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Distance-decay effect in stone tool transport by wild chimpanzees

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Stone tool transport leaves long-lasting behavioural evidence in the landscape. However, it remains unknown how large-scale patterns of stone distribution emerge through undirected, short-term transport behaviours. One of the longest studied groups of stone-tool-using primates are the chimpanzees of the Taï National Park in Ivory Coast, West Africa. Using hammerstones left behind at chimpanzee *Panda* nut-cracking sites, we tested for a distance-decay effect, in which the weight of material decreases with increasing distance from raw material sources. We found that this effect exists over a range of more than 2 km, despite the fact that observed, short-term tool transport does not appear to involve deliberate movements away from raw material sources. Tools from the millennia-old Noulo site in the Taï forest fit the same pattern. The fact that chimpanzees show both complex short-term behavioural planning, and yet produce a landscape-wide pattern over the long term, raises the question of whether similar processes operate within other stone-tool-using primates, including hominins. Where hominin landscapes have discrete material sources, a distance-decay effect, and increasing use of stone materials away from sources, the Taï chimpanzees provide a relevant analogy for understanding the formation of those landscapes.

1. Background

Primates regularly move materials from one place to another, mainly for display [1], foraging [2], and tool use [3,4]. Because the majority of materials involved are organic, these behaviours are often invisible in the absence of direct observation. Stone tools, as durable markers of past activity, offer an opportunity to record the long-term effects of primate behaviour on the landscape. Among the stone-tool-using primates—West African chimpanzees (*Pan troglodytes verus*) [5], Burmese long-tailed macaques (*Macaca fascicularis aurea*) [6], and bearded capuchin monkeys (*Sapajus libidinosus*) [7]—stone tool transport is receiving increasing attention for its role in niche construction [8], site formation [9], and energetic costs [10].

Movement of stone materials has also been instrumental in reconstructing the ranging patterns of early members of the human lineage, the hominins [11,12]. Stone transport especially helps with identifying early hominin tool use, when materials are carried from their original context to a site [13]. A number of studies have shown that Early Pleistocene hominins were selectively transporting stone materials that were suitable for the tasks at hand [11,14–19]. Along with the requirement to bring together suitable stone materials and target prey in one place [20], tool transport has been suggested to attest to planning or other cognitive abilities in early hominins [21].

However, time averaging of the archaeological record—in which multiple activities occurring in the same place at different times are indistinguishable—obscures our ability to identify the individual behavioural sequences included [22]. One technique used to overcome this limitation and elucidate the stepwise behavioural patterns behind the archaeological record has been to use agent-based modelling. These models examine how a composite record can result from a series of unplanned individual movements [23,24]. Their findings suggest that such tool transport patterns lead to the emergence of a distance-decay effect as a default when the driving factors behind movements are undirected.

The distance-decay [25] effect is defined as a negative correlation between the weight of stone materials at a site, and the site's distance from the raw material source, and it has been identified from various Early Stone Age hominin archaeological sites [25–28]. This effect has been postulated to occur for two main reasons: (i) heavier stones are energetically more expensive to carry longer distances and (ii) stones further from sources have typically been used for longer and are more completely broken down (either deliberately flaked or accidentally fractured) as a result [25].

Despite the insights that time-averaged archaeological sites and computational models can provide, they both lack essential information. For the models, the missing information relates to real-world behavioural complexity, and for the hominin sites, it is an understanding of the individual behavioural steps that have been compressed to form the archaeological record. In this situation, primate archaeology [29–32] gives us a unique opportunity to record those aspects of the data that are missing from other approaches. Here, we present the results of the first study of wild chimpanzee long-distance stone tool transport, and its relation to stone source distributions, on a landscape scale to assess whether or not non-human primates show a distance-decay effect.

