

RESEARCH ARTICLE

Dental wear patterns reveal dietary ecology and season of death in a historical chimpanzee population

Julia Stuhlträger^{1,2*}, Ellen Schulz-Kornas^{1,3}, Ottmar Kullmer^{4,5}, Marcel M. Janocha^{4,5}, Roman M. Wittig^{6,7}, Kornelius Kupczik¹

1 Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany, **2** Konrad Lorenz Institute for Evolution and Cognition Research, Klosterneuburg, Austria, **3** Department of Cariology, Endodontics and Periodontology, University of Leipzig, Leipzig, Germany, **4** Department of Palaeoanthropology, Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt am Main, Germany, **5** Department of Palaeobiology and Environment, Institute of Ecology, Evolution, and Diversity, Goethe University Frankfurt, Frankfurt am Main, Germany, **6** Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany, **7** Taï Chimpanzee Project, CSRS, Abidjan, Ivory Coast

* julia_stuhltraeger@eva.mpg.de



OPEN ACCESS

Citation: Stuhlträger J, Schulz-Kornas E, Kullmer O, Janocha MM, Wittig RM, Kupczik K (2021) Dental wear patterns reveal dietary ecology and season of death in a historical chimpanzee population. PLoS ONE 16(5): e0251309. <https://doi.org/10.1371/journal.pone.0251309>

Editor: Cyril Charles, Ecole Normale Supérieure de Lyon, FRANCE

Received: December 10, 2020

Accepted: April 25, 2021

Published: May 10, 2021

Copyright: © 2021 Stuhlträger et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All raw data from 3D surface texture and occlusal fingerprint analysis supporting the findings of this study are accessible through the open access data repository of the Max Planck Society (via <https://dx.doi.org/10.17617/3.54>).

Funding: This research was funded by the Max-Planck-Society (www.mpg.de). Further, Julia Stuhlträger was supported by the writing-up fellowship from the Konrad Lorenz Institute for Evolution and Cognition Research (www.kli.ac.at).

Abstract

Dental wear analyses have been widely used to interpret the dietary ecology in primates. However, it remains unclear to what extent a combination of wear analyses acting at distinct temporal scales can be beneficial in interpreting the tooth use of primates with a high variation in their intraspecific dietary ecology. Here, we combine macroscopic tooth wear (occlusal fingerprint analysis, long-term signals) with microscopic 3D surface textures (short-term signals) exploring the tooth use of a historical western chimpanzee population from north-eastern Liberia with no detailed dietary records. We compare our results to previously published tooth wear and feeding data of the extant and continually monitored chimpanzees of Taï National Park in Ivory Coast. Macroscopic tooth wear results from molar wear facets of the Liberian population indicate only slightly less wear when compared to the Taï population. This suggests similar long-term feeding behavior between both populations. In contrast, 3D surface texture results show that Liberian chimpanzees have many and small microscopic wear facet features that group them with those Taï chimpanzees that knowingly died during dry periods. This coincides with historical accounts, which indicate that local tribes poached and butchered the Liberian specimens during dust-rich dry periods. In addition, Liberian females and males differ somewhat in their 3D surface textures, with females having more microscopic peaks, smaller hill and dale areas and slightly rougher wear facet surfaces than males. This suggests a higher consumption of insects in Liberian females compared to males, based on similar 3D surface texture patterns previously reported for Taï chimpanzees. Our study opens new options for uncovering details of feeding behaviors of chimpanzees and other living and fossil primates, with macroscopic tooth wear tracing the long-term dietary and environmental history of a single population and microscopic tooth wear addressing short-term changes (e.g. seasonality).

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Introduction

The diet of chimpanzees (*Pan troglodytes*) is highly variable, and includes fruits, leaves and other vegetative plant parts as well as animal resources [e.g. 1–5]. Specific dietary proclivities vary by chimpanzee subspecies, population, and/or social structure [3, 5–8]. For example, *P. t. troglodytes* of the Lopé Reserve (Gabon) feed more on fruits and less on leaves compared to a population of the same subspecies from the Goualougo Triangle (Democratic Republic of Congo) [2, 9–11]. Moreover, dietary preferences even differ between neighboring communities of the same population, as was recently published for two western chimpanzee (*P. t. verus*) communities of the population from the Taï National Park (Ivory Coast) [12]. Both communities feed mainly on fruits and other plant parts, but with varying number of plant species. Furthermore, the north community is more engaged in ant feeding, while the south community feeds less on ants but more on honey and bees [12]. Feeding preferences of chimpanzees are also age and sex specific, and depend upon the seasonal availability of food [13, 14]. Generally, female chimpanzees engage more in nut cracking than males [1, 15], and they more often consume insects while males consume more meat from hunted vertebrates [13, 16]. Additionally, environmental factors such as grit and dust have a strong effect on the feeding ecology of chimpanzees. For example, western chimpanzees of the Taï National Park are recurrently exposed to large amounts of wind-borne dust particles during specific dry periods of the year affecting their chewing and digestive efficiency [13].

