nature ecology & evolution

BRIEF COMMUNICATION

https://doi.org/10.1038/s41559-019-0904-4

Three thousand years of wild capuchin stone tool use

Tiago Falótico[1,2,6], Tomos Proffitt[3,6*], Eduardo B. Ottoni[1], Richard A. Staff[4] and Michael Haslam[5]

The human archaeological record changes over time. Finding such change in other animals requires similar evidence, namely, a long-term sequence of material culture. Here, we apply archaeological excavation, dating and analytical techniques to a wild capuchin monkey (*Sapajus libidinosus*) site in Serra da Capivara National Park, Brazil. We identify monkey stone tools between 2,400 and 3,000 years old and, on the basis of metric and damage patterns, demonstrate that capuchin food processing changed between ~2,400 and 300 years ago, and between ~100 years ago and the present day. We present the first example of long-term tool-use variation outside of the human lineage, and discuss possible mechanisms of extended behavioural change.

Our understanding of long-term human behavioural evolution is primarily built following changes in stone technology. Palaeolithic archaeologists and palaeoanthropologists use this variation to infer changes in hominin cognition[1] and manual dexterity[2], as well as subsistence strategies and environmental adaptations[3]. However, there is no long-term record of tool use variation in any other animal lineage. Excavations of western chimpanzee (*Pan troglodytes verus*) nut-cracking sites have highlighted the potential antiquity of primate stone tools[4], but without finding changes in tool function[5]. Similarly, although previous excavations of wild Burmese long-tailed macaque (*Macaca fascicularis aurea*) and bearded capuchin monkey (*Sapajus libidinosus*) sites have identified a range of stone tool behaviour[6,7], we have lacked evidence of behavioural variation over time. Here we show that wild bearded capuchins in Brazil have been using stone tools for at least the past ~3,000 years, with marked variation in tool use through this period. This discovery presents the first example of long-term tool use variation outside of the human lineage, providing comparative data on the mechanisms of extended behavioural change.

The wild *S. libidinosus* of Serra da Capivara National Park (SCNP) use stone tools in a wider variety of behaviours than any living animal other than *Homo sapiens*. These activities include nut cracking, seed processing, digging, stone-on-stone percussion, sexual displays and fruit processing[8–12]. For percussive tasks, the SCNP capuchins use rounded quartzite cobbles as hammerstones, which are readily available in the immediate landscape. For anvils they use tree roots and limbs, as well as loose cobbles and conglomerate blocks[10].

The current study focuses on Caju BPF2, an open-air site located in the Baixão da Pedra Furada (BPF) valley (08° 49.740′ S, 42° 33.292′ W) in SCNP[7] (Fig. 1). Wild capuchins currently bring stones to this site to process endemic cashew nuts (*Anacardium* spp.), resulting in the accumulation of cashew-residue-covered hammerstones and broken cashew shells, along with heavy percussive damage on local cashew trees. Our most recent excavations build on the those previously reported[7] and extend the site's limits and time depth.

A total of 16 radiocarbon dates closely associated with percussive stone tools demonstrate that capuchins have used this location during four separate chronological phases (I–IV; Supplementary Table 1). Caju BPF2 consists of two separate excavated areas, Caju BPF2 East (20 m^2) and Caju BPF2 West (47 m^2). Combined, a total area of 67 m^2 was excavated to a maximum depth of 0.77 m, with 1,699 lithics >2 cm recovered of which 123 (7.2%) exhibited percussive damage. The excavation was separated into 16 arbitrary 5-cm spits, grouped into four chronological phases based on radiocarbon dating, Phase I being the most recent and Phase IV representing the oldest currently known capuchin occupation. The sedimentology (fine sand with frequent small, rounded pebbles) is consistent throughout, with no discernible change between spits or levels. Gaps in the radiocarbon dating, however, suggest periods of low sedimentation rates. Dates for the lowest levels push the earliest known capuchin occupation at SCNP back to approximately 3000–2400 cal BP, quadrupling the time depth of evidence for non-ape tool use. A natural control sample representative of the raw materials available to capuchins within the landscape was sampled (see Supplementary Information).

