



## 3.3 million years of stone tool complexity suggests that cumulative culture began during the Middle Pleistocene

Jonathan Paige<sup>a,1</sup> and Charles Perreault<sup>b</sup>

Edited by Richard Klein, Stanford University, Stanford, CA; received November 1, 2023; accepted May 8, 2024

Cumulative culture, the accumulation of modifications, innovations, and improvements over generations through social learning, is a key determinant of the behavioral diversity across *Homo sapiens* populations and their ability to adapt to varied ecological habitats. Generations of improvements, modifications, and lucky errors allow humans to use technologies and know-how well beyond what a single naive individual could invent independently within their lifetime. The human dependence on cumulative culture may have shaped the evolution of biological and behavioral traits in the hominin lineage, including brain size, body size, life history, sociality, subsistence, and ecological niche expansion. Yet, we do not know when, in the human career, our ancestors began to depend on cumulative culture. Here, we show that hominins likely relied on a derived form of cumulative culture by at least ~600 kya, a result in line with a growing body of existing evidence. We analyzed the complexity of stone tool manufacturing sequences over the last 3.3 My of the archaeological record. We then compare these to the achievable complexity without cumulative culture, which we estimate using nonhuman primate technologies and stone tool manufacturing experiments. We find that archaeological technologies become significantly more complex than expected in the absence of cumulative culture only after ~600 kya.

cultural evolution | human evolution | imitation | stone tools | cumulative culture

Humans have expanded into and adapted to diverse habitats thanks to a culturally transmitted body of knowledge that has evolved over generations, including complex technologies. The population process of cumulative cultural evolution is the primary mode of human adaptation, and it supports all aspects of human subsistence (1–3). The human reliance on cumulative cultural evolution places them squarely in a “cultural niche.” However, the evolutionary history of this ability is unclear. When did hominins begin to rely on, pass on, and modify complex technologies? Is this a derived trait of modern humans or a primitive trait shared across hominins? Answering these questions will help our understanding of the role technology and culture played in shaping hominin evolution.

Here, we study changes in the complexity of stone tool manufacturing sequences across hominin evolution. Chipped stone tools are the oldest, longest-lasting, and most widespread technology in the archaeological record. After their appearance over 3 Mya in East Africa (4, 5), stone tools gradually became a central component of the forager’s toolkit. Hominins explored many stone tool-making practices, from simple Oldowan pebble-core reduction, which requires only a few actions performed in sequence, to the more complex production of Polynesian quadrangular adzes made by craft specialists in complex societies (6).

But why should hominins ever rely on complex technologies? In many circumstances, expedient tools that are quick and easy to learn and make, such as simple flakes, may be preferable to more complex ones. Thus, and unsurprisingly, simple flaked tools remained present across the 3 My of the archaeological record.

Nonetheless, exploring new regions of the design space for stone tool technology to gain efficiency and function will inevitably require increased complexity. There are, for example, only so many types of tools that can be made by striking a handheld core with a hard hammer, and these are simple and easy to master relative to later technologies (7–9). As new knapping techniques are discovered, the frontiers of the possible design space expand. For example, soft hammer percussion and pressure flaking make bifaces much thinner than possible through hard hammer percussion (10). These more complex technologies are also more difficult to discover, master, and teach (7–9, 11, 12).

Complexity also begets complexity. An important innovation engine is recombining existing traits to form new ones (13–19). In stone tools, recombining existing steps in novel ways may lead to new forms and tool types and increase the likelihood of new technologies being discovered. For example, the development of hafting would have

### Significance

Our species, *Homo sapiens*, occupies a uniquely diverse set of ecological habitats. Humans expanded into tropical forests and arctic tundra through cumulative culture. Cumulative culture is the accumulation of modifications, innovations, and improvements over generations through social learning. Generations of variant accumulations allow humans to use technologies and know-how well beyond what a single naive individual could invent independently within their lifetime. We analyzed the stone tools made during the last 3.3 My. We found that these stone tools remained simple until about 600,000 B.P. After that point, stone tools rapidly increased in complexity. Consistent with findings from other research teams, we suggest that this transition signals the development of cumulative culture in the human lineage.

Author affiliations: <sup>a</sup>Department of Anthropology, University of Missouri, Columbia, MO 65211; and <sup>b</sup>School of Human Evolution and Social Change, Institute of Human Origins, Arizona State University, Tempe, AZ 85281

Author contributions: J.P. and C.P. designed research; performed research; contributed new reagents/analytic tools; analyzed data; and wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2024 the Author(s). Published by PNAS. This article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

Although PNAS asks authors to adhere to United Nations naming conventions for maps (<https://www.un.org/geospatial/mapsgeo>), our policy is to publish maps as provided by the authors.

<sup>1</sup>To whom correspondence may be addressed. Email: [jpnr@missouri.edu](mailto:jpnr@missouri.edu).

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2319175121/-/DCSupplemental>.