Both biotic (food) and abiotic (dust) factors lead to dental tissue loss during mastication, which manifests itself macroscopically by generating complementary wear facets on antagonistic occlusal tooth surfaces and microscopically by forming pits/dales and scratches/furrows on these wear facets [e.g. 13, 17–20]. Therefore, tooth wear analysis has been widely used as a tool for reconstructing diets and environmental changes in living and fossil primates and other mammals, often where primary ecological or environmental data were incomplete or lacking [e.g. 21–26].

For example, occlusal fingerprint analysis (OFA) is used to assess the spatial position, size and distribution of wear facets and informs about occlusal 3D jaw movements [23, 27, 28], i.e. the occlusal power stroke that is divided into the incursive shearing phase I and the excursive grinding phase II [29]. It therefore assesses macroscopic wear changes and provides a longer-term signal of wear, accumulated over several months or years [e.g. 30–32]. For example in a human case study, macroscopic wear patterns of a lifetime raw food vegetarian showed inclined wear facets which the authors related to this specific dietary behavior [23]. Moreover, a more recent study on modern and archaeological human teeth showed that hard and tough dietary items produce flat and large wear facets, while a diet consisting mainly of meat produces steeper wear facets [24]. Thus, these studies suggest that distinct dietary differences result in diverging macroscopic tooth wear patterns.

Three-dimensional (3D) surface texture (3DST) analysis, on the other hand, quantifies various micrometer sized geometric aspects on molar wear facet surfaces, such as surface micro-features height, orientation, density, and complexity [33]. This technique therefore reveals short-term signals on a dental wear facet, i.e. it provides information on the diet consumed up to the last few days prior to an individual's death [34–36].

Previous studies showed that there is a correlation between macro- and microscopic tooth wear signals. For instance, studies on Neanderthals have demonstrated that both macro- and microscopic wear signals carry an environmentally driven wear signal [24, 37]. Neanderthals from open environments showed enlarged and steep wear facets that formed in a shearing action during mastication [24], while the microscopical surface textures found on these facets were less complex and heterogeneous [37]. Yet, both analyses indicated an increased reliance

upon tough, fibrous food such as meat [24, 37]. In recent feeding experiments on rabbits [19], goats [38], and guinea pigs [39] it has been shown that both increased macroscopic tooth wear and microscopic wear signals (high surface roughness and high mean density of pits and furrows) were positively correlated with the amount, shape and size of internal and external dietary abrasives ingested.

Here we aim to infer the dietary ecology and tooth use of a historical population of western chimpanzees (*P. t. verus*) from northeastern Liberia for which there are no detailed behavioral and ecological records available. These chimpanzees were poached in the 1950s, and subsequently their skulls were collected and accessioned into the collection of the Senckenberg Research Institute and Natural History Museum Frankfurt. We employ macro- and microscopic wear analyses on both upper and lower first and second molars (M1/M2) as well as deciduous fourth premolars (dp4) and compare the results to those of the extant Tai National Park chimpanzee population whose dietary ecology has been extensively studied since 1979 [1]. Given their geographic proximity in evergreen lowland rain forests [40] (Fig 1A), both populations are assumed to have been exposed to similar climatic and environmental factors such as a bi-annual rainfall pattern, monthly precipitation rate [1, 41] and dust deposition through the Harmattan trade wind during the more pronounced dry periods of a year [42–44]. Using both OFA (long-term macroscopic tooth wear) and 3DST analysis (short-term microscopic tooth wear) we specifically explore (1) whether both populations show similar tooth wear patterns, and (2) whether we can reveal season-specific (dry/rainy) wear patterns within the historical Liberian chimpanzee population, similar to what has previously been found in the Tai chimpanzees [13]. In addition we test for sex-specific differences in tooth wear patterns (both macroscopic and microscopic tooth wear).