At the Taï National Park, Ivory Coast, chimpanzees use stone hammers and mainly wooden anvils to crack open different nut species. Most commonly processed are *Coula edulis* nuts; these nuts are rather easy to crack and allow chimpanzees to choose between stone and wooden tools. Another commonly cracked nut species is *Panda oleosa*. In contrast with *Coula* this nut is very hard, requiring greater force, and can only be cracked with large stone tools that typically weigh several kilograms [5]. As large stones are rare in this tropical rainforest, chimpanzees often leave a suitable hammerstone that they have brought to a tree which is currently producing nuts. They frequently re-use this tool for as long as the tree bears fruit. Over time this leads to the development of intense use-damage to the hammerstone, in the form of central pits and stone fracture [33].

To test for the distance-decay effect in wild chimpanzee stone transport at Taï, we concentrated on granite tools. The Taï National Park is located on a Precambrian granite peneplain, with several isolated granite inselbergs formed from plutonic intrusions, which made this material the most amenable to studying chimpanzee stone redistribution. Granite is also a preferred material for chimpanzees when cracking *Panda* nuts. We, therefore, compared stone availability at the inselbergs with that of other environments in the home range of the Taï chimpanzees, predicting that the availability of large granite stones suitable for cracking the hard *Panda* nuts would be highest at the inselbergs.

We then mapped the location, recorded size and raw material of hammerstones used at *Panda* nut-cracking sites throughout the chimpanzee home range. We additionally recorded the use-wear on each hammerstone, as a means of assessing the intensity of previous use. Taking use-damage as a proxy for the length of time that a stone had been used allowed us to determine whether (i) small hammerstones were being transported further before use, or (ii) stones became smaller over time through intense re-use, and travelled further due to a longer latency from the first movement away from the original source.

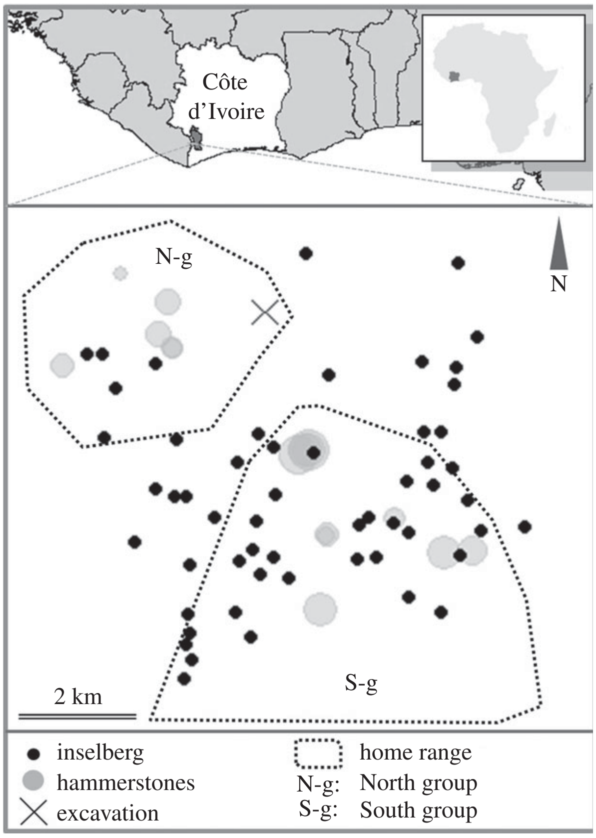

Figure 1. Position of inselbergs (black) and located hammerstones (grey) in the Taï National Park. The size of the grey circles (hammerstones) corresponds to the weight of the hammerstone material at a site. The two polygons represent the home range of the North and the South group. The cross symbol represents the location of the excavated Noulo chimpanzee site.

Our data are more closely aligned with previous archaeological work than fine-scale ethological observations, in that we collected information on the palimpsest of stone distribution that has been built up by the chimpanzees over time. However, we are additionally able to integrate direct observations of chimpanzees into our analysis to shed light onto the development of stone tool distribution patterns throughout the landscape.

2. Material and methods

The study was conducted in the home range of two chimpanzee communities in the Taï National Park. The two study groups ranging in this area were fully habituated to human observers, and focal follows have been determining their home range since 1985 (North group) and 2005 (South group).

