



No sustained increase in zooarchaeological evidence for carnivory after the appearance of *Homo erectus*

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Edited by Metin I. Eren, Anthropology, Kent State University, Kent, OH; received August 23, 2021; accepted December 15, 2021 by Editorial Board Member C. O. Lovejoy

The appearance of *Homo erectus* shortly after 2.0 Ma is widely considered a turning point in human dietary evolution, with increased consumption of animal tissues driving the evolution of larger brain and body size and a reorganization of the gut. An increase in the size and number of zooarchaeological assemblages after the appearance of *H. erectus* is often offered as a central piece of archaeological evidence for increased carnivory in this species, but this characterization has yet to be subject to detailed scrutiny. Any widespread dietary shift leading to the acquisition of key traits in *H. erectus* should be persistent in the zooarchaeological record through time and can only be convincingly demonstrated by a broad-scale analysis that transcends individual sites or localities. Here, we present a quantitative synthesis of the zooarchaeological record of eastern Africa from 2.6 to 1.2 Ma. We show that several proxies for the prevalence of hominin carnivory are all strongly related to how well the fossil record has been sampled, which constrains the zooarchaeological visibility of hominin carnivory. When correcting for sampling effort, there is no sustained increase in the amount of evidence for hominin carnivory between 2.6 and 1.2 Ma. Our observations undercut evolutionary narratives linking anatomical and behavioral traits to increased meat consumption in *H. erectus*, suggesting that other factors are likely responsible for the appearance of its human-like traits.

zooarchaeology | *Homo erectus* | human diet | carnivory | sampling

Although chimpanzees are known to hunt and consume other animals (1, 2), modern humans are distinct among anthropoid primates to the extent to which animal tissues comprise a major component of our diets (3). Increased carnivory has long been hypothesized by paleoanthropologists to be a major catalyst of human evolution. Originally invoked as an explanation for early hominin divergence from our closest hominoid relatives (4, 5), increased carnivory later came to be associated with *Homo erectus/ergaster* (hereafter *H. erectus*) (6–11), which first appears in eastern Africa at 1.9 Ma at East Turkana (12). Compared with earlier hominin species, *H. erectus* exhibits an adaptive package that has been linked to increased carnivory: larger brains, reduction in gut size, larger body size, and modern human-like limb proportions (10, 13–18). This suite of evolutionary changes is encapsulated by the “meat made us human” hypothesis (6), which causally links the adaptations of *H. erectus* with a greater reliance on carnivory than its predecessors. While widespread, this view has been criticized on the grounds that stone-tool-assisted animal tissue consumption significantly predates the anatomical and behavioral adaptations that it is purported to explain (19). Alternative hypotheses invoking provisioning of plant foods by grandmothers (20, 21) and the development of controlled fire for increasing nutrient availability through cooking (22) have been advanced to explain the evolution of modern human characteristics, including increased encephalization.

The zooarchaeological record is commonly interpreted as supporting the “meat made us human” hypothesis (6, 17, 23). Direct

evidence for hominin modification of bones prior to 2 Ma is sparse and sometimes controversial (24–29). At approximately 2 Ma, evidence from the FwJj 20 site suggests that some hominins had diversified their diet by incorporating aquatic resources (30), and contemporaneous evidence from Kanjera points to the repeated use of a single location for processing carcasses (31). Between 1.8 and 1.4 Ma, the large numbers of modified bones from sites at East Turkana (32–35) and Olduvai Gorge (23, 36–41) clearly demonstrate that hominins were consuming animal resources. Evidence from a few sites that are particularly old (FwJj 20 and Kanjera) or particularly well preserved (the FLK 22 Zinj site) have loomed large in debates over the evolution of hominin carnivory (42), but there has been no quantitative synthesis of the zooarchaeological record designed to evaluate the prevalence of hominin carnivory at the regional scale. Analyzing this question at the regional scale is important because any behavioral change that supports key anatomical changes defining a species (e.g., increased brain and body size in *H. erectus* supported by elevated carnivory) is expected to be found widely across the constituent populations of that species. Moreover, we expect increased evidence for this shift to be temporally sustained because the morphological traits that carnivory is argued to support (e.g., increased brain size) persist across the nearly 2 million