Materials and methods

Cranial material

The sample of cranial material used in the present study originates from Liberia. It belongs to a large assemblage of chimpanzee skulls housed in the collections of the Department of Paleoanthropology in the Senckenberg Research Institute and Natural History Museum Frankfurt (Frankfurt am Main, Germany, N = 36) and the Phyletic Museum (Jena, Germany, N = 6). In total, we analyzed 100 upper and lower cheek teeth (M1: N = 47, M2: N = 41, dp4: N = 12) of 42 specimens (S1 Table). The crania originate from individuals of a free-ranging western chimpanzee (*P. t. verus*) population (“Liberian chimpanzees”) in the northeastern part of Nimba County (Liberia). Those individuals were killed, butchered and their skulls usually kept as trophies by locals, called Dan and Kran [46, 47], and later gathered and bought during expeditions led by the German ethnologist and medical doctor Hans Himmelheber in 1952/53 and 1955/56. The individuals originate from a restricted area, which was bounded to the east by the Cess River and to the west by the St. John River. Himmelheber reported the sex of 24 chimpanzees, which was later confirmed by Dierbach [48].

We used a second set of cranial material originating from a free-ranging chimpanzee population of the same subspecies from the Tai National Park (Ivory Coast) to address intraspecific variation in macro- and microscopic tooth wear. This cranial material is part of the osteological collection of the Tai Chimpanzee Project [49] hosted by the Departments of Human Evolution and Primatology of the Max Planck Institute for Evolutionary Anthropology (MPI-EVA Leipzig, Germany). For this population we included 95 upper and lower cheek teeth (M1: N = 49, M2: N = 26, dp4: N = 20) of 41 specimens (S1 Table). Data for the microscopic tooth wear analysis were taken from Schulz-Kornas et al. [13] and Stuhlträger et al. [14].

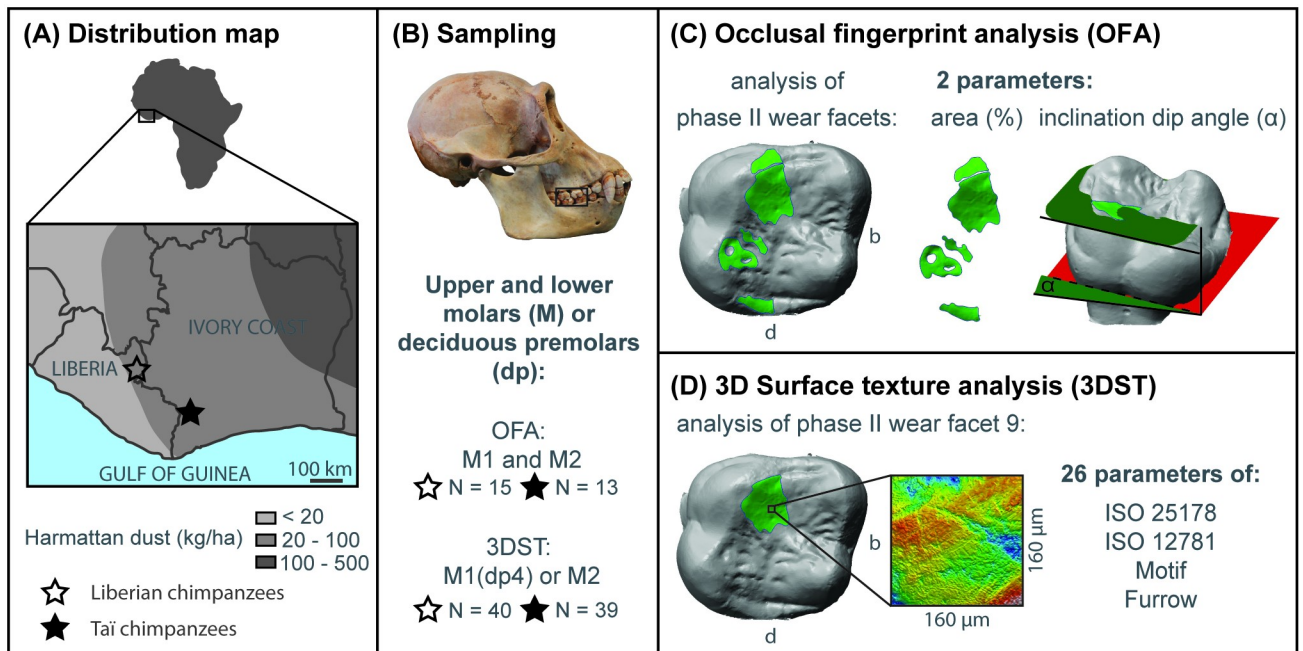


Fig 1. Distribution map and methodological setup. Map with the distribution range of the Liberian chimpanzee population, the locality of the Taï National Park (Ivory Coast) and the distribution of Harmattan dust loads in those areas (A). The map and the Harmattan distribution was redrawn and adapted according to the data presented in Lesschen et al. [45]. Sampling procedure (B) for occlusal fingerprint analysis (macroscopic tooth wear) (C) and 3D surface texture analysis (microscopic tooth wear) (D) shown for the upper first molar (b = buccal, d = distal).