(a) Field data collection

During February and March 2015, we located 25 active *Panda* nut-cracking sites (seven in the North group and 18 in the South group territory) by revisiting sites used by the chimpanzees in the prior 18 months (figure 1). For each hammerstone, we recorded its GPS position and weight. We consistently

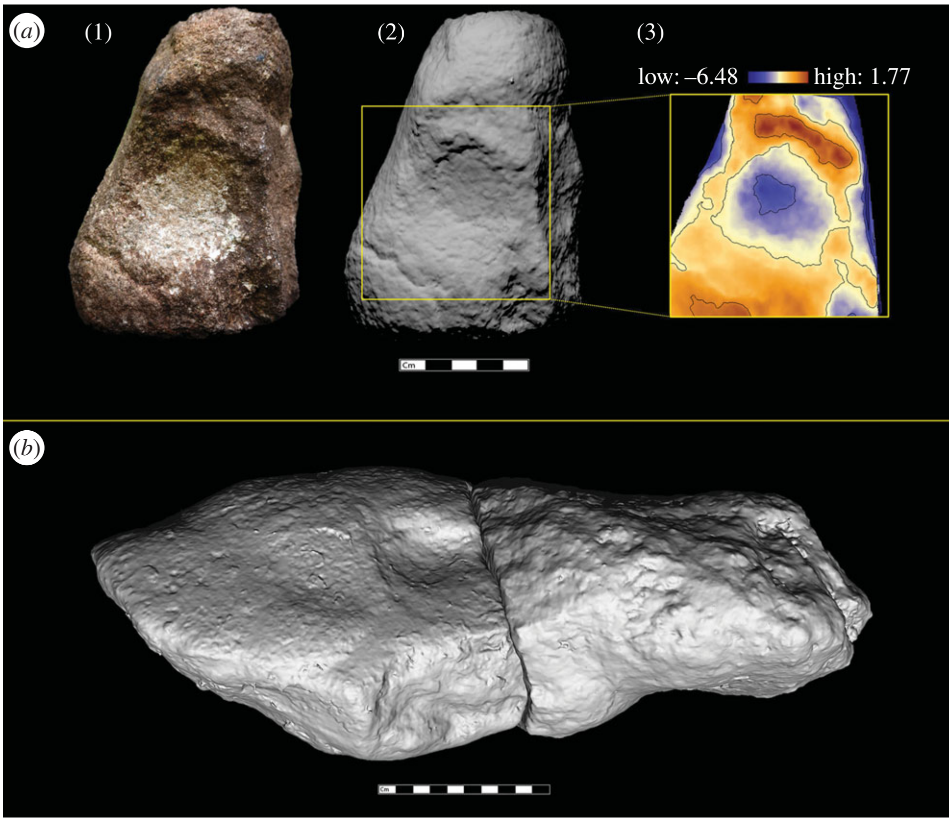

Figure 2. (*a*) Assessing pit depth from *Panda* nut-cracking hammerstones using three-dimensional models. (1) Photograph (Sony Nex6); (2) three-dimensional scan (NextEngine laser scanner); (3) topographic model of the pitted area (Geographic Information System (GIS)). (*b*) Refit of broken hammerstone, each part was independently used as a hammer at two *Panda* cracking sites that were 37 m apart.

found only one hammerstone per nut-cracking site. To determine use-wear of these hammerstones, we produced a three-dimensional model of each hammerstone using a NextEngine laser scanner. If stones found at one site were clearly broken into several parts, we combined all parts belonging to a single stone in our calculations (electronic supplementary material, table S1).

On the basis of GPS reference points taken at landmarks within the chimpanzee home range, we digitized a map of the Taï National Park (originally created by Organisation mondiale de la Santé) that showed the locations of inselbergs. Inselbergs are defined as elevated granite outcrops, marked on the map as polygons. We accounted for the possibility that outcrops without elevation are missing from the map (see below). On average, the inselbergs are rarely larger than 100 m radius. For each inselberg, we determined one coordinate using the centre point of the maximum length and width of the inselberg (figure 1). For each hammerstone, we calculated the distance to all granite inselbergs ($n = 55$) located in the two chimpanzee home ranges. In our analysis, we excluded quartzite (South group $N = 4$) and laterite (North group $N = 1$) *Panda* hammerstones, because they cannot be allocated to a specific location of origin and, therefore, we were not able to estimate transport distances.