Published June 17, 2024.

opened up many possibilities for new forms, knapping strategies, and kinds of tools to be used and invented (20). When recombination is an important driver of innovation, complexity can increase rapidly as the number of known traits increases and the number of possible recombinations expands exponentially (15).

## Cumulative Culture

Cumulative culture refers to the accumulation of modifications, innovations, and improvements over generations through social learning. Generations of improvements, modifications, and lucky errors can generate technologies and know-how well beyond what a single naive individual could invent independently within their lifetime. When a child inherits her parent's generation's culture, she inherits the outcome of thousands of years of lucky errors and experiments.

Cumulative culture produces three related outcomes. First, it increases a population's knowledge pool over time. Second, cumulative culture finds improbable solutions, much like biological evolution does. Ecological challenges can have many possible solutions that are too difficult for individuals to discover or invent on their own. Cumulative culture allows populations to explore large fitness landscapes and, step-by-step, discover local optima (21). This allows populations to develop useful practices even when individuals have only a partial causal understanding of it (1, 22). Third, cumulative culture tends to increase the complexity of technologies and other know-how. Cumulative culture allows for useful distinct parts and structures in a finished tool form (23) or steps and procedures in the manufacture of an object (24, 25) to accumulate over time, resulting in increasingly diverse, efficient, and specialized toolkits.

Observational and experimental evidence suggest that nonhuman ape culture does not rely on copying know-how (26, 27). Instead, nonhuman ape cultures appear to emerge from an interplay of genes, environments, and social learning, which all channel the development of know-how without directly copying the particular steps involved in these behaviors (27). While these mechanisms can support ape traditions and technologies that are complex to a degree (28, 29), they cannot achieve the complexity of traditions passed on and elaborated on through copying know-how more directly. Humans, in contrast, can copy behavioral processes and their results, which likely enables cumulative culture (27).

Reliance on cumulative culture placed humans in a new cultural niche that profoundly impacted behavior and biology (1). As the cultural pool of observable behaviors evolved, so did the genes that control learning. This may explain why specialized cognitive abilities emerge early in life (1, 30, 31). The cultural adaptation of cooking created new selective pressures on our bones, muscles, teeth, and guts (32). Other products of this gene-culture coevolution process may include an increase in relative brain size, a prolonged life history, and other keystone traits underlying human uniqueness (33, 34).

But when did humans enter the cultural niche? Suggestions have ranged from the early Oldowan to this being unique to modern humans in the late Pleistocene (35–38). Answering this question demands measuring proxies of cumulative culture, such as technological complexity, over evolutionary time scales. It also requires an expectation for what such a proxy should look like without cumulative culture. We expect the advent of cumulative culture to leave two signatures in the archaeological record: 1) it will produce behaviors more complex than what extant nonhuman primates are capable of and more complex than what individual humans can learn on their own (21, 35), and 2) it will lead to a

rapid increase in the degree of cultural complexity hominins were capable of achieving. Because we do not expect simple tools always to be replaced by more complex ones, these two signatures should leave their mark at the upper limit of the distribution of technological complexity over time.

## Materials and Methods

We collected data on stone tool manufacture sequences from published studies. We aimed for a broad spatial and temporal coverage, surveying lithic technology from the Pliocene to the Holocene in Africa, Eurasia, Oceania, and the Americas. The decision to code a particular published study was based on the degree of detail in descriptions of the lithic technology, including information on how cores were managed, how pieces were retouched, and the presence of illustrations (39–41) (*SI Appendix*).

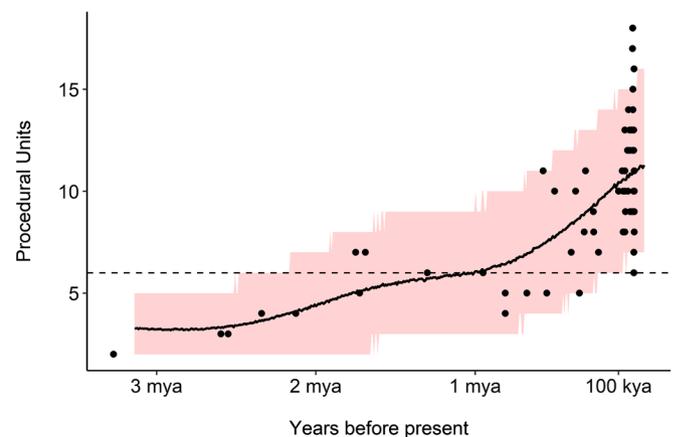
We measured the complexity of manufacturing sequences by counting the number of procedural units it involved. Procedural units are discrete, mutually exclusive manufacturing steps that can be chained together in the production of technologies (25, 41, 42). We considered 33 possible procedural units in stone tool-making sequences that were marked as either present or absent within each sequence (43, 44). These procedural units include steps involved in core preparation, the tools used to produce flakes, and retouching (*SI Appendix, Table S1*).