We recovered 122 clearly identifiable capuchin stone artefacts, weighing 46.7 kg in total, from the Caju BPF2 excavations. Percussive evidence on these tools includes multiple individual impact points, incipient cones of percussion, adherent residue, crushing of the stone surface or a combination of these (Supplementary Information). The Caju BPF2 artefacts include active percussive tools, as well as passive elements and fragments (Supplementary Table 2), with the majority being quartzite pebbles and cobbles (97.1%) and the remainder sandstone. Raw material representation parallels that of the landscape at SCNP (Supplementary Information), with the closest lithic material source being a seasonally dry streambed about 25 m to the east. All recovered hammerstones are considerably larger than the natural background stones, indicating capuchin tool selection throughout the site's occupation.

The earliest hammerstones at the site (Phase IV, circa 2993–2422 cal BP) are heavily damaged by percussive battering (Fig. 2), and the large majority of hammerstones with flake detachments were found in this level (Supplementary Information). Tools from this phase possess considerably more impact points across more surfaces, have more extensive use-wear and are much smaller and lighter than those from the more recent Phases I and II. These damage

[1]Department of Experimental Psychology, Institute of Psychology, University of São Paulo, Butantã, Brazil. [2]Neotropical Primates Research Group, Butantã, Brazil. [3]Institute of Archaeology, University College London, London, UK. [4]Scottish Universities Environmental Research Centre, East Kilbride, UK. [5]Independent Researcher, London, UK. [6]These authors contributed equally: T. Falótico, T. Proffitt. *e-mail: t.proffitt@ucl.ac.uk