To assess the availability of large granite stones, in 2011 we systematically placed 131 line transects of 2 m widths through the North group and South group ranges. We divided the environmental conditions encountered on transects into three conditions: forest, inselberg, and swamp. Each transect was 500 m in length and ran north-to-south, separated from one another by 500 m (total transect length = 65.5 km). We counted and measured each stone larger than 3 cm within a maximum range of 1 m to either side of the transect, and classified them into one of 10 weight categories (1: 0.1–0.25 kg; 2: >0.25–0.5 kg; 3: >0.5–0.75 kg; 4: >0.75–1 kg; 5: >1–2 kg; 6: >2–4 kg; 7: >4–6 kg; 8: >6–8 kg; 9: >8–10 kg; 10: >10 kg). We only included granite material in the analysis.

(b) Use-wear intensity

Our approach to the use-wear assessment was similar to previous studies that have pioneered the use of GIS analysis of both archaeological and primate percussive tools, focusing on hammerstones [34] and stone anvils [35,36] (figure 2*a*). After visually assessing pits on three-dimensional models of all hammerstones, we exported the models as 'Stereo Lithography (STL) files to Meshlab at a resolution of 0.127 mm, where we calculated total model volume and isolated and cropped the pitted surfaces. Cropped three-dimensional surfaces were then oriented so the pitted surface was horizontal using Nett Fab™ and exported as xyz files. Each xyz file was imported into ArcGIS® 10.2 and converted to triangular irregular network models in order to subsequently convert the three-dimensional surface to a raster Digital Elevation Model (DEM) surface.

The total extent of the pit was derived using a topographic position index (TPI) calculated with the land facet analysis plugin for ArcGIS® [37], which calculated the difference in the elevation of each cell against the average elevation of the surrounding cells in order to identify relative high and low regions of the three-dimensional surface. We used a circular scale of 25 mm to determine the surrounding neighbourhood of cells. We applied contour lines using the TPI raster layer in order to consistently delimit the extent of the pitted region of the hammer, and the delimiting contour line was used as a mask in order to extract a DEM raster of the pit. We calculated the total depth of the pit using the DEM raster layer from a bounding box layer. Using this methodology, we were able to record the maximum depth of the pit(s) on each hammerstone.

(c) Statistical analysis (models)

To investigate whether the weight of granite hammerstones at a given nut-cracking site was influenced by the distance between the site and the closest inselberg (as the possible origin), we used linear models [38]. Overall we expected that chimpanzees select a stone source close to a cracking site. For each hammerstone, we determined the distance to the nearest inselberg and included that as a fixed effect in our first model.

To complement archaeological analysis, we added direct observations to the dataset and controlled for the different group that ranged in the designated territories. To evaluate potential inter-group differences, we investigated whether the distances between the inselbergs and hammerstone locations differed between the North and South groups. We applied the same model as described above with a two-way interaction between the distance to the nearest inselberg and social group as a fixed effect.

To analyse whether the distance of the hammerstone to the nearest inselberg correlated with the amount of usage the tool had been exposed to over the years, we assessed use-wear intensity for all *Panda* nut-cracking tools. As a proxy of use-wear intensity, we measured maximum pit depth of hammerstones. We ran a linear regression with the depth of a use-worn pit as the response, and the distance to the nearest inselberg to a given *Panda* nut-cracking site as a fixed effect.

For all models, we checked various diagnostics of model validity and stability (Cook's distance, DFBetas, DFFits, and leverage) and for the assumptions of normally distributed and homogeneous residuals by visually inspecting a qqplot and the residuals plotted against fitted values. We found no obvious deviations from these assumptions [38]. The significance of the full model as compared to the null model was established using a likelihood ratio test (LRT; R function ANOVA with argument test set to 'F') (for the first and third model it was equivalent to [39]). The *p*-values were established using LRTs [40]. The models were implemented in R [41] using the function lm from the base package.