To build an expectation of technological complexity achievable by early hominid individuals without cumulative culture, we collected data on 1) nonhuman primate technologies, 2) the complexity of stone tool technologies spontaneously invented by naive flintknappers, and 3) the complexity of technologies observed during randomized flaking experiments (*SI Appendix, Table S2*).

We fitted a descriptive statistical model to the data. We modeled procedural unit counts as a Poisson regression with a smooth spline to describe its relationship with age (*SI Appendix*) (43).

## Results

The complexity of tool-making sequences sampled in our dataset increases over time (Fig. 1), in line with previous assessments of trends in complexity over the Paleolithic period (7, 25, 45). The simplest technologies are the ~3.3 ma bipolar percussion sequences from Lomewki (3 PU), Oldowan pebble cores from EG12 (~2.6 ma, 3 PU), and the simple flakes produced at Bokol Dora 1 in Ethiopia (~2.6 ma, 3 PU). The most complex sequences are from the Holocene: A pressure blade technology involving 19 procedural



**Fig. 1.** Count of procedural units ( $n = 64$ ) as a function of time. The line represents the mean of the statistical model posterior predictions, and the shaded ribbon is the 80th percentile interval. Posteriors are sampled from the global grand mean with no site-specific deviations. The horizontal dash line at  $PU = 6$  marks the most complex nonhuman primate technology, i.e., the brush-tipped termite probe production reported among chimpanzee groups (29). Other nonhuman primates and human experiment values fall below this line (*SI Appendix, Table S2*).

units was found in ~10 ka deposits at the Early Mesolithic site of Sujala, Finland (46).

The sequences from nonhuman primates, naive human experiments, and random-flaking experiments vary from 1 to 6 PU (SI Appendix, Table S2). We assume here a baseline of 6 PU for the complexity that can be achieved without cumulative culture.

The upper limit of the complexity distribution over time can be divided into three periods. The first period started around 3.3 Mya and ended ~1.8 Mya. During this time, the manufacture sequences ranged between 2 and 4 procedural units in length—below the most complex baseline.

The second period spans ~1.8 to ~0.6 Mya and includes much of the Acheulean industry. The ceiling of complexity during this period ranges from 4 to 7 PU. This range overlaps and surpasses our baseline value by one PU. The predictions drawn from our statistical model's posteriors include PU counts above what has been observed empirically, such as eight or even nine PU by 1.8 Mya. We think this is a limitation of the model. Our overall understanding of the stone tools of the period is greater than the eight data points in our dataset. There are, for example, 175 published Acheulean sites reported in the ROCEEH database (47), and they do not contain complex technologies like a blade, Levallois core, or tranchet flaking. We expect that the absence of observed technologies with a complexity PU of 7 or greater is a real empirical trend, not a sampling error.

The third period starts near the beginning of the Middle Pleistocene, around 600 kya, and extends into the late Holocene, as early as ~800 kya, given the uncertainty in the statistical model's parameters. During the third period, hominin species relied on technologies more complex than the experimental and nonhuman primate technological baselines. The complexity observed ranges from 5 to 18 PU. By ~300 kya, some technologies are twice as complex as perishable chimpanzee tools. This suggests that hominins consistently relied on technologies that likely required cumulative culture to develop and persist across generations. Technologically, the rapid increase in maximum complexity is marked by the development of blade production, Levallois reduction, soft hammer, and pressure flaking.

The development of cumulative culture may predate the divergence of the Neanderthal and Modern Humans and be a shared derived feature of both lineages. This is reflected in the overlap in the complexity of both groups during the late Pleistocene. The complexity of technologies made by Neanderthals ranges from 9 to 13 PU ( $n = 6$ ), and those produced by Modern Humans during the Pleistocene range from 8 to 15 PU ( $n = 11$ ). This is in line with other independent lines of evidence that have found that Neanderthal Middle Pleistocene Levallois technologies are more complex than the blade technologies associated with Modern Humans in the late Pleistocene (7, 8).

## Discussion

The long-term pattern of rise in complexity relative to what we described above can be accounted for by at least two evolutionary scenarios: an early entry into the cultural niche and a late one. In both scenarios, hominins relied on cumulative culture by ~600 kya.

**An Early Entry into the Cultural Niche Scenario.** According to this scenario, hominins stepped into the cultural niche before 600 kya and possibly as early as 3.3 Mya. After all, complexity levels below our baseline of PU~6 may be consistent with an absence of cumulative culture, but they don't exclude it. Thus, the rise in the cumulative maxima of the distribution of PU over time may be due, in its entirety, to a mixture of gene-culture coevolution and cumulative culture.

Tool-assisted meat extraction may have been an impetus for the evolution of cumulative culture. The earliest potential evidence for these extractive, tool-assisted behaviors in the hominin lineage is represented in the tool marks at Dikkika ~3.4 Mya (48), slightly older than earliest percussive and flaked stone tools date to ~3.3 Mya at Lomekwi 3, and predating later Oldowan flaked tools ~2.8 Mya (5). Early hominins may have relied on percussive tools to access marrow (49) and chipped stone tools to scavenge meat (50–52). After ~2 Mya, the evidence for a reliance on hunting as a method of obtaining protein and fat becomes more persistent (53, 54), and this increase in access to meat would have helped provide the energy for the increases in brain and body size observed across hominin evolution (55).