Significance

Many quintessential human traits (e.g., larger brains) first appear in *Homo erectus*. The evolution of these traits is commonly linked to a major dietary shift involving increased consumption of animal tissues. Early archaeological sites preserving evidence of carnivory predate the appearance of *H. erectus*, but larger, well-preserved sites only appear after the arrival of *H. erectus*. This qualitative pattern is a key tenet of the “meat made us human” viewpoint, but data from sites across eastern Africa have not been quantitatively synthesized to test this hypothesis. Our analysis shows no sustained increase in the relative amount of evidence for carnivory after the appearance of *H. erectus*, calling into question the primacy of carnivory in shaping its evolutionary history.

Author contributions: W.A.B., J.R., A.D., and J.T.F. designed research; W.A.B., B.P., J.R., A.D., and J.T.F. performed research; W.A.B., B.P., and J.R. contributed new reagents/analytic tools; W.A.B. analyzed data; and W.A.B., B.P., J.R., A.D., and J.T.F. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. M.I.E. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at <http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2115540119/-DCSupplemental>.

Published January 24, 2022.

years of *H. erectus* existence (43). This kind of durable shift in behavior cannot be demonstrated with evidence from any single stratigraphically limited archaeological site, but can be seen only by compiling the record of sites across the region (44).

However, we recognize that the raw quantity of zooarchaeological evidence of hominin carnivory may be misleading because sampling effort is not uniform through time. Holding constant the true behavioral frequency of hominin carnivory, we would expect well-sampled intervals to preserve more zooarchaeological evidence of carnivory than poorly sampled intervals. Any behaviorally meaningful accounting of the regional prevalence of carnivory must account for this variation in how intensively the record has been sampled.

With this in mind, we tested a key prediction of the “meat made us human” hypothesis by characterizing the temporal patterns in the quantity of evidence for hominin carnivory between 2.6 and 1.2 Ma across eastern Africa, while controlling for variation in sampling effort through time. Because bones can enter the zooarchaeological record through both anthropogenic and nonanthropogenic means, our measures of hominin carnivory focus solely on the portion of the record that bears direct evidence of hominin modification (i.e., the count of modified bones, and counts of sites and levels bearing modified bones). Our measures of carnivory are designed to quantify the size of the zooarchaeological record only and do not address questions of carcass-processing efficiency.

Results

Our compilation of data from nine major research areas in eastern Africa (Fig. 1A) includes 59 site levels dating between 2.6 and 1.2 Ma (Fig. 1B). The temporal distribution of site levels clearly illustrates the abundance of levels postdating 1.9 Ma from East Turkana and Olduvai Gorge, which gives rise to the widespread impression that the amount of evidence for carnivory increases with the appearance of *H. erectus* (the approximate temporal ranges for several hominin species are illustrated in Fig. 1C). The raw time series of paleontological sampling intensity and zooarchaeological evidence for hominin carnivory are shown in Fig. 2, using bins with a duration of 100 kyr (additional

time bin durations are examined in *SI Appendix* with comparable results).

The earliest interval from 3.4 to 2.6 Ma (blue diamonds in Fig. 2) has very robust paleontological sampling, but is excluded from our analyses because there is no zooarchaeological record from this period, with the sole exception of the disputed specimens from Dikika at 3.39 Ma (25, 29). The next interval from 2.6 to 1.9 Ma (yellow circles in Fig. 2) has notably poor paleontological sampling, together with low-frequency evidence for hominin carnivory in six of the seven 100-kyr time bins. Finally, the period from 1.9 to 1.2 Ma (red triangles in Fig. 2) shows robust paleontological sampling coupled with a high frequency of evidence for hominin carnivory. Though not the primary focus of our analysis, we observe that the count of modified bones in each time bin is strongly correlated with the total count of lithic artifacts in the associated assemblages (*SI Appendix*, Fig. S4).

