wet Zone and Intermediate Zone rainforest, as well as human reliance on...
Methods

Chronology and thin section micromorphology. Fa-Hien Lena (80° 12' 55" E, 6° 38' 55" N), located in Sri Lanka's Wet Zone region, near the town of Bulathsinhala, some 75 km southeast of Colombo in a lowland evergreen and semi-evergreen rainforest environment44,45. The cave, on the slope of a gneiss cliff, has a vicinities of rivers and lakes40,41. By contrast, following its evolution in Africa c. 300 ka42, our species came to occupy higher-elevation niches than its hominin predecessors, as well as deserts, palaeoarctic settings, and tropical rainforest habitats stretching across Asia, Melanesia, and North, Central, and South America4. Moreover, it was even able to alter and manage environments, such as tropical forests, to meet its own subsistence and cultural needs through ever-intensifying niche-construction39,43. Detailed paleoecological and archeological analysis, such as that presented here, offers to yield more insights into the variety of cultural and subsistence strategies that facilitated the eventual colonization of all of the world’s continents, and resilience to increasingly extreme Pleistocene climatic fluctuations, that left H. sapiens the last hominin standing on the face of the planet.

Artifact analysis. The technological study of the lithic assemblages of Fa-Hien Lena was carried out following the chaîne opératoire concept68,69, a methodological framework that defines the reconstruction of the various processes of flake production from the procurement of raw materials, through the phases of manufacture and utilization until the final discard. The chaîne opératoire concept provides systematic sequences of the flaking activities in which it is possible to determine the temporal phase and the position of the artifact produced70. The lithic material is composed of 5070 items (Supplementary Tables 43–44). The predominant raw material is quartz, which is abundantly available in the streams nearby. Two chert blanks were also found and include: a silex flake fragment in context 131 (Phase A); two flakes and a fragment in context 136 (Phase B): a flake fragment in context 141; and one flake and one blade from context 248 (Phase C).

For the analysis of osseous artifacts, the materials were examined using a Zeiss Stemi 508 stereomicroscope fitted with an Axiocam 105 camera. Taphonomic and anthropogenic alterations were identified based on published works85–87 and mapped on photographs taken with a Canon digital SLR camera.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The authors declare that all data supporting the findings of this study are available upon request from the authors. The artifacts and faunal remains from the Fa-Hien Lena excavations are curated at the Department of Archeology, Government of Sri Lanka, under the site code RFP and the suffixes 10, 11, and 12 (denoting the year of excavation). Some materials remained housed at the Max Planck Institute for the Science of Human History to be returned to the Department of Archeology, Government of Sri Lanka by the end of 2019. All of the data reported in the paper are presented in the main text or in the Supplementary Notes, Tables, and Figures.

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References

1. Roberts, P. & Stewart, B. A. Defining the ‘generalist specialist’ niche for Pleistocene Homo sapiens. Nat. Hum. Behav. 2, 542–550 (2018).
2. Finlayson, C. Neanderthals and Modern Humans: An Ecological and Evolutionary Perspective. (Cambridge Univ. Press, Cambridge, 2004).
3. Domínguez-Rodrigo, M. Is the “Savanna Hypothesis” a dead concept for explaining the emergence of the earliest hominins? Curr. Anthropol. 55, 59–81 (2014).

Zooarchaeology and taphonomy. We analyzed faunal remains recovered from the 2009 and 2012 excavations of Fa-Hien Lena. All bone fragments from sedimentary contexts with secure radiocarbon dates (including those from deposits sandwiched by dated layers) were included in the analysis. All specimens, including diaphyses and rib shafts, were sorted, counted, and measured (length, width, and thickness) using a digital caliper (Mitutoyo 500–463). Identified specimens were encoded in detail using codes for anatomical zones31 (e.g., Supplementary Figure 5) that allow the description of bone preservation/fragmentation patterns. Diagnostic dental and skeletal elements were identified to the highest possible taxonomic level using vertebrate comparative collections from the Laboratory of Comparative Anatomy of the Muséum national d’Histoire naturelle (MNHN) in Paris and photographs from the mammalian collections of the Field Museum of Natural History and American Museum of Natural History. Following von den Driesch52, individual dental specimens and specific anatomical features of diagnostic skeletal elements were measured to differentiate between closely related taxa. The naming of identified taxa follows the nomenclature for mammalian species of Wilson and Reeder53. The taxa identified in the sites were assigned to size class based on live weight (modified from refs. 54,55): (a) micromammals: 100 g to 1 kg, (b) small mammals: 1 kg to 25 kg, (c) large mammals class 1: 25 kg to 200 kg, (d) large mammals class 2: 200 kg to 1000 kg, and (e) large mammals class 3: > 1000 kg. All fragments were examined for natural, animal, and anthropic modifications, including weathering56,57, abrasion58, burning, staining, and butchery marks59. Bone surface modifications were recorded/observed using an Olympus BX53 light microscope and a Keyence VHX-6000 digital microscope. Burnt bone fragments were identified by color56. They were distinguished into different classes based on the degree of burning60: (1) partially burnt, (2) charred (blackened), and (3) calcined (partial and complete calcination). Burnt bones were quantified by determining the percentage of the total bone fragments that is comprised of burnt specimens62,63.