<https://doi.org/10.1371/journal.pone.0251309.g001>

Habitat information

The northeastern part of Nimba County (Liberia) and the Taï National Park (Ivory Coast) comprise evergreen lowland rain forest with the latter remaining the largest one in west Africa [1, 40]. Both chimpanzee habitats are in close proximity (approximately 200 km apart, Fig 1A), and underlie similar periodic environmental changes. In the Taï forest the annual rainfall from 1950 to 1975 and from 1988 to 1995 was approximately 1800 mm [1], but declined to around 1400 mm annually between 2000 and 2008 (Taï Chimpanzee Project, unpublished data). For Liberia we selected an appropriate location (N6° 43' 12", W8° 36' 36") and time period (1931–1960) based on historical rainfall data of the Climatic Research Unit of University of East Anglia [41], which documented an average annual rainfall of 1900 mm. In both habitats, the precipitation follows a bi-annual pattern, with two rainy periods (March–June, September–November), separated by months with a decline in rainfall. This decline is strongest from December to February. During this time the rainfall does only vary approximately from 25 mm to 48 mm per month in the Taï forest ([1]; Taï Chimpanzee Project, unpublished data), whereas in northeast Liberia the rainfall does not exceed 42 mm per month (for detailed information on the climate of the Taï forest see [1, 50]). Hence, the period from December to February is considered as a dry period [1]. Furthermore, this particular dry period is accompanied by the Harmattan, a cold desert wind from the Western Sahara, which results in dust deposition in both habitats [42–44].

Occlusal fingerprint analysis (OFA)

The OFA is a virtual method for the characterization and quantitative comparison of dental macroscopic tooth wear patterns (wear facet pattern) which result from the alteration of the

occlusal primary relief in tooth crowns through dental tissue loss during the occlusal power stroke (phase I and phase II) of chewing and other dental activities [23, 27, 51]. A fully developed wear facet pattern in a hominid molar usually consists of a maximum of 13 wear facet positions [52]. Wear facets 1–4 belong to phase I buccal, wear facets 5–8 to phase I lingual, and wear facets 9–13 are attributed to phase II of the occlusal power stroke movements [28]. Here we focused on the upper and lower M1 and M2 complementary wear facets of phase II of the power stroke (Fig 1B and 1C), those wear facets should carry a surface texture induced mainly by food properties, since they are essentially worn through tooth-food-tooth contacts. During chewing, food is trapped, compressed and comminuted between antagonistic phase II facets at the end of phase I and during phase II power stroke movements [53]. To reduce the effect of age and for better comparability we only chose specimens with M1 and M2 in wear stages 3 and 4 according to Smith [54]. Consequently, and compared to the 3DST analysis, we could include only 15 specimens of the Liberian chimpanzees and 13 specimens of the Tai chimpanzees of the OFA study sample.

The OFA uses digital 3D polygonal models of crowns usually generated from high-quality dental casts [55] applying white-light 3D-surface scanning with a spatial minimum point-to-point distance in x-y-z of $\sim 55\mu\text{m}$ (smartSCAN 3D C-5, Breuckmann GmbH). Polyworks[®] 2017 (InnovMetric Inc.) 3D metrology software was used for post-processing of the computer models. The Polyworks[®] Modeler module provides digital tools for a manual segmentation of each wear facets using a close polyline fitted onto the surface of the model while having the original casts under a binocular alongside for a best-practice segmentation [51]. Afterwards the polyline of all wear facets were integrated into the model surface by a re-triangulation of the model surface. Accordingly, wear facet areas were analyzed following the procedures recently described in detail by Kullmer et al. [51]. The OFA method applied here for the wear facet quantification consists of three sequential steps: determination of a reference plane through cervical margin, wear facet segmentation and mapping, and the calculation of wear facet area size and dip angle in respect to the reference plane of the molar crown, while fitting a best-fit plane through wear facet surface data points.