Over the 2.6- to 1.2-Ma interval, time bins with more thorough paleontological sampling have more abundant zooarchaeological evidence of carnivory, and therefore paleontological evidence of carnivory, and therefore paleontological evidence of species richness (our proxy for sampling effort, justified in the *Materials and Methods* and *SI Appendix*) is a positive predictor of all three carnivory proxies (count of levels $R^2 = 0.44$, count of sites $R^2 = 0.36$, total modified bones $R^2 = 0.40$) (*SI Appendix*, Fig. S1 and Table S1). Because recovery of zooarchaeological evidence is contingent on the preservation and sampling of fossil animal remains, we interpret this correlation as indicating that temporal patterns in the observed zooarchaeological record have been structured by sampling effort. Residuals from regressions of the three carnivory proxy variables against richness serve as our metrics for residual evidence of carnivory (REC) relative to paleontological sampling.

There is no sustained increase in REC after the appearance of *H. erectus* at 1.9 Ma (Fig. 3). While several time bins—including the bin centered on 1.85 Ma associated with the appearance of *H. erectus*—have large positive REC values, there is no point between 2.6 and 1.2 Ma at which REC values show a sustained increase. This pattern holds when alternate bin durations are considered (*SI Appendix*, Fig. S2).

Separate from the prediction that the regional-scale quantity of evidence for carnivory increased with the appearance of

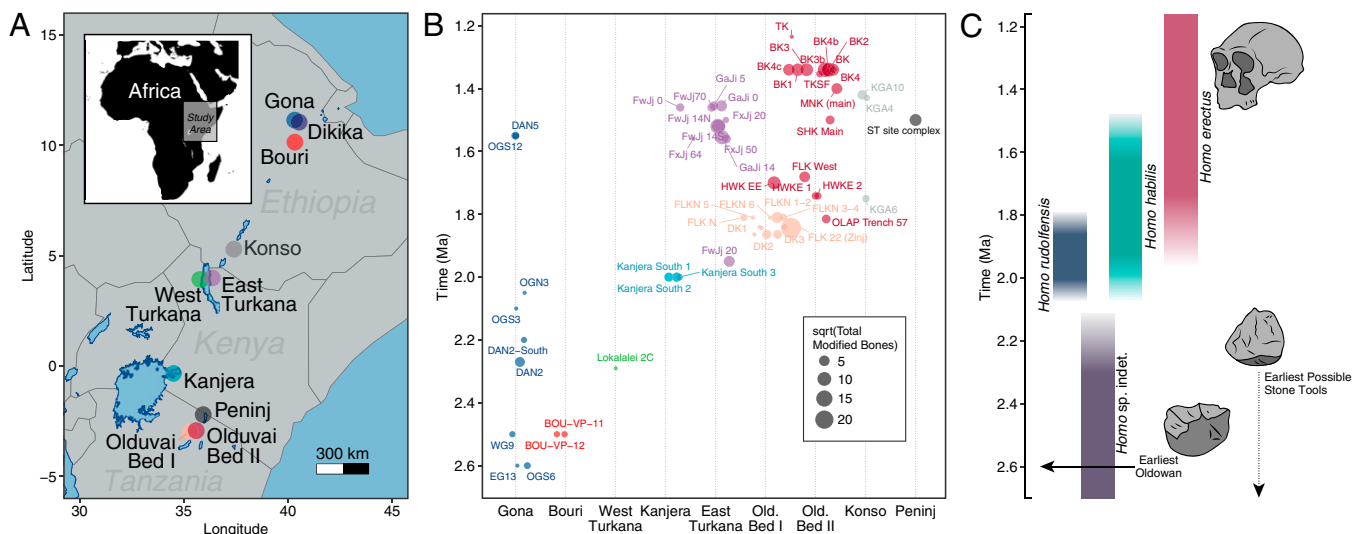


Fig. 1. Spatiotemporal distribution of zooarchaeological evidence synthesized in this study. (A) Regional map showing spatial distribution of major research areas. (B) Temporal distribution of zooarchaeological levels plotted according to their date on the vertical axis. Labels are color coded by major study area. The size of each circle is drawn proportional to the square root of the number of modified bones reported from the corresponding zooarchaeological assemblage. The position of each level on the horizontal axis is randomly jittered to improve legibility. (C) Schematic illustration of the temporal ranges of selected hominin species in eastern Africa over the temporal duration of this study.