The minimum number of element (MNE) and minimum number of individual (MNI) counts were calculated following a modification of Dobney and Rickley’s equation system. This system is based on the recording of morphologically distinct zones in a skeletal element. The MNE was taken as the total number of non-repeatable zones (i.e., greater than 50% of the diagnostic zone present) for every skeletal element of a taxon. The highest MNE value, considering side and age (epiphyseal fusion and dental wear), was used to estimate the MNE counts. The MNE counts were converted to minimum animal unit (MAU) values by taking into account the number of times the element occurs in the skeleton. The normed MAU values (% MAU) were used to compare skeletal part representation in the different phases of cave occupation56.

The length and circumference of long bone fragments were also recorded in relation to complete specimens to measure the extent of bone fragmentation in the assemblage. Long bone fragments were assigned the following fragment circumference and length scores66,67: (1) fragments with less than half of the circumference/length of the complete specimen, (2) fragments with more than half of the circumference/length of the complete specimen, and (3) fragments with the complete circumference/length of the complete specimen.

As a consequence, the utilization of these energetically expensive resources developed in the absence of resource pressure, documents the behavioral and technological flexibility of H. sapiens. These complex subsistence strategies appear to be part of the adaptive ecological plasticity of our species that enabled it to inhabit diverse Late Pleistocene habitats across the world. The primary niche of non-H. sapiens hominins within and beyond Africa appears to be diverse forest and grassland mosaics in the vicinity of rivers and lakes40,41. By contrast, following its evolution in Africa c. 300 ka42, our species came to occupy higher-elevation niches than its hominin predecessors, as well as deserts, palaeoarctic settings, and tropical rainforest habitats stretching across Asia, Melanesia, and North, Central, and South America4. Moreover, it was even able to alter and manage environments, such as tropical forests, to meet its own subsistence and cultural needs through ever-intensifying niche-construction39,43. Detailed paleoecological and archeological analysis, such as that presented here, offers to yield more insights into the variety of cultural and subsistence strategies that facilitated the eventual colonization of all of the world’s continents, and resilience to increasingly extreme Pleistocene climatic fluctuations, that left H. sapiens the last hominin standing on the face of the planet.
4. Mellars, P. Going east: new genetic and archaeological perspectives on the modern human colonization of Eurasia. Science 313, 796–800 (2006).

5. Marean, C. The transition to foraging for dense and predictable resources and its impact on the evolution of modern humans. Philos. Trans. Roy. Soc. B 371, 1698 (2016).

6. Stiner, M. C. Thirty years on the “Broad Spectrum Revolution” and paleolithic demography. PNAS 98, 6993–6998 (2001).

7. Shi, S. J. Homo sapiens is as Homo sapiens was: behavioral variability versus “behavioral modernity” in Paleolithic archaeology. Curr. Anthropol. 52, 1–35 (2011).

8. Bird, M. I., Taylor, D. & Hunt, C. Palaeoenvironments of insular Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? Quat. Sci. Rev. 24, 2228–2242 (2005).

9. Boivin, N., Fuller, D. Q., Dennell, R., Allaby, R. & Petraglia, M. D. Human Dispersal across Diverse Environments of Asia during the Upper Pleistocene. Quat. Int. 300, 32–47 (2013).

10. Martin, P. S. & Klein, R. G. Quaternary Extinctions: A Prehistoric Revolution (University of Arizona Press, Tucson, 1984).

11. Rule, S. et al. The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. Science 355, 1483–1486 (2012).

12. Sandom, C., Faubry, S., Sandel, R. & Svenning, J.-C. Global late quaternary megafauna extinctions linked to humans, not climate change. Philos. Trans. Roy. Soc. B 28, 20133254 (2014).

13. Barker, G. & Farr, L. (eds) Archaeological Investigations in the Niah Caves. McDonald Institute for Archaeological Research, Cambridge, (2016).

14. Summerhayes, G. R. et al. People of the ancient rainforest: Late Pleistocene foragers at the West Mouth and Lobang Hangus. In Hien Rock Shelter. J. Hum. Evol. 60, 102–118 (2011).

15. Perera, N. et al. Bone Technology from Late Pleistocene Archaeological Sites. Natural History Museum, London, 354–356 (2014).

16. Roberts, P. et al. Direct evidence for human reliance on rainforest resources in Late Pleistocene Australia. Philos. Trans. R. Soc. B 373, 1486–1509 (2018).

17. van Vliet, N., Milner-Gulland, E. J., Bousquet, F., Saqqal, M. & Nasi, R. Effect of small-scale heterogeneity of prey and hunter distributions on the sustainability of bushmeat hunting. Conserv. Biol. 37, 1327–1337 (2010).

18. Greenberg, L. et al. The kelp highway hypothesis: marine environment, the coastal migration theory, and the peopling of the Americas. J. Island. Coast. Archael. 2, 161–170 (2017).