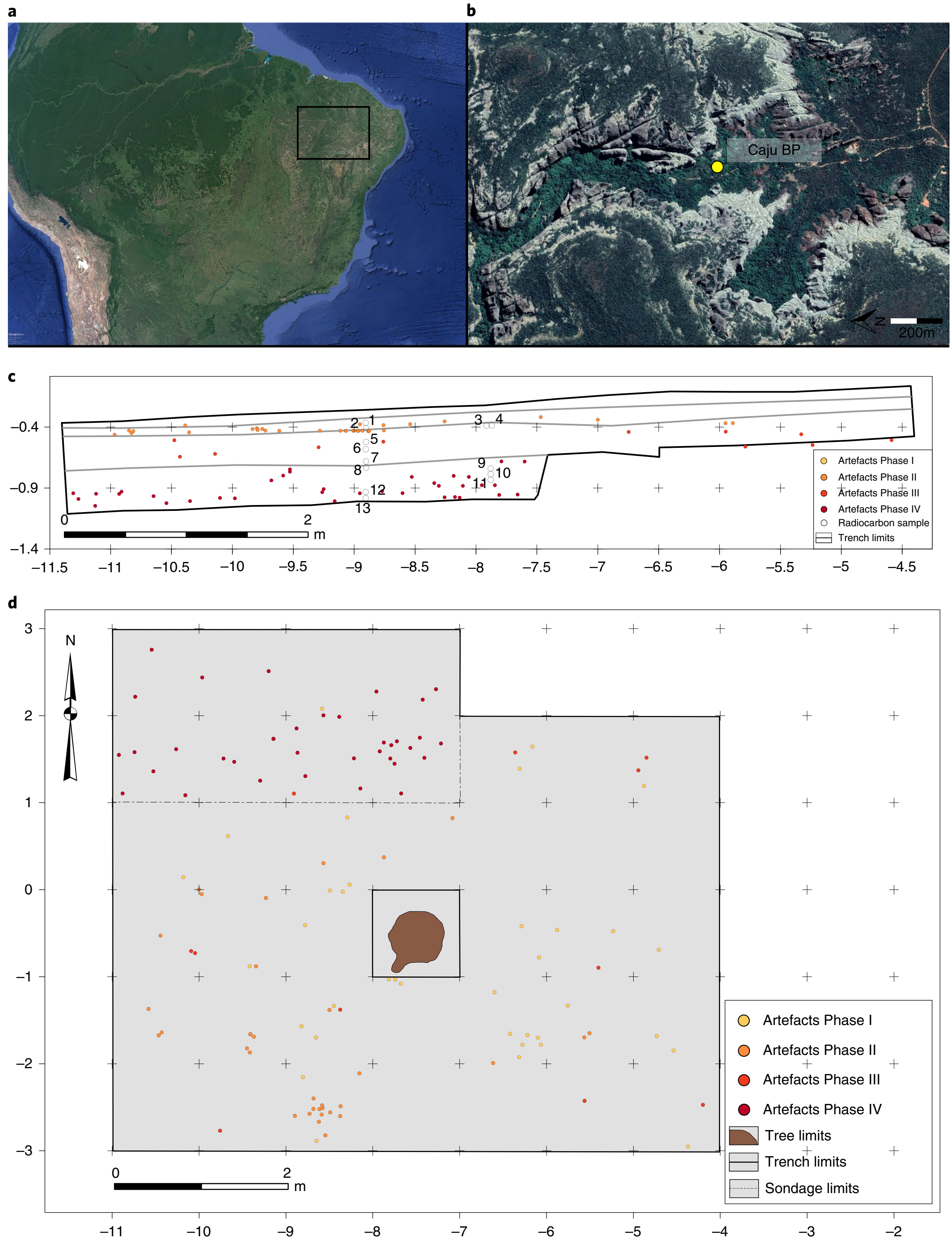

Fig. 1 | The Caju BPF2 site, Serra da Capivara National Park, Brazil. a, Map of Brazil with the location of Serra da Capivara National Park. **b**, The Baixão da Pedra Furada with the location of the Caju BPF2 excavation. **c**, Stratigraphic cross-section of Caju BPF2 West with locations of radiocarbon dating samples and artefacts. 1, Oxford radiocarbon accelerator unit (OxA) identifier—31432; 2, OxA—31433; 3, OxA—31858; 4, OxA—31859; 5, OxA—31434; 6, OxA—31860; 7, OxA—31861; 8, OxA—831435; 9, OxA—33134; 10, OxA—33135; 11, OxA—33136; 12, OxA—33137; 13, OxA—33138. All radiocarbon samples are listed in Supplementary Table 1. Note overlapping artefacts due to slope of excavation.**d**, Plan of Caju BPF2 West **a**, Map data Google Earth, JS Dept of State Geographer, 2018 Google, SIO, NOAA, US Navy, NGA, GEBCO, Landsat/Copenicus. **b**, 2019 CNES / Airbus, 2018 Google.

patterns most probably resulted from strikes that contacted the underlying substrate in addition to the target, suggesting that small foods were the main target; however, variation in tool use behaviour and repeated tool use should not also be overlooked. Furthermore, observations of modern wild *S. libidinosus* have shown that stone tool dimensions and weights correlate positively with food hardness