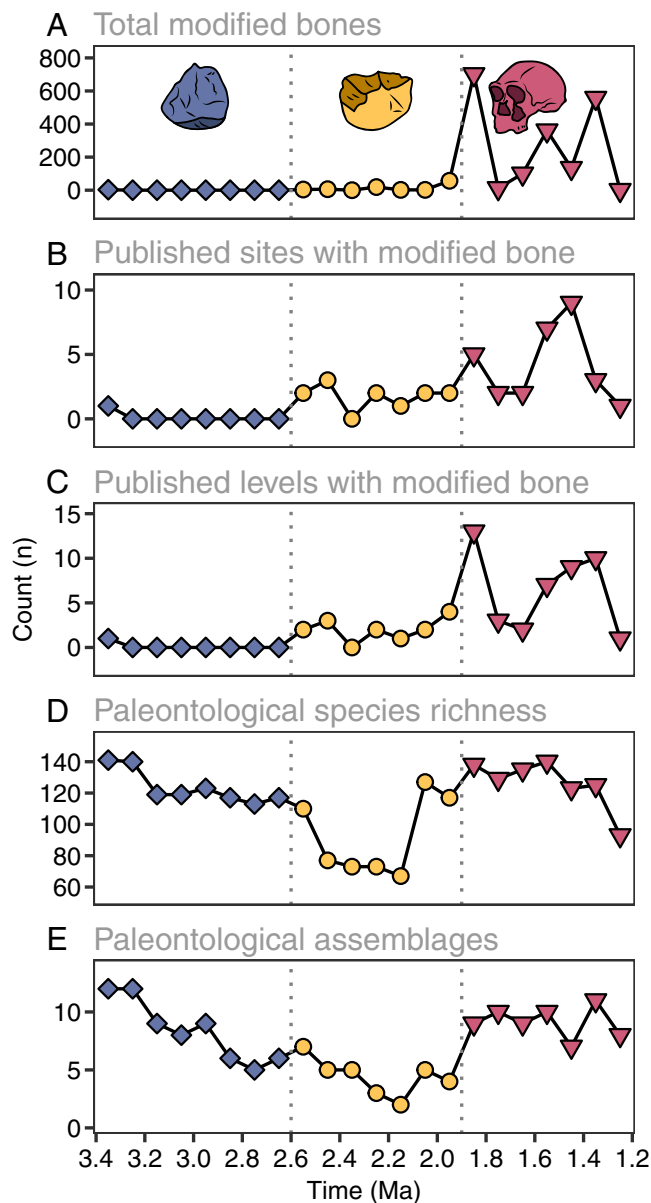


Fig. 2. Time series of amount of evidence for hominin carnivory and paleontological sampling effort. (A) Time series of count of total modified bones. (B) Time series of count of zooarchaeological sites. (C) Time series of count of separately published stratigraphic levels. (D) Time series of paleontological species richness. (E) Time series of count of paleontological assemblages. Plotting symbols and colors are for heuristic illustration of the pre-Oldowan period (blue diamonds), the Oldowan period prior to the appearance of *H. erectus* (yellow circles), and the period after the appearance of *H. erectus* (red triangles). Time bin duration is 100 kyr. Sites with dates falling on the boundary between bins are assigned to the younger bin. Vertical lines are at 2.6 and 1.9 Ma.

H. erectus, the larger size of zooarchaeological assemblages postdating 1.9 Ma has been argued to be behaviorally significant (45). In this context, size refers to the quantity of carnivory evidence preserved relative to the number of sites or levels, not to the area or volume of the excavation. While it is obvious that some of the well-known zooarchaeological assemblages postdating 1.9 are very large (e.g., FLK 22 Zinj), we evaluate patterns in site size through time to determine whether there is a persistent change toward larger sites after 1.9 Ma, which would be consistent with a widespread behavioral shift at this time. Our proxies for site size in each bin include: residuals from the

regression of the number of levels against the number of sites; residuals from the regression of the total number of modified bones against the number of site levels; and residuals from the regression of the total number of modified bones against the number of sites (SI Appendix, Fig. S3).