The reference plane was calculated from a selection of data points 0.2 mm above and below a manually fitted polyline along the cervical margin (step 1). It was used to orientate the crown model in the Cartesian xy-plane [23, 27, 51, 56, 57]. The closed polyline tool and the grouping of surface data points in Polyworks[®] 2017 (InnovMetric Inc.) allows the segmentation and labeling of each wear facet (step 2) on the 3D surface model. In the current study the wear facet area size value in mm^2 and the inclination dip angles of each phase II wear facet are calculated between the reference plane (xy-plane) and the wear facet best-fit plane (step 3). Wear facet areas of phase II facets are calculated as percentage values of the portion of area of wear facets of phase II in respect to the area percentage of all wear facets.

3D surface texture (3DST) analysis

The standard phase II wear facet for primate dietary reconstructions [29, 52] is wear facet 9 on both upper and lower molars. In this study, we selected first and second molars on either the right or left side and, where present, of the fourth deciduous premolars. The teeth were cleaned with acetone and molds were taken using a high resolution silicone imprint (Provil[®] novo Light C.D.2 regular set; Type 3; Heraeus Kulzer, Dormagen, Germany), following the procedure of Schulz et al. [33, 58] and Calandra et al. [25]. We used the high-resolution confocal disc-scanning surface measuring system μsurf mobile (NanoFocus AG, Oberhausen, Germany) with a 100x long distance objective and a numerical aperture of 0.8 to acquire 3DST measurements. Three to four not overlapping scans (each $160\mu\text{m} \times 160\mu\text{m}$) of each facet with

a resolution of 0.16 μm in x and y, and a step size of 0.06 μm in z were taken and averaged (mean) for further analyses. Measurements with less than 95% surface points were excluded from further analyses.

The obtained data were analyzed using 26 3DST parameters (Fig 1D, S2 Table) following the 3D areal surface texture standards ISO 25178 [59], ISO 12781 [60] as well as motif (dales and hill recognition using watershed segmentation algorithms) and furrow (surface vectorization) analyses [58] using the μsoft analysis premium software version 7.4.8076 (NanoFocus AG, Oberhausen, Germany; a derivative of Mountains[®] Analysis software by Digital Surf, Besançon, France). These 3DST parameters relate to criteria such as area (*Sha*, *Sda*, *mea*), density (*Spd*, *Sal*, *medf*), height (*Sq*, *Sp*, *Ssk*, *S5p*, *S5v*, *FLTv*, *FLTp*, *meh*, *madf*, *metf*), volume (*Vv*, *Vvc*, *Vmp*, *mev*), plateau size (*Smr*, *Smc*), anisotropy (*Str*), texture direction (*Std*), complexity (*Sdr*), and slope (*Sdq*).

Statistics

For all comparisons, we analyzed upper and lower molars separately. For OFA we used both, the first and the second molar, because this method is more affected by the degree of tooth wear. For the 3DST analysis the first permanent molar was the preferred one, i.e. only if this molar was not available, we used the second molar to increase the specimen number. Deciduous fourth premolars were only used for the 3DST comparison of the two populations ($\text{dp4}_{\text{Liberia}}$ vs. dp4_{Tai}) to test whether the possible wear differences already appear in younger individuals. All tests were run between the two populations and between sexes.

We used a circular statistic for OFA to analyze the wear facet dip angles, which we conducted in the software Oriana© (version 3.21, 1994–2010, Kovach-Computing services, Anglesey, Wales, Great Britain) [61–64]. We performed a groupwise Watson-Williams-Test between the mean angles. For the comparison of the phase II wear facet areas, we first checked whether the data are normally distributed. Therefor we used a histogram for visual exploration, as well as the Shapiro-Wilk test that affirmed a normal distribution for our data. Hence, we used the Welch Two Sample t-test in the software R 3.4.3 [65] (using the function “t.test”) to check for statistical significance. The means of wear facet dip angle and area were calculated separately for UM1, LM1, UM2 and LM2.

All the statistical analyses related to the 3DST were performed using the software R 3.4.3 [65] by using the R packages *xlsx* version 0.4.2 [66], *doBy* version 4.5.3 [67], and *R.utils* version 1.12.1 [68]. We used the robust Welch–Yuen heteroscedastic omnibus test (WYT) coupled with a heteroscedastic pairwise comparison test (analog to Dunnett’s T3 test). If both tests detected a significant difference ($p = \leq 0.05$) a heteroscedastic rank based test (according to Cliff’s method) was used to detect significant differences between trimmed (15%) means. The trimming method excludes the highest and lowest parts of the data set and is used to compensate for non-normality [25]. For a detailed description of the statistical tests including the R-scripts see Calandra et al. [25, 69].