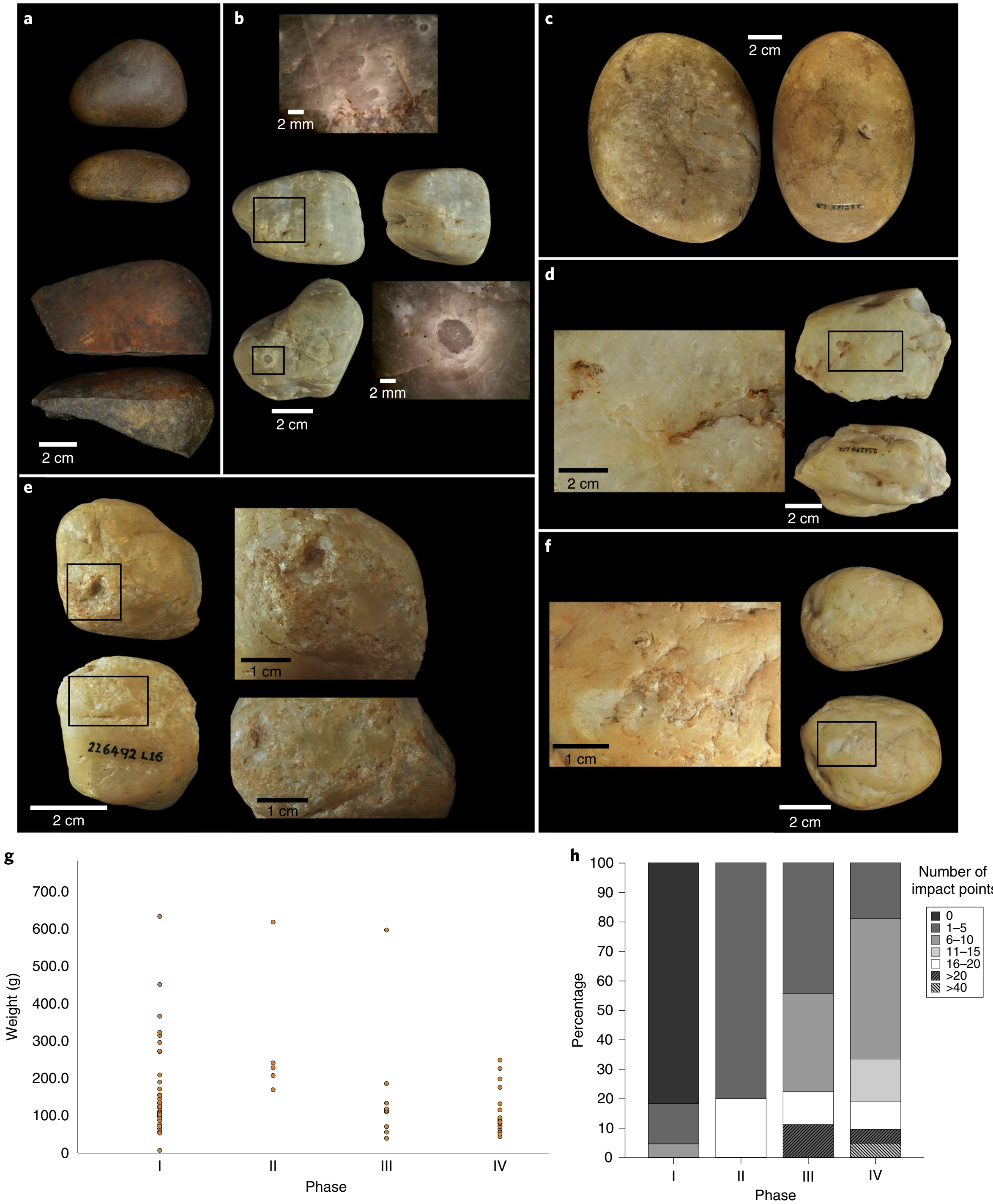

Fig. 2 | Examples of hammerstones and anvils from Caju BPF2. a, Examples of cashew-residue-covered hammerstones from Phase I. **b**, Hammerstone from Phase II with clear incipient cones of percussion. **c**, Example of an anvil from Phase II. **d–f**, Examples of hammerstones with typical capuchin percussive damage from Phase IV. **g**, Weights of all hammerstones and hammerstones with flake detachments from all phases. **h**, Relative frequency of impact points on all hammerstones and hammerstones with flake detachments from all phases.

or resistance[13,14,15]. Compared with the known use of the site for cashew processing in Phase I, this association points to the low weight of hammerstones in Phase IV, probably resulting from processing smaller, less resistant, food sources than cashews.

The lithic assemblage from Phase III (circa 640–565 cal BP) is not radically different from either the preceding or following phases in terms of hammerstone dimensions and weight (Supplementary Information). Percussive damage is similar to that seen in Phase IV, suggesting a continued reliance on small foods, while the relatively high percentage of anvils is most similar to the later Phase II. In its wider site context, this phase therefore preserves an intermediate capuchin pounding behaviour. Hammerstones in Phase II (circa 257–27 cal BP) are much larger than the cashew-processing material from Phase I (Fig. 2). Coupled with the fact that large anvils and anvil fragments make up the majority of artefacts from this level, the evidence suggests that capuchin percussive activity at the site during this period also centred less exclusively on cashews, and more on the opening of harder foods.