The 1.85- and 1.35-Ma time bins have large positive residuals for the number of modified bones against the number of sites (Fig. 4A), as well as the count of published levels against the number of sites (Fig. 4B). Residuals of the total number of modified bones against the number of levels (Fig. 4C) for these time bins are also positive, but are not strong outliers as they are for the other site size proxies. This suggests that the exceptional number of modified bones observed during the 1.85- and 1.35-Ma bins is driven by a proliferation of sites with multiple stratigraphic levels. There is no sustained increase in any measure of site size (Fig. 4A–C) after the appearance of *H. erectus* at 1.9 Ma.

Discussion

Our synthesis of the eastern African zooarchaeological record makes clear that sampling effort constrains the zooarchaeological visibility of hominin carnivory. While the raw abundance of modified bones and the number of zooarchaeological sites and

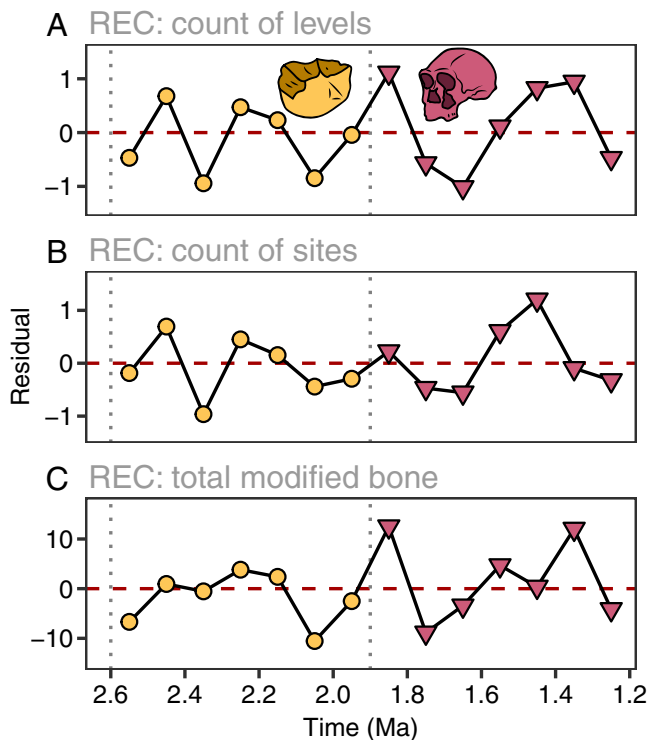


Fig. 3. REC plotted through time. REC reflects the residuals from the ordinary least squares regression of each carnivory proxy against the number of paleontological species (richness) in a bin. Points that fall near the red dashed line at zero have the expected amount of carnivory evidence within a time bin as predicted by paleontological sampling effort. Points falling above or below the red line show more or less (respectively) evidence for carnivory than expected based on paleontological sampling effort. There is no sustained increase in REC in bins postdating 1.9 Ma. Both dependent and independent variables were square root transformed prior to the regressions from which these residuals were derived. (A) Residuals from regression of count of levels against species richness. (B) Residuals from regression of count of zooarchaeological sites against species richness. (C) Residuals from regression of count of levels against species richness. Color and shape of points are as in Fig. 2. Vertical dotted lines are at 2.6 and 1.9 Ma.