3. Results

(a) Tool weight versus distance to source

Granite hammerstones had a mean weight of 8.7 ± 4.4 kg (range 2.6–17.2 kg), while distances between the nut-cracking sites and the nearest inselbergs averaged 704.5 ± 604.3 m (range 114–2 265 m). Our first model revealed a significant distance-decay effect, with the weight of the hammerstones found at nut-cracking sites decreasing with increasing distance to the nearest inselberg (LRT: estimate $= -3.726$, standard error (s.e.) $= 1.675$, $t = -2.225$, $p = 0.043$; figure 3; electronic supplementary material, table S2).

Furthermore, we did not find a difference in the effect on distance to the inselberg on the weight of the hammerstone between North and South groups (LRT: estimate $= -3.198$, s.e. $= 4.101$, $t = -0.78$, $p = 0.451$; electronic supplementary material, table S3). Our results suggested that the distance-decay effect is, therefore, not influenced by potential cultural behaviour of the social group but is a universal effect of long-distance tool transport.

(b) Use-wear versus distance to source

Use-wear intensity increased significantly with increasing distance to the closest inselberg. Linear regression revealed that the pit of a given hammerstone is deeper, the greater the distance between a site and the nearest mountain (LRT: estimate $= 0.009$, s.e. $= 0.003$, $t = 2.718$, $p = 0.017$; figure 4; electronic supplementary material, table S4). Therefore, the depth of a pit reflected the potential distance the stone was carried to the current cracking site. We take these results

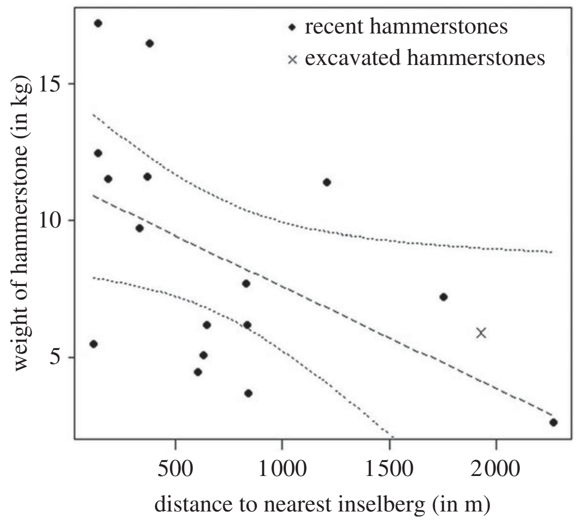

Figure 3. Weight of stone tools as a function of the distance to the nearest inselberg. Each circle represents a stone tool (black circle: this study, cross: excavated stones from [42]). The dashed line shows the fitted model and the dotted lines the 95% confidence interval. (The excavated material was not included in the model and only placed on the graph for visual aid.)

with a note of caution, as pit depth could be affected by other variables for which we do not have data, such as slight variation in the stone material composition, or in the intensity and frequency the hammerstone was used at specific locations throughout its transport. Nevertheless, over the time-averaged dataset in this study, use-wear pit depth is positively correlated with distance to the nearest inselberg.

(c) Stone distribution and availability

To assess granite stone distribution throughout the territory, line transects covered 50.57 km of tree forest, 1.34 km over inselbergs, and 13.59 km through swamps. Because we were interested in the distribution of natural stones, we excluded hammers at nut-cracking sites from this analysis. On all inselbergs that were sampled representatively, we found large stones in the size range of suitable *Panda* hammerstones which could function as a raw material source. In total, we found 133 suitable hammerstones for *Panda* nut cracking (more than 2 kg) on the inselberg transects (average of 12.9 suitable hammerstones per 100 m line transect), three suitable hammerstones in the forest condition (0.006 suitable hammerstones per 100 m line transect), and no stones suitable for *Panda* nut cracking in the swamps (figure 5). Two of the three stones located in the forest area do fit the common scheme of the distance-decay effect which could suggest that these hammerstones mark locations of deceased *Panda* trees.