The slow increase in complexity over the first 2.5 My of stone tool history, including long periods of stasis at complexity levels below the degree of complexity seen in perishable chimpanzee technologies, could be the signature of gradual and step-wise gene-culture coevolution. As cumulative culture begins to produce adaptive know-how, selective pressures on brains and developmental processes facilitate the acquisition, storage, and use of that cultural information (56, 57). The timing and tempo of the evolution of these biological traits, in turn, could put a check on cumulative culture (3, 58). For instance, replicative knapping experiments suggest that skill and motor control requirements increased across the Paleolithic (7, 59). Early hominins likely did not have the same capacity for both delicate and forceful manual manipulation that would have made some of the tool-making actions seen in the later record, like platform preparation, easier to perform and which enabled things like thinned bifaces and Levallois cores (10, 59). The plateau in maximum complexity after 1.8 Mya may be due to a stasis in skill and motor control that improved only after ~600 kya. However, technological stasis can occur for many other reasons besides biology (3). Technology may have reached a plateau in difficulty that required to be escaped the discovery of a hard-to-find solution. The hominin foraging niche before ~600 kya may not have favored innovation and investment in complex technologies (60). In addition, since cumulative culture is a population process, demography, population structure, and environmental change can affect innovation rates (14, 61), the maintenance of complex traits, or the longevity of technologies (62, 63).

**A Late Entry into the Cultural Niche Scenario.** In this scenario, hominins entered the cultural niche late during the Middle Pleistocene when they began producing technologies with complexity levels not observed in contexts with no cumulative culture. While other forms of social learning may have influenced stone tool-making before this, it is only around 600 kya that hominins relied on process copying (35). This timeline is similar to prior work suggesting culture was truly cumulative in the Middle Pleistocene (20, 38, 64, 65).

We also think this is the more likely scenario. First, experiments have shown that early knapping technologies can be learned through individual learning alone (66) or minimal information, such as observing flakes, but not the flintknapping process (63). The experimental studies that have found how easily randomized flaking actions can produce handaxe-like artifacts lend credence to the hypothesis that handaxe technology results from serial reinvention instead of cultural transmission (35). In contrast, the stone tools developed after 600,000 y have a high learning cost, even with the benefit of formal teaching expertise in other flintknapping domains (8, 12).

Second, the rapid and continuous increase in complexity after ~600 kya is consistent with how cumulative culture operates in a way that million-years-long gaps at low levels of complexity are not. Third,

this late-entry scenario is supported by many separate lines of archaeological and fossil evidence. Several lines of behavioral evidence show substantial differences in complexity between the record before and after ~600 kya. Indeed, a similar pattern of relative stasis before 600 kya, followed by rapid diversification, can be detected in the diversity of reduction methods and tool types found in archaeological sites worldwide (Fig. 2, *Top*). A similar trend can also be seen in the efficiency of reduction strategies at producing sharp working edges per unit of mass (Fig. 2, second panel from the top). The efficiency data have a gap in its coverage between ~800 and ~250 ka, but it shows that efficiency remained low and unchanging between 2 ma and 800 ka and that by 250 kya, it has doubled and, at times, tripled. Other hominin behaviors only developed in this recent period (Fig. 2, lower panel) and most markedly during the Middle Stone Age of Africa, after ~300,000 y (67, 68). The middle Pleistocene also bears some of the most substantial evidence for hearths and domestic spaces, likely essential components of the development of cumulative culture (69, 70). Wooden structures, constructed with logs hewn using hafted tools, represent a combinatorial and additive technological behavior, dating to at least 476 kya (64). Finally, patterns in phonemic diversity across space suggest that language also emerged over the last 500,000 y (71).