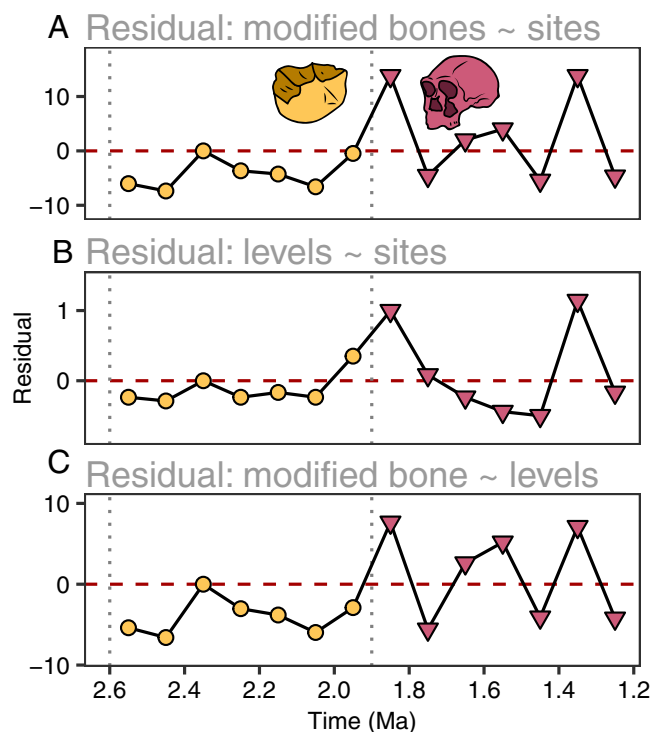


Fig. 4. Site size through time. (A) Time series of residuals from a regression of total modified bones against the count of sites in a time bin. (B) Time series of residuals from a regression of number of published levels against the number of sites in a time bin. (C) Time series of residuals from total number of modified bones regressed against the number of published levels in a time bin. Dashed red line shows the expected value of zero. Color and shape of points are as in Fig. 2. Vertical lines are at 2.6 and 1.9 Ma. All variables were square root transformed prior to regression.

levels all demonstrably increase after 1.9 Ma, these increases are mirrored by a corresponding rise in paleontological sampling intensity, as inferred from species richness (Fig. 2). Indeed, a substantial portion of the increased quantity of evidence for carnivory after 2.6 Ma can parsimoniously be attributed to the improved sampling of the record over the same interval (R^2 ranging from 0.36 to 0.44) (SI Appendix, Table S1). The sampling-controlled record of hominin carnivory after 1.9 Ma is best characterized as showing bursts of high abundance of evidence, punctuated by periods of low abundance of evidence (Fig. 3). Bins postdating 1.9 Ma do not consistently have more levels or more modified bones than predicted based on the number of sites, although the 1.85- and 1.35-Ma bins are very large positive outliers (Fig. 4 A–C). These outliers illustrate what we refer to as the “Olduvai effect,” where an intensive, sustained research effort has resulted in the discovery and publication of far more site levels (Fig. 1B) than expected based on the amount of paleontological sampling. However, the other time bins in the 1.85- to 1.35-Ma interval are less well sampled at Olduvai (Fig. 1B), despite being reasonably well sampled paleontologically at the regional scale (Fig. 2 D and E). These bins, which are less impacted by the Olduvai effect, have more moderate levels of evidence of carnivory (Fig. 3 A–C). We therefore interpret the abundance of evidence of carnivory in the 1.85- and 1.35-Ma time bins as most parsimoniously reflecting the intensive sampling effort in Olduvai Bed I and Bed II rather than necessarily reflecting a persistent and widespread change in hominin behavior.

Our study demonstrates that the temporal pattern in the amount of evidence of hominin carnivory from 2.6 to 1.2 Ma is essentially flat (Fig. 3), with no sustained increase through time.

Though archaeologists have interpreted the lack of large zooarchaeological assemblages prior to 1.9 Ma in behavioral terms (45), our results imply that this observation is parsimoniously interpreted as driven by sampling—the interval prior to 1.9 Ma is very poorly sampled paleontologically (Fig. 2 D and E), which we suspect strongly limits zooarchaeological visibility of carnivory. Our analysis controlling for sampling effort does not find support for the “meat made us human” hypothesis linking behavioral and anatomical innovations in *H. erectus* with an increased dietary reliance on animal tissues. Our results run counter to claims that *H. erectus* showed elevated levels of carnivory, at least early in this species’ evolutionary history (i.e., 1.9 to 1.2 Ma). Based on present published evidence, we therefore conclude that the earliest shift toward increasing carnivory in the hominin lineage cannot be tied to the appearance of *H. erectus*.

Decoupling increased carnivory from the appearance of *H. erectus* has important implications for the role of animal tissue consumption in human evolution. The fact that the quantity of evidence for hominin carnivory shows no persistent increase after the appearance of *H. erectus* suggests that alternative adaptive explanations for modern anatomical and behavioral traits are required. The novel characteristics of *H. erectus* may instead be related to other factors besides carnivory. Some researchers have suggested that the provisioning of plant foods by grandmothers (20, 21) or the development of novel methods of food preparation using fire (22) may have contributed to the evolution of the modern human-like features of *H. erectus*. However, we caution that direct archaeological evidence for all these scenarios is tenuous, and significant uncertainties remain.