4. Discussion

Wild chimpanzee nut-cracking tools from the Taï National Park show a clear distance-decay effect. Hammerstone weights at *Panda* nut-cracking sites decreased with increasing distance to the nearest location of suitable raw material. Suitable *Panda* nut-cracking raw material was located at the inselbergs, while the forest and swamps did not have large granite stones available naturally, demonstrating that such stones found at nut-cracking sites have been carried there by the chimpanzees. Our data recorded the longest known

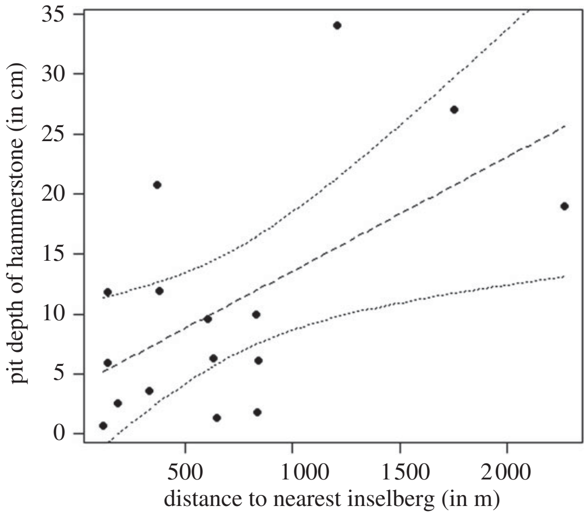

Figure 4. Use-wear pit depth as a function of the distance to the nearest inselberg. Each dot represents one stone tool. The dashed line shows the fitted model and the dotted lines the 95% confidence interval.

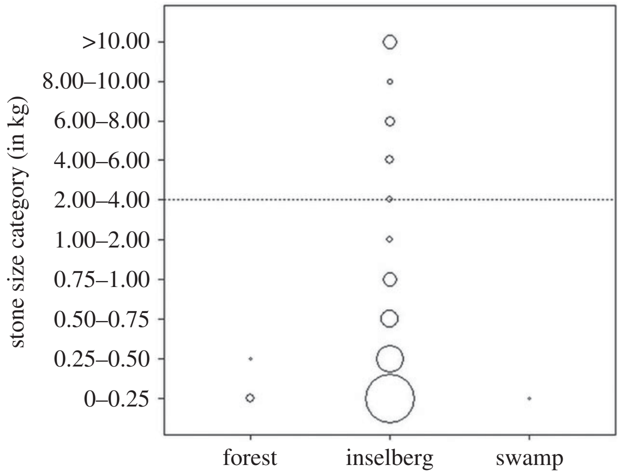

Figure 5. Granite stone distribution in the chimpanzee home range in the Taï National Park. Available stone size is corrected for the area sampled in the three different ecological conditions (forest, inselberg, swamp). The horizontal line represents the minimum weight of a suitable *Panda* hammerstone (assessed through our sample size).

stone tool transport by wild chimpanzees, cumulatively reaching over 2 km. Additionally, tools found further from raw material sources were used and re-used more intensively, as measured by the development of pits on their surface.

The oldest known chimpanzee tools to date were excavated from within the range of the Taï North group [42]. Interestingly, the combined weight of granite *Panda* tool fragments found at that site (Noulo) fits the distance-decay curve derived from our observations of the modern landscape, indicating that this behaviour may have remained unchanged for at least 4 000 years (figure 3). The continuity of this pattern over millennia suggests that stone tool transport over the long term is not influenced by cultural factors, instead it follows the pattern resulting from accumulated, unplanned, short-term transport events.