Heavy percussive damage to the roots and branches of the cashew trees at Caju BPF2 indicates their use as anvils during Phase I, which may help explain the lower percentage of large stone anvils in this phase. All stone artefacts from this period are discoloured with identifiable cashew residue[7]. Residue analysis on older artefacts is, however, impossible due to a lack of preservation of any identifiable adhering residue[7]. It is likely that this is due to a combination of mechanical removal and water-based dilution of residues over time. This finding indicates either a diminished role of cashew processing in the past or the decomposition of cashew nut residue over time. Combined with modern-day observations, the archaeological data confirm that the primary recent activity at Caju BPF2 was cashew nut processing.

The higher frequency and degree of percussive damage in the oldest level of the site, as well as an increased frequency of flaked hammerstones, support the inference of a change in pounding behaviour between Phase IV and Phases II and I, sometime between ~2,500 and ~300 years ago. Hammerstones used for low-resistance food processing are much smaller and lighter than those used for all other capuchin percussive tasks[10,14–17], and the Phase IV hammerstones fall within the mean dimensions of those used for this activity. As noted, the increased damage noted on Phase IV tools is probably a consequence of frequent and repeated impacts between the hammerstone and an anvil stone, as a result of the smaller size of the processed food. Low-resistance foods such as seeds also do not require a large anvil surface area, which would help explain why there are no large anvils in the earliest level. It may be that the corresponding passive elements at that time were hard natural substrates or quartzite pebbles of the same dimensions as hammerstones. The latter would mean that hammers and anvils in Phase IV may, in fact, be interchangeable, as observed in present-day capuchins at SCNP.

Although SCNP has a rich human archaeological record[18,19], the capuchin percussive lithic material identified at Caju BPF2 is clearly non-human in origin. The assemblage lacks knapped material such as exploited cores, flakes and retouched material. In addition, the capuchin hammerstones at Caju BPF2 do not show the same percussive damage as typical human knapping hammerstones. Instead, they consist of repeated, superimposed incipient cones of percussion often located on flat surfaces, typical of capuchin percussive activities[8]. The Caju BPF2 site also lacks non-lithic material, such as ceramics or concentrated burnt areas, which is ubiquitous in Late Holocene human archaeological sites at SCNP[20].

In traditional Early Stone Age lithic analyses, assemblage variation has been interpreted in a number of ways. Distinct substantial technological changes unique to hominins, such as the Oldowan to Acheulean transition, have been used to infer hominin evolutionary adaptations, such as the appearance of a new species[21] or cognitive developments[22]. However, more nuanced lithic differences within one technological tradition are interpreted in an equally varied manner. For example, both synchronic and diachronic variation within the Oldowan have been used to suggest regional adaptations to local environmental and raw material factors[23], as well as varying cultural groups and traditions[24]. Furthermore, variation of artefact form within a single technological category, such as percussive artefacts within the Oldowan, has been used to suggest change in function[25,26] and hominin subsistence strategies[27]. This study shows that similar inferences can now be made regarding non-human primate technological variation.

The exact reasons behind the apparent diachronic technological change for the SCNP capuchins is currently unknown. SCNP is home to numerous capuchin groups, and these monkeys have been reported to acquire nut-cracking stone tool use behaviour by social learning processes[28]. If the same situation held true in antiquity, then the diachronic variation observed at Caju BPF2 may be a consequence of cultural variation in foods targeted with stone tools. That is, it may represent the archaeological signature of multiple capuchin populations that frequented this location, each of which used stones for different encased foods. Equally, it might instead record long-term site re-occupation by a single capuchin population undergoing tool use change. Outside of social explanations, the stone tool variation at Caju BPF2 may also reflect a past lack of cashew trees at this location. Although the palaeo-environmental record at SCNP indicates a relatively continuous presence of dry savannah forest in this region[20], the presence of cashew trees may have fluctuated in this specific location.