The earliest evidence of Oldowan hominin carnivory from 2.6 to 2.2 Ma comes from sites at Gona (46), Bouri (24) (but see ref. 27), and Lokalalei (47, 48). While the raw number of modified bones and zooarchaeological levels is low across this interval (Fig. 2), the residual number of sites preserving evidence of hominin carnivory is approximately what is expected based on the notably poor paleontological sampling characterizing this period (Fig. 3). Previous work has pointed to the potentially confounding effects of low sampling intensity on understanding the early Oldowan (49). Our analysis suggests that the limited published evidence of carnivory during the earliest Oldowan could be due to poor sampling rather than reflecting a low behavioral incidence of hominin carnivory. In fact, when sampling is considered, the early Oldowan evidence for carnivory is more compelling than it appears at face value. Ongoing paleoanthropological research at recently discovered sites in the 2.6- to 2.2-Ma interval (50, 51) will continue to augment sample sizes and improve our understanding of the prevalence of hominin carnivory during this key early interval.

Materials and Methods

B.P. (with contributions from W.A.B.) compiled published data from zooarchaeological assemblages ($n = 59$, Dataset S1) from Ethiopia, Kenya, and Tanzania over the period 3.4 Ma to 1.2 Ma. All published and securely dated zooarchaeological sites in this interval were considered (Dataset S1), including Bouri (24), Dikika (25), Konso (52), Gona (46, 53, 54), East Turkana (30, 32, 34, 55–57), Hadar (58), West Turkana (47, 48), Kanjera (31), Naiyena Engol (59), Olduvai (36, 38, 41, 60–73), and Peninj (74). Each site was assigned to a 100-kyr temporal bin (additional details on site inclusion and binning are in SI Appendix).

Numerous aspects of zooarchaeological assemblages may be quantified. However, our study is focused on capturing the amount of evidence for carnivory in a time bin using simple metrics that can be gleaned from all the included zooarchaeological studies. For each bin, we computed several proxies for hominin carnivory: the number of zooarchaeological sites preserving modified bones; the total count of modified bones across sites; and the number of separately reported stratigraphic levels (multiple levels from a single site may be published separately, especially when they are interpreted to reflect discrete occupations).

We account for variation in sampling effort through time by tallying the number of paleontological assemblages and the species richness (number of species) of large (>18 kg) mammals in each time bin. It is well documented that sampling effort is a major determinant of observed species richness in fossil samples, with greater sampling effort (e.g., more specimens, more localities) leading to the recovery of more species (75–78). It follows that time bins with elevated species richness have greater sampling effort, yielding more fossils and/or more fossil-bearing localities. We regressed each of our proxies for carnivory against richness (all variables were square root transformed), and the residuals from these regressions comprise our proxies for REC. Separate regressions using the number of paleontological sites as a predictor also showed positive relationships with carnivory proxies, but had lower R^2 values (SI Appendix, Table S1, further discussion in SI Appendix). Because the count of sites is well correlated with species richness ($R^2 = 0.58$) there is redundancy in these two proxies for sampling effort, and for clarity we present results only for species richness.

To evaluate patterns of site size through time we regressed the number of published levels against the number of sites ($R^2 = 0.94$), and we also regressed

the total number of modified bones against the number of site levels ($R^2 = 0.82$) and the number of sites ($R^2 = 0.67$). These regressions were constrained to pass through the origin (SI Appendix, Fig. S3, see further explanation in SI Appendix). Note that all variables were square root transformed). We interpret the residuals from these regressions as measures of site size, with positive residuals indicating time bins that have a greater quantity of modified bones or site levels than predicted based on the number of sites or levels. These residual estimates of site size are plotted as time series in Fig. 4.

Data Availability. All study data are included in the article and/or SI Appendix.

ACKNOWLEDGMENTS. We thank the reviewers and editor for constructive comments on previous versions of this paper. B.P. acknowledges the work of Kara Peters and Jessica Thompson in collecting some of the data from the zooarchaeological literature for other projects. W.A.B. acknowledges the members of the PAPER group at The George Washington University for several fruitful conversations about this paper.

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