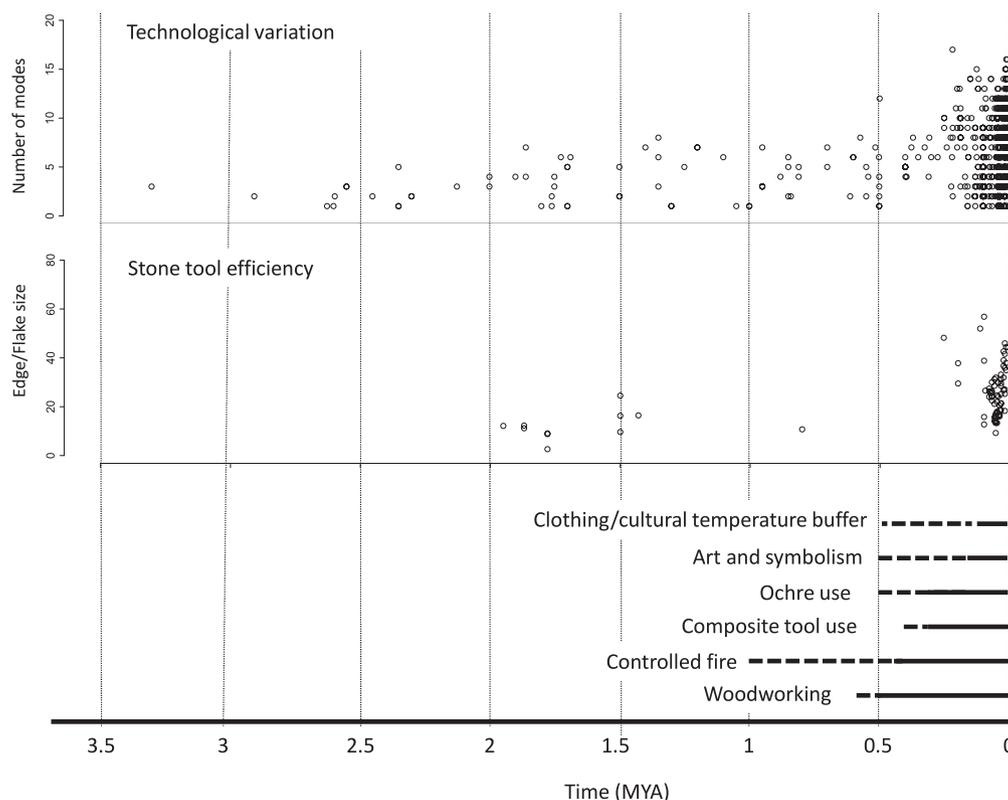
Encephalization also increased rapidly in absolute and relative terms over the last 600,000 y (80). Before this, increases in brain mass are linked to increases in body mass and are marked by a prolonged period of stasis that extends through 1.8 Mya. In line with our result, this trend includes Neanderthal and modern humans (81). Sequences of dental development indicate that the early *Homo* species, including *erectus*, had a pace of life history similar to that of contemporary and fossil African apes. The prolonged life-history schedule of modern humans appears in the later stages of human evolution and possibly, again, with the origin of Neanderthals and modern humans (82), an

inference supported by many other aspects of the fossil record (83–85). The fast tempo of maturity of early *Homo* species suggests that mere larger brains and body sizes were not the primary selective agent for prolonged maturity and extended life stages (82–84). A better candidate selective force may be a reliance on cumulative culture that started ~600 kya.

## Conclusion

Discriminating between an early and a late entrance into the cultural niche will largely hinge on assessing more accurately how the procedural units and the various ways they can be combined are accessible to individual learners who are culturally isolated. Further randomized flaking experiments and knapping experiments with chimpanzees and humans remain promising. These experiments, of course, are not without caveats. They tend to be of short duration (hours, days), whereas, in the past, an individual would have a lifetime to experiment and learn from trial and error, as well as a lifetime to learn from others. Moreover, to what extent chimpanzees and modern humans are good models of early hominin cognition and manual dexterity is unclear. Modern humans may be able to converge through trial and error alone on manufacturing sequences that are more complex than what early hominins could have achieved, even with cultural transmission.

Finally, taphonomic biases, chief among them that technologies based on organic material are mostly invisible archaeologically, necessarily distort our view of technological behavior over evolutionary timescales. We note, in particular, that the most complex nonhuman primate technology in our sample is based on organic data. It is possible that early hominins relied on cumulative culture to develop complex social, foraging, and technological behaviors that are archaeologically invisible.



**Fig. 2.** *Top* panel. The total number of tool and core types present across assemblages is summarized using the technological Modes A-I system (39, 72–75) (N = 1,192). *Middle* panel: The efficiency of stone tool technology is measured as the ratio between edge length and flake size. Data represent the median ratio among N = 81 assemblages (76). *Bottom* panel: Hominin behavioral timeline (20, 64, 77–79).

**Data, Materials, and Software Availability.** All data described and R code for the statistical analysis are available on Zenodo except the chimpanzee termite brush manufacture sequence, which is provided in the main text: <https://doi.org/10.5281/zenodo.11398650> (43). The codebook used to generate the procedural unit data (version 1.1) is also stored on Zenodo: <https://doi.org/10.5281/zenodo.7847876> (44).

**ACKNOWLEDGMENTS.** We thank the members of the Adaptation, Behavior, Culture, and Society Research Group, especially Deanna Dytchowskyj, Tom Morgan, Kevin Langergraber, and Rob Boyd for their feedback over the course of the development of this project. We also thank Matthew Peeples, Michael Barton, Marcus Hamilton, Amy Clark, and three anonymous reviewers who provided very helpful comments on this manuscript. The views expressed in this paper are solely those of the authors.