Whichever is the case, while capuchins operated within the same basic stone tool percussive tradition over at least 3,000 years of activity at Caju BPF2, they implemented this technology to different ends. The lithic material recovered from four chronologically distinct phases represents around 450 generations of repeated, but not necessarily continuous, capuchin tool use within the SCNP landscape. The predominant behaviour between 2993 and 565 cal BP was probably the processing of small, low-resistance foods, whereas by 257 cal BP this behaviour had altered to encompass larger and harder resources than cashew processing seen in modern times. Our identification of diachronic stone tool behavioural change in the primate archaeological record indicates that humans are not unique in terms of long-term artefactual variation. This recognition of millennial-scale technological change outside the human lineage opens the door for future investigations into how stone tool-using animals adapt to long-term ecological trends, as well as potentially broadening the comparative scope of primate models for Plio-Pleistocene hominin technological variation in the archaeological record.

Methods

Lithic analysis. Strict selection criteria were employed during the excavation process. All lithics, both natural and artefactual larger than 2 cm, were collected. These were separated into natural unmodified pieces and artefacts that possessed clear percussive damage. A six-way inter-analyst agreement was used to assign an artefact as either a capuchin percussive tool or fragment; if an individual analyst disagreed, the artefact was not recorded as capuchin-used. In this way we have been extremely conservative in our identification and recovery of capuchin cultural material. It is very likely that the true frequency of capuchin artefacts in each chronological phase at Caju BPF2 is greater, as ambiguous capuchin artefacts were set aside, as well as those that showed no percussive damage but may have been lightly used. However, by employing a conservative estimate, we have ensured that only the most diagnostic artefacts are included. One large, highly rounded hammerstone from Phase II may be either anthropogenic or capuchin-used (or both) and was excluded from this analysis, leaving 122 artefacts for our analyses. As Caju BPF2 is still frequented by capuchin groups, we decided that hammerstones on the surface should be kept in circulation so as not to disrupt the animals' natural behaviour. The location of these surface hammerstones was plotted, and they were documented in terms of dimensions and weight; however, these were not collected and not subjected to technological analysis. These hammerstones have been included in our analysis of tool dimensions but have been excluded from our comparisons of percussive damage. The remaining artefacts were measured, weighed and subjected to a full technological lithic analysis. Technological classifications were based on criteria previously used to describe primate percussive material[8], and shown to be adequate in describing the range of artefacts associated with capuchin percussive behaviour.

Statistical analysis. Both categorical and nominal data were used to assess inter-phase variability. Depending on the data distribution, parametric and non-parametric tests were employed. A combination of Chi-squared and Cramer's V (for categorical data) and Kruskal–Wallis and Mann–Whitney *U*-tests (for numerical data) was used to test for overall diachronic variation. The 0.05 significance level was applied as the threshold for each statistical test. Post hoc analyses were employed to identify individual sources of variation between assemblages. For Kruskal–Wallis and Mann–Whitney *U*-tests, post hoc pairwise comparisons were undertaken. For significant Chi-squared results, adjusted residuals were calculated to identify significant trends within the data; values of 2.0 and −2.0 were taken to assess significance at a 0.05 confidence level. All data manipulation and statistical testing were undertaken in Excel and SPSS.

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

Data availability
All data pertaining to the study are included within the text and Supplementary Information. Access to the collections is available upon request.

Received: 24 January 2019; Accepted: 18 April 2019;
Published online: 24 June 2019