19. Roberts, P. et al. Fruits of the forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~36 to 3 ka) Sri Lanka. J. Hum. Evol. 106, 102–118 (2017).

20. Gamble, C. Timewalkers: The Prehistory of Global Colonization. (Alan Sutton Press, Gloucester UK, 1993).

21. Gamble, C. Mapping the Earth: The Archaeology of Deep Human History. (Cambridge University Press, Cambridge, 2013).

22. Rubel, R. J. Bone and tusk tools from the West Mouth and Lobang Hangus. In Archaeological Investigations in the Niah Caves, Sarawak (eds. Barker, G. & Farr, L.) 301–324 (McDonald Institute for Archaeological Research, Cambridge, 2016).

23. Perera, N. A. & Dolman, P. Density compensation in Neotropical primate communities: Evidence from 56 hunted and non-hunted Amazonian forests of varying productivity. Oecologia 122, 175–189 (2000).

24. Fortier, J. The ethnography of south Asian foragers. Ann. Rev. Anthropol. 38, 99–114 (2009).

25. Fortier, R. A. Effects of hunting on rain forest primates. In Primate Conservation in the Tropical Rainforest (eds. Marsh, C. W. & Mittermeier, R. A.) 109–146 (Liss, New York, 1987).

26. Stiner, M. C. The use of mortality patterns in archaeological studies of human efficiency and focus of blowpipe hunting among Semaq Beri hunter-gatherers of Peninsular Malaysia. Hum. Ecol. 16, 271–305 (1988).

27. Cranbrook, E. & Labang, D. Bearded pigs (Sus barbatus): tooth-wear and aging wild populations in Sarawak. Sarawak Museum. Journal 58, 163–182 (2003).

28. Piper, P. J. & Rabet, R. J. Vertebrate fauna from the Niah Caves. In Archaeological Investigations in the Niah Caves, Sarawak (eds. Barker, G. & Farr, L.) 401–438 (McDonald Institute for Archaeological Research, Cambridge, 2016).

29. Brandt, J. H. The Southeast Asian Negrito: further notes on the Negrito of Malaysia. J. Arch. Sci. 32, 305–311 (2005).

30. Cunningham, A. J. The sociocultural basis for the conservation of the Toque monkey (Macaca sinica). In Primate Conservation (eds. Rainier III & Bourne, J. H.) 327–365 (Cambridge University Press, Cambridge, UK, 1994).

31. Radley, R. & Dyer, D. Mammal Species of the World. (John Hopkins University Press, Baltimore, MD, 2005).

32. Thomas, D. H. Great basin hunting patterns: a quantitative method for testing faunal remains. Am. Antiq. 34, 392–401 (1969).

33. Wilson, D. E. & Reeder, D. M. (eds). The Mammal Species of the World. (John Hopkins University Press, Baltimore, MD, 2005).

34. Behrensmeier, A. K. Taphonomic and ecological information from bone weathering. Paleobiology 4, 150–162 (1978).

35. Shah, S. K. & Bradbury, A. The spatial distribution of zooarchaeological remains in a prehistoric foraging community. J. Arch. Sci. 22, 147–153 (1995).

36. Shipman, P. & Rose, J. Bone tools: an experimental approach. In Scanning Electron Microscopy in Archaeology (eds. Olsen, S. L.) 303–335 (British Archaeological Reports International Series, Oxford, 1988).

37. Shipman, P., Foster, G. & Schoening, M. Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. J. Arch. Sci. 11, 307–325 (1984).

38. Johnson, E. Human modified bones from early southern Plains Sites. In Bone Modification (eds. Bonnie-Lynn, B. & Sorg, M.) 431–471 (Center for the Study of First Americans, Orono, ME, 1989).

39. Brain, C. K. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. (Chicago University Press, Chicago, IL, 1981).

40. Cain, C. R. Using burned animal bone to look at middle stone age occupation and behavior. J. Arch. Sci. 32, 873–884 (2005).

41. O’Connell, J., Petraglia, M. D. & Preuschoft, H. Taphonomy and zooarchaeology of the Upper Paleolithic cave of Dzudzuanu, Republic of Georgia. Int. J. Osteoarchaeol. 18, 131–151 (2008).

42. Klein, R. G. & Cruz-Uribe, K. The Analysis of Animal Bones from Archaeological Sites. (Chicago University Press, Chicago, IL, 1984).

43. Lyman, R. L. Vertebrate Taphonomy. (Cambridge Manuals in Archaeology, Cambridge University Press, Cambridge, UK, 1994).
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Author contributions
O.W., N.A., M.D.P., and P.R. designed the research; O.W., N.A., M.C.L., K.D., J.B., A.C., S.D., N.K., I.S., A.P., N.B., M.D.P., and P.R. collected the data; O.W., N.A., M.C.L., K.D., J.B., A.C., S.D., N.K., I.S., A.P., N.F., N.B., M.D.P., and P.R. analyzed the data; O.W., N.A., M.C.L., K.D., J.B., A.C., S.D., N.K., I.S., A.P., N.F., N.B., M.D.P., and P.R wrote the paper.

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