- R. Boyd, P. J. Richerson, J. Henrich, The cultural niche: Why social learning is essential for human adaptation. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 10918–10925 (2011).
- S. Mathew, C. Perreault, Behavioural variation in 172 small-scale societies indicates that social learning is the main mode of human adaptation. *Proc. R. Soc. B* **282**, 20150061 (2015).
- T. J. H. Morgan, Testing the cognitive and cultural niche theories of human evolution. *Curr. Anthropol.* **57**, 370–377 (2016).
- S. Harmand *et al.*, 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* **521**, 310–315 (2015).
- D. Braun *et al.*, Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 11712–11717 (2019).
- D. Malo, *The Hawaiian Antiquities (Moolelo Hawaii)* (Honolulu Hawaiian Gazette Co., 1903).
- A. Muller, C. Clarkson, C. Shipton, Measuring behavioural and cognitive complexity in lithic technology throughout human evolution. *J. Anthropol. Archaeol.* **48**, 166–180 (2017).
- J. Pargeter, N. Khreisheh, J. J. Shea, D. Stout, Knowledge vs. know-how? Dissecting the foundations of stone knapping skill. *J. Hum. Evol.* **145**, 102807 (2020).
- J. Pargeter, N. Khreisheh, D. Stout, Understanding stone tool-making skill acquisition: Experimental methods and evolutionary implications. *J. Hum. Evol.* **133**, 146–166 (2019).
- D. Stout, J. Apel, J. Commander, M. Roberts, Late Acheulean technology and cognition at Boxgrove, UK. *J. Archaeol. Sci.* **41**, 576–590 (2014).
- M. I. Eren, S. J. Lycett, C. I. Roos, C. G. Sampson, Toolstone constraints on knapping skill: Levallois reduction with two different raw materials. *J. Archaeol. Sci.* **38**, 2731–2739 (2011).
- S. J. Lycett, N. von cramon-taubadel, M. I. Eren, Levallois: Potential implications for learning and cultural transmission capacities. *Lithic Technol.* **41**, 19–38 (2015), 10.1179/2051618515Y.0000000012.
- G. Bassala, "Continuity and discontinuity" in *The Evolution of Technology*, G. Bassala, Ed. (Cambridge: Cambridge University Press, New York, EUA, 1988), pp. 26–63.
- M. Derex, C. Perreault, R. Boyd, Divide and conquer: Intermediate levels of population fragmentation maximize cultural accumulation. *Philos. Trans. R. Soc. B: Biol. Sci.* **373**, 20170062 (2018).
- M. Enquist, S. Ghirlanda, K. Eriksson, Modelling the evolution and diversity of cumulative culture. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 412–423 (2011).
- E. Miu, N. Gulley, K. N. Laland, L. Rendell, Innovation and cumulative culture through tweaks and leaps in online programming contests. *Nat. Commun.* **9**, 2321 (2018).
- R. V. Solé *et al.*, The evolutionary ecology of technological innovations. *Complexity* **18**, 15–27 (2013).
- H. Youn, D. Strumsky, L. M. A. Bettencourt, J. Lobo, Invention as a combinatorial process: Evidence from US patents. *J. R. Soc. Interface.* **12**, 20150272 (2015).
- W. B. Arthur, *The Nature of Technology: What It Is and How It Evolves* (Simon and Schuster, 2009).
- L. Barham, *From Hand to Handle: The First Industrial Revolution* (OUP Oxford, 2013).
- A. Mesoudi, A. Thornton, What is cumulative cultural evolution? *Proc. R. Soc. B* **285**, 20180712 (2018).
- J. A. Harris, R. Boyd, B. M. Wood, The role of causal knowledge in the evolution of traditional technology. *Curr. Biol.* **31**, 1798–1803.e3 (2021).
- W. H. Oswald, *An Anthropological Analysis of Food-Getting Technology* (Wiley, 1976).
- M. N. Haidle, Working-memory capacity and the evolution of modern cognitive potential: Implications from animal and early human tool use. *Curr. Anthropol.* **51**, S149–S166 (2010).
- C. Perreault, J. Brantingham, S. L. Kuhn, S. Wurz, X. Gao, Measuring the complexity of lithic technology. *Curr. Anthropol.* **54**, S397–S406 (2013).
- C. Tennie, Focusing on relevant data and correcting misconceptions reaffirms the ape ZLS. Comment on "Blind alleys and fruitful pathways in the comparative study of cultural cognition" by Andrew Whiten. *Phys. Life Rev.* **44**, 94–98 (2023).
- A. Acerbi, W. D. Snyder, C. Tennie, Ape cultures do not require behavior copying. bioRxiv [Preprint] (2020). <https://doi.org/10.1101/2020.03.25.008177> (Accessed 27 March 2020).
- S. Musgrave, E. Lonsdorf, D. Morgan, C. Sanz, The ontogeny of termite gathering among chimpanzees in the Goulougo Triangle, Republic of Congo. *Am. J. Phys. Anthropol.* **174**, e24125 (2020).
- C. Sanz, J. Call, D. Morgan, Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* **5**, 293–296 (2009).
- S. Wohlgeleuter, G. Diesendruck, L. Markson, What is a conventional object function? The effects of intentionality and consistency of use. *J. Cognit. Dev.* **11**, 269–292 (2010).
- D. E. Lyons, A. G. Young, F. C. Keil, The hidden structure of overimitation. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 19751–19756 (2007).
- P. J. Richerson, R. Boyd, J. Henrich, Gene-culture coevolution in the age of genomics. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 8985–8992 (2010).
- K. Hill, M. Barton, A. M. Hurtado, The emergence of human uniqueness: Characters underlying behavioral modernity. *Evol. Anthropol. Issues, News, and Rev.* **18**, 187–200 (2009).
- M. Muthukrishna, M. Doebeli, M. Chudek, J. Henrich, The cultural brain hypothesis: How culture drives brain expansion, sociality, and life history. *PLoS Comput. Biol.* **14**, e1006504 (2018).
- C. Tennie, D. R. Braun, L. S. Premo, S. P. McPherron, "The island test for cumulative culture in the paleolithic" in *The Nature of Culture: Based on an Interdisciplinary Symposium 'The Nature of Culture', Tübingen, Germany, Vertebrate Paleobiology and Paleoanthropology*, M. N. Haidle, N. J. Conard, M. Bolus, Eds. (Springer, Netherlands, 2016), pp. 121–133.
- O. Bar-Yosef, The upper paleolithic revolution. *Annu. Rev. Anthropol.* **31**, 363–393 (2002).