Additionally, we performed a Factor Analysis (FA) to compare the Liberian chimpanzees with the Tai chimpanzees from dry and rainy periods (for details see S1 Text). We selected 11 of the initial 26 3DST parameters (*Sq*, *Sp*, *Vmp*, *Sdr*, *Sdq*, *Sal*, *Smc*, *meh*, *medf*, *metf*, *mea*) using varimax rotation and the function “factanal”. The rotation “varimax” is recommended for a small sample size and rotates the factors in a way that each variable has a large absolute loading on only one factor, while its loadings on the other factors are close to zero [70]. The 3DST parameters were selected due to approximately normal distribution and no missing values. The Kaiser-Meyer-Olkin measure of sampling adequacy (value > 0.5), using the function “paf” of the R package *rela* [71], showed that the FA was justified. The FA scores of factors

with Eigenvalues ≥ 1 were extracted to perform a one-way ANOVA with a post-hoc Tukey's Honestly Significant Difference (HSD) test in order to explore significant variations between groups.

Results

The OFA results reveal that both populations differ to some extent in their macroscopic wear pattern; the angle of facet inclination shows a trend towards steeper phase II wear facets (larger angle of inclination) and smaller phase II wear facet areas in the Liberian population of chimpanzees compared to Taï chimpanzees (Fig 2, Table 1). This difference is significant only on the upper second molars (facet inclination: $p_{\text{Watson-Williams}} = 0.004$, facet area: $p_{\text{Welch Two Sample t-Test}} = 0.047$) (Table 1), reflecting differences in the occlusal relief of the molars. Steeper and smaller wear facets point to lower rates of tissue loss in the Liberian chimpanzees indicating differences in chewing activity.

The combination of the Welch–Yuen heteroscedastic omnibus test, a heteroscedastic pairwise comparison test and a heteroscedastic rank based test using a total of 26 3DST variables reveal that both populations (mixed sex) distinctly differ in their microscopic wear pattern (S3 Table) on both upper and lower M1/M2 and dp4. The surface textures of the Liberian chimpanzees M1/M2 and dp4 are significantly flatter (*Sq*, *S5v*, *FLTv*, *FLTp*), less voluminous (*Vv*, *Vvc*), and show a higher density of peaks (*Spd*) and furrows (*medf*) with small hill areas (*Sha*, *mea*) and dale areas (*Sda*) than those of the Taï chimpanzees (S3 Table).

When testing for presence of a seasonality signal, using FA with two factors we found that the 3DSTs of the Liberian upper and lower M1s and M2s overlap with those individuals of the Taï chimpanzees that died during the dry period (upper facet 9: $p_{\text{TUkey}} = 1$, lower facet 9: $p_{\text{TUkey}} = 0.865$) but are significantly different from those that died during the rainy period (upper facet 9: $p_{\text{TUkey}} = 0.005$, lower facet 9: $p_{\text{TUkey}} = 0.007$) (Fig 3, Table 2). For both, upper and lower facet 9, the factor loadings suggest that the height parameters (*Sq*, *Sp*, *meh*, *metf*) as well as the parameters *Vmp* (volume) and *Smc* (plateau size) contribute most to factor 1, whereas *Sdr* (complexity), *Sdq* (slope), *mea* (area) and *medf* (density) contribute most to factor 2 (S4 Table). The separation of Liberian chimpanzees from Taï chimpanzees that died during a rainy period is mainly driven by factor 2 (Fig 3), indicating more complex 3DSTs with a higher density of furrows in the Liberian chimpanzees.

The analysis of a sex-specific wear pattern reveals that female chimpanzees from Liberia have significantly steeper phase II wear facets on their upper second molars than females from Taï ($p_{\text{Watson-Williams}} = 0.022$), while males of both populations exhibit a similar macroscopic tooth wear pattern (Fig 4A and 4B). Liberian females also have slightly smaller phase II wear facet areas compared to Taï females, but none of these differences are significant (Table 1). Furthermore, females and males within both populations do not differ in their phase II wear facet areas (Table 1). Additionally, Liberian and Taï females differ in their 3DSTs to a greater degree than Liberian and Taï males (S5 Table). Specifically, Liberian females have more complex (*Sdr*) surface textures with significantly more peaks and less plateaus than Taï females as indicated on the upper molars by *Ssk* (Fig 4C) and on the lower molars by *Spd* (Fig 4D), *medf* and *Sda* (S6 Table). Males of both chimpanzee populations show greater similarity in their 3DSTs, differing exclusively in the characteristics of peaks (Fig 4D, S5 Table).