References
1. Stout, D. *Philos. Trans. R. Soc. B* **366**, 1050–1059 (2011).
2. Harmand, S. et al. *Nature* **521**, 310–315 (2015).
3. Potts, R. *Curr. Anthropol.* **53**, S299–S317 (2012).
4. Mercader, J. et al. *Proc. Natl Acad. Sci. USA* **104**, 3043–3048 (2007).
5. Proffitt, T., Haslam, M., Mercader, J., Boesch, C. & Luncz, L. V. *J. Hum. Evol.* **124**, 117–139 (2018).
6. Haslam, M. et al. *J. Hum. Evol.* **96**, 134–138 (2016).
7. Haslam, M. et al. *Curr. Biol.* **26**, R521–R522 (2016).
8. Proffitt, T. et al. *Nature* **539**, 85–88 (2016).
9. Falótico, T. & Ottoni, E. B. *PloS ONE* **8**, e79535 (2013).
10. Falótico, T. & Ottoni, E. B. *Behaviour* **153**, 421–442 (2016).
11. Falótico, T., Siqueira, J. O. & Ottoni, E. B. *Sci. Rep.* **7**, 6278 (2017).
12. Mannu, M. & Ottoni, E. B. *Am. J. Primatol.* **71**, 242–251 (2009).
13. Spagnoletti, N. et al. *J. Hum. Evol.* **61**, 97–107 (2011).
14. Ferreira, R. G., Emidio, R. A. & Jerusalinsky, L. *Am. J. Primatol.* **72**, 270–275 (2010).
15. Visalberghi, E. et al. *Am. J. Phys. Anthropol.* **132**, 426–444 (2007).
16. Falótico, T. et al. *Primates* **59**, 385–394 (2018).
17. Moraes, B. L. C. D., Souto, A. D. S. & Schiel, N. *Am. J. Primatol.* **76**, 967–977 (2014).
18. Boëda, E. et al. *Antiquity* **88**, 927–941 (2014).
19. Lahaye, C. et al. *Quat. Geochronol.* **30**, 445–451 (2015).
20. Pessiss, A.-M., Martin, G. & Guidon, N. *Os Biomas e as sociedades Humanas Na Pré- História Da Região Do Parque Nacional Serra Da Capivara, Brasil* Vol. II-B (FUMDAHM, 2014).
21. Leakey, M. D. *Olduvai Gorge* Vol. 3 (Cambridge Univ. Press, 1971).
22. Torre, Idela & Mora, R. *J. Archaeol. Method Theory* **21**, 781–823 (2014).
23. Braun, D. R. et al. *J. Hum. Evol.* **55**, 1053–1063 (2008).
24. Leakey, M. D. *After the Australopithecines: Stratigraphy, Ecology, and Culture Change in the Middle Pleistocene* (eds Butzer, K. W. & Isaac, G. L.) 477–493 (Mouton, 1975).
25. Arroyo, A. & de la Torre, I. *J. Archaeol. Sci.* **74**, 23–34 (2016).
26. Arroyo, A. & de La Torre, I. *J. Hum. Evol.* **20**, 402–421 (2018).
27. Mora, R. & de la Torre, I. *J. Anthropol. Archaeol.* **24**, 179–192 (2005).
28. Eshchar, Y., Izar, P., Visalberghi, E., Resende, B. D. & Fragaszy, D. M. *Anim. Cogn.* **19**, 605–618 (2016).

Acknowledgements
The study was funded by a European Research Council Starting Investigator Grant (No. 283959) to M.H.; a São Paulo Research Foundation award to T.F. (No. 2013/05219-0) and E.B.O. (No. 2014/04818-0); a CNPq PQ Grant (No. 308746/2017-1) to E.B.O.; a Leverhulme Trust Early Career Fellowship (No. ECF-2015-396) awarded to R.A.S.; and a British Academy Fellowship (No. pf170157) awarded to T.P. Support for fieldwork and analysis was provided by N. Guidon and G. Daltrini Felice of FUMDHAM. Fieldwork at SCNP was approved by Brazilian environmental protection agencies (IBAMA/ICMBio Nos. 37609-5 and 37615-5). We thank L. V. Luncz for assistance in identification of primate material and R. F. de Oliveira for assistance in coordinating the excavation team and identification of primate material.

Author contributions
T.F. and M.H. undertook excavation and initial data collection. T.F., T.P., M.H. and E.B.O. conceived the study. T.P. conducted the technological analysis. R.A.S. conducted radiocarbon dating of samples and produced associated figures and tables. T.P. and T.F. wrote the paper and Supplementary online material, with contributions from M.H., E.B.O. and R.A.S. T.P. generated all figures and graphs.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-0904-4.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to T.P.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.