- D. Stout, M. J. Rogers, A. V. Jaeggi, S. Semaw, Archaeology and the origins of human cumulative culture: A case study from the Earliest Oldowan at Gona, Ethiopia. *Curr. Anthropol.* **60**, 309–340 (2019).
- C. P. van Schaik, G. R. Pradhan, C. Tennie, Teaching and curiosity: Sequential drivers of cumulative cultural evolution in the hominin lineage. *Behav. Ecol. Sociobiol.* **73**, 1–11 (2019).
- J. Paige, *The Evolution of Stone Tool Traditions* (Arizona State University, Tempe, Arizona, 2022).
- J. Paige, A codebook for collecting data on the presence or absence of stone tool making techniques from the literature (v 1.1.0). Zenodo. 10.5281/zenodo.7847876. Deposited 20 April 2023.
- J. Paige, C. Perreault, A dataset describing the manufacturing of stone tools over 3 million years. *J. Open Archaeol. Data* **11**, 12 (2023).
- T. R. Maloney, Towards quantifying teaching and learning in prehistory using stone artifact reduction sequences. *Lithic Technol.* **44**, 36–51 (2019).
- J. Paige, C. Perreault, "Paige Perreault 2024 (PNAS) Analysis. v.1.0". Zenodo. 10.5281/zenodo.11398650. Deposited 31 May 2024.
- J. Paige, "A Codebook for Collecting Data on the Presence or Absence of Stone Tool Making Techniques from the Literature v.1.1". Zenodo. 10.5281/zenodo.7847876. Deposited 20 April 2023.
- S. L. Kuhn, *The Evolution of Paleolithic Technologies* (Routledge, 2020).
- T. Rankama, J. Kankaanpää, First evidence of eastern Preboreal pioneers in arctic Finland and Norway. *Quartär* **58**, 32 (2011).
- A. W. Kandel *et al.*, The ROCEEH Out of Africa Database (ROAD): A large-scale research database serves as an indispensable tool for human evolutionary studies. *PLOS One* **18**, e0289513 (2023).
- S. P. McPherron *et al.*, Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* **466**, 857–860 (2010).
- R. J. Thompson, S. Carvalho, C. W. Marean, Z. Alemseged, Origins of the human predatory pattern: The transition to large-animal exploitation by early hominins. *Curr. Anthropol.* **60**, 1–23 (2019).
- R. J. Blumenshine, M. M. Selvaggio, Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* **333**, 763–765 (1988).
- M. Dominguez-rodrigo, R. Pickering, S. Semaw, M. Rogers, Cutmarked bones from Pliocene Archaeological sites at Gona, Afar, Ethiopia: Implications for the function of the world's oldest stone tools. *J. Hum. Evol.* **48**, 109–121 (2005).
- S. Semaw *et al.*, 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *J. Hum. Evol.* **45**, 169–177 (2003).
- F. Diez-Martin *et al.*, The origin of the acheulean: The 1.7 million-year-old site of FLK West, Olduvai Gorge (Tanzania). *Sci. Rep.* **5**, 17839 (2015).
- J. V. Ferraro *et al.*, Earliest archaeological evidence of persistent hominin carnivory. *PLoS One* **8**, e62174 (2013).
- D. Braun *et al.*, Early Hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 10002–10007 (2010).
- J. Henrich, *The Secret of Our Success: How Culture is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter* (Princeton University Press, 2017).
- P. J. Richerson, R. Boyd, *Not By Genes Alone: How Culture Transformed Human Evolution* (University of Chicago Press, 2008).
- T. Morgan *et al.*, Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nat. Commun.* **6**, 6029 (2015).
- A. J. M. Key, C. J. Dunmore, Manual restrictions on palaeolithic technological behaviours. *PeerJ* **6**, e5399 (2018).
- D. E. Lieberman, "Being a carnivorous hominin in the Lower Paleolithic: A biological perspective on convergence and stasis" in *Convergent Evolution in Stone-Tool Technology*, M. J. O'Brien, B. Buchanan, M. I. Eren, Eds. (The MIT Press, 2018), pp. 91–106.
- M. Derex, R. Boyd, Partial connectivity increases cultural accumulation within groups. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 2982–2987 (2016).
- O. Kolodny, N. Creanza, M. W. Feldman, Evolution in leaps: The punctuated accumulation and loss of cultural innovations. *Proc. Natl. Acad. Sci. U.S.A.* **112**, E6762–E6769 (2015).
- A. Powell, S. J. Shennan, M. G. Thomas, Late Pleistocene demography and the appearance of modern human behavior. *Science* **324**, 1298–1301 (2009).
- L. Barham *et al.*, Evidence for the earliest structural use of wood at least 476,000 years ago. *Nature* **622**, 107–111 (2023).
- R. J. Planer, E. Bandini, C. Tennie, Hominin tool evolution and its (surprising) relation to language origins. OSF. <https://osf.io/rztx7>. Accessed 18 January 2024.
- W. D. Snyder, J. S. Reeves, C. Tennie, Early knapping techniques do not necessitate cultural transmission. *Sci. Adv.* **8**, eabo2894 (2022).
- C. W. Marean *et al.*, Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* **449**, 905–908 (2007).
- S. McBrearty, A. S. Brooks, The revolution that wasn't: A new interpretation of the origin of modern human behavior. *J. Hum. Evol.* **39**, 453–563 (2000).
- A. E. Clark, S. Ranlett, M. C. Stiner, Domestic spaces as crucibles of Paleolithic culture: An archaeological perspective. *J. Hum. Evol.* **172**, 103266 (2022).
- S. L. Kuhn, M. C. Stiner, Hearth and home in the Middle Pleistocene. *J. Anthropol. Res.* **75**, 305–327 (2019).
- C. Perreault, S. Mathew, Dating the origin of language using phonemic diversity. *PLoS One* **7**, e35289 (2012).
- J. J. Shea, Lithic modes A-I: A new framework for describing global-scale variation in stone tool technology illustrated with evidence from the East Mediterranean Levant. *J. Archaeol. Method Theory* **20**, 151–186 (2013).
- J. J. Shea, *Prehistoric Stone Tools of Eastern Africa: A Guide* (Cambridge University Press, 2020).
- Y. Nishiaki *et al.*, Spatiotemporal variability in lithic technology of Middle-to-Upper Paleolithic Asia: A new dataset and its statistical analyses. *Q. Int.* **596**, 144–154 (2021), 10.1016/j.quaint.2021.03.022.
- J. J. Shea, *Stone Tools in Human Evolution: Behavioral Differences among Technological Primates* (Cambridge University Press, 2016).