Discussion

Tooth wear analysis is a valuable tool to reconstruct the dietary ecology of fossil and extant primates at the interspecific and intraspecific level. For example, interspecific and intraspecific studies on early *Homo sapiens* and different groups of Neanderthals showed that both

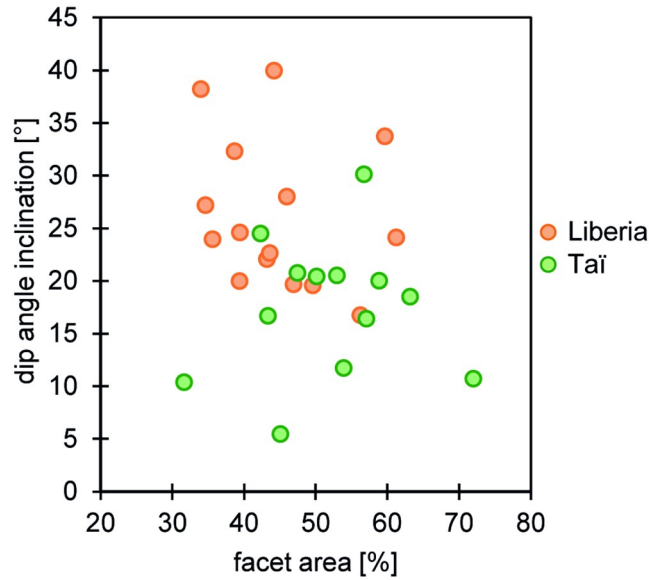


Fig 2. Facet area and dip angles of phase II wear facets of the upper second molars compared between both chimpanzee populations.

<https://doi.org/10.1371/journal.pone.0251309.g002>

Table 1. Descriptive statistics for dip angles and areas for phase II wear facets.

Test variable 1 vs. 2	Teeth	phase II dip angle [°]							phase II area [%]						
		Test variable 1			Test variable 2			p-value ^a	Test variable 1			Test variable 2			p-value ^b
		N	Mean	SD	N	Mean	SD		N	Mean	SD	N	Mean	SD	
<i>Liberia vs. Tai</i>	UM1	15	21.45	7.4	15	20.77	7.39	0.689	15	39.85	7.72	12	44.71	6.44	0.087
	LM1	14	27.23	5.53	7	25.16	7.27	0.476	14	43.88	8.59	7	49.98	9.82	0.191
	UM2	15	25.57	7.01	13	17.51	6.59	0.004	15	44.81	8.06	13	51.89	10.32	0.047
	LM2	14	27.62	7.07	9	25.23	4.14	0.368	14	44.71	10.96	9	47.96	7.92	0.419
<i>Liberian females vs. Tai females</i>	UM1	4	18.85	9.05	7	15.37	4.41	0.406	4	38.9	5.77	7	43.81	3.88	0.194
	LM1	4	26.61	6.75	4	23.73	7.09	0.577	3	41.5	8.98	4	48.03	9.9	0.406
	UM2	4	26.34	9.33	8	14.66	5.82	0.022	4	41.05	10.4	8	52.01	11.72	0.144
	LM2	4	27.65	11.81	5	26.83	4.47	0.886	5	51.81	12.15	5	47.06	7.02	0.476
<i>Liberian males vs. Tai males</i>	UM1	8	21.03	5.38	5	21.15	5.99	0.971	7	38.12	6.42	5	45.97	9.39	0.152
	LM1	7	27.85	4.11	3	27.06	8.59	0.844	6	46.26	5	3	52.58	11.17	0.434
	UM2	8	23.76	4.71	5	22.07	5.37	0.563	7	42.41	4.89	5	51.69	8.89	0.081
	LM2	7	27.53	3.57	4	23.23	3.08	0.076	6	39.73	5.17	4	49.09	9.93	0.156
<i>Liberian females vs. Liberian males</i>	UM1	4	18.85	9.05	8	21.03	5.38	0.604	4	38.90	5.77	7	38.12	6.42	0.842
	LM1	4	26.61	6.75	7	27.85	4.11	0.711	3	41.50	8.98	6	46.26	5	0.462
	UM2	4	26.34	9.33	8	23.76	4.71	0.528	4	41.05	10.40	7	42.41	4.89	0.819
	LM2	4	27.65	11.81	7	27.53	3.57	0.975	5	51.81	12.15	6	39.73	5.17	0.091
<i>Tai females vs. Tai males</i>	UM1	7	15.37	4.41	5	21.15	5.99	0.082	7	43.81	3.88	5	45.97	9.39	0.648
	LM1	4	23.73	7.09	3	27.06	8.59	0.596	4	48.03	9.9	3	52.58	11.17	0.604
	UM2	8	14.66	5.82	5	22.07	5.37	0.042	8	52.01	11.72	5	51.69	8.89	0.957
	LM2	5	26.83	4.47	4	23.23	3.08	0.214	5	47.06	7.02	4	49.09	9.93	0.744

UM = upper molars, LM = lower molars, N = number of individuals, SD = standard deviation, p = level of significance,

^a p-values from Watson-Williams-Test,

^b p-values from Welch Two Sample t-Test.