Based on direct observations, chimpanzees very rarely move large hammerstones significant distances in one transportation event [5]. *Panda* trees often occur in clusters and are not homogeneously distributed throughout the territory. To date, transport of *Panda* hammerstones has been observed only within these clusters [33]. Also, hammerstones do not follow a linear transport path away from the source, but the long-term net effect of several sequential movements is to radiate material further and further away from the source the longer the hammerstone has been in use. We, therefore, suggest that chimpanzees do not intentionally plan long-distance transport, and that stone tool distribution across the landscape has developed through the long-term interplay of ecological constraints, energetic requirements, and foraging behaviour.

Recent studies reported remarkable spatial memory [43], planning of daily foraging routes [44], and planned short-distance tool transport bouts [45] in the Taï chimpanzees. In contrast with the time-averaged tool distributions that we report here, these daily activities do not adequately reflect the long-term stone deposition on a landscape scale. Distance of current stone location to source, therefore, cannot be used as a proxy for abilities linked to planned transport for the Taï chimpanzees. However, we also note that sophisticated planning abilities may still be responsible for short-term day-to-day activities, even where these are subsequently blurred by time.

We were able use these direct observations of individual events to inform on the processes that led to the current situation. For example, two *Panda* hammerstones found 37 m apart, at two different nut-cracking locations, illustrate how the distance-decay effect might have developed. Repeated use of a tool eventually breaks it at its weakest points, typically on the edges [9] or, as in this case, across the deepening pit in the centre (figure 2*b*). Both segments of the broken stone continued to be used as separate hammers, coupled with continued transportation. The result is a fragmentation of the original behavioural record, but the emergence of the archaeological pattern.

Our results empirically support the results of prior agent-based models, by showing that short-term, undirected movements can produce a time-averaged distance-decay curve. This situation occurs even though the assumptions underlying these models are simplified versions of the environmental and social conditions that the chimpanzees have to negotiate. This concordance suggests that studies of hominin stone transport that emphasize complex drivers such as advanced planning abilities [12,46–48] may be over-interpreting the hominin evidence, where that evidence is indistinguishable from the model outcomes.

Hominin stone tool distance-decay patterns have been explained as outcomes of the curation of raw material [26], natural topographic barriers [25], the mitigation of risk related to the need to possess sharp cutting edges [26], or planning for future needs [20]. Stone tool deposition might have, furthermore, been influenced by the ranging pattern of carnivores and ecological factors such as water sources and clusters of shelter trees.

The data presented in this study add the time-averaged result of multiple short-distance transport bouts to the range of possible hominins behaviours associated with this spatial patterning of lithic material, and may go some way to developing a better understanding of the 'middle range' behaviours between raw material acquisition and artefact deposition.

If archaeological circumstances provide similar evidence as seen in chimpanzee stone tool transport patterns—discreet and identifiable raw material sources within the landscape as well as a decreasing mass of material and increase in reduction intensity from raw material sources—then the behavioural processes observed for wild chimpanzees should be the starting reference point for behavioural reconstructions. Our study emphasizes that the final observed distribution of material is rarely under the control of the tool user, and should not be interpreted as such without supporting contextual evidence.

We have demonstrated that landscape-wide patterning of materials applies to the Taï chimpanzees, and is identifiable using archaeological methods. For both chimpanzees and hominins, investigations can now proceed to help explain how these patterns emerge from the interplay of short- and long-term behavioural processes.

Ethics. All our work was conducted in compliance with appropriate animal care regulations and national laws. Data collection was non-invasive and in compliance with the requirements and guidelines of the 'Ministère de l'enseignement supérieure et de la recherche scientifique' and adhered to the legal requirements of the Côte d'Ivoire. We further strictly adhered to the regulations of the Deutsche Tierschutzgesetz or the ASP principles for the ethical treatment of non-human primates.

Data accessibility. The dataset supporting this article has been uploaded as part of the electronic supplementary material, table S1.

Authors' contributions. L.V.L. designed the study, carried out the data collection and analysis, and wrote the manuscript; T.P. carried out analysis and wrote the manuscript; L.K. carried out the analysis and wrote the manuscript; M.H. designed the study and wrote the manuscript; R.M.W. designed the study and edited the paper.

Competing interests. We have no competing interests.

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