76. Ž Režek, H. L. Dibble, S. P. McPherron, D. R. Braun, S. C. Lin, Two million years of flaking stone and the evolutionary efficiency of stone tool technology. *Nat. Ecol. Evol.* **2**, 628–633 (2018).
77. E. Y. Hallett *et al.*, A worked bone assemblage from 120,000–90,000 year old deposits at Contrebandiers Cave, Atlantic Coast, Morocco. *iScience* **24**, 102988 (2021).
78. J. Galway-Witham, J. Cole, C. Stringer, Aspects of human physical and behavioural evolution during the last 1 million years. *J. Q. Sci.* **34**, 355–378 (2019).
79. J. Wilkins, B. J. Schoville, K. S. Brown, M. Chazan, Evidence for early hafted hunting technology. *Science* **338**, 942–946 (2012).
80. C. B. Ruff, E. Trinkaus, T. W. Holliday, Body mass and encephalization in Pleistocene Homo. *Nature* **387**, 173–176 (1997).
81. J.-J. Hublin, S. Neubauer, P. Gunz, Brain ontogeny and life history in Pleistocene hominins. *Phil. Trans. R. Soc. B* **370**, 20140062 (2015).
82. C. Dean *et al.*, Growth processes in teeth distinguish modern humans from Homo erectus and earlier hominins. *Nature* **414**, 628–631 (2001).
83. D. R. Bolter, A. L. Zihlman, "Chapter 15 - Evolution of human growth" in *Human Growth and Development*, N. Cameron, L. M. Schell, Eds. (Academic Press, ed. 3, 2022), pp. 425–448.
84. R. Hogg *et al.*, A comprehensive survey of Retzius periodicities in fossil hominins and great apes. *J. Hum. Evol.* **149**, 102896 (2020).
85. T. A. Monson, A. P. Weitz, M. F. Brasil, L. J. Hlusko, Teeth, prenatal growth rates, and the evolution of human-like pregnancy in later Homo. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2200689119 (2022).