<https://doi.org/10.1371/journal.pone.0251309.t001>

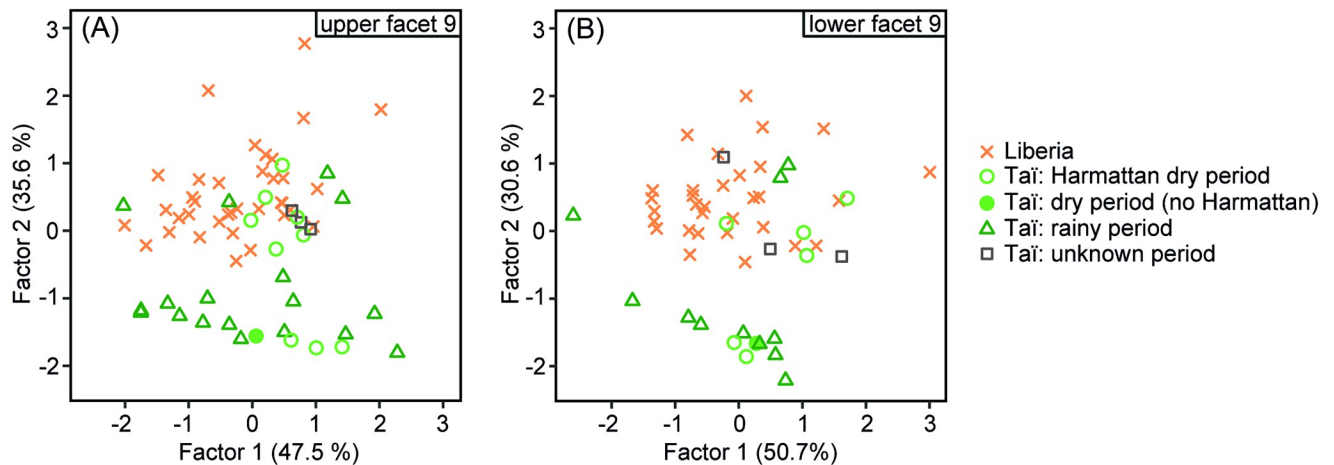


Fig 3. Factor analysis of wear facet 9 comparing the Liberian chimpanzee population to Tai chimpanzees from dry and rainy periods. (A) upper molars; (B) lower molars; 3DST data for Tai chimpanzees taken from Schulz-Kornas et al. [13].

<https://doi.org/10.1371/journal.pone.0251309.g003>

macroscopic (long-term) and microscopic (short-term) tooth wear analyses can be informative about dietary (biotic) and environmental (abiotic) factors [e.g. 24, 37]. Therefore, the aim of the present study was to infer the feeding ecology and environmental settings of a historical western chimpanzee population from northeastern Liberia by comparing its macroscopic and microscopic tooth wear patterns to those of a reference sample from the Tai chimpanzee population whose dietary ecology is well established. We specifically asked (1) whether both populations show similar tooth wear signals and thus share a similar feeding ecology given their geographic proximity, and (2) whether any seasonal fluctuations (dry and rainy periods) in the environment and sex-based feeding habits could be detected in the Liberian chimpanzee population. We found that both populations have distinct tooth wear patterns with Liberian chimpanzees having macroscopically slightly steeper dip angles and smaller phase II wear facet areas and microscopically flatter and less rough wear facet surface textures with a higher density of small peaks and furrows than Tai chimpanzees (see Table 1, Figs 2 and 3). This suggests a higher concentration of small internal (e.g. phytoliths) or external (e.g. dust) abrasives in the diet of the Liberian chimpanzees, at least shortly before their death [e.g. 13, 25]. Moreover, and similar to the observed sex-specific differences among Tai chimpanzees, female and male Liberian chimpanzees differ in their microscopic tooth wear patterns. However, at this point these differences need to be considered cautiously due to the limited sample size for male Liberian

Table 2. Post-hoc Tukey’s Test for the scores of factor 1 and 2 of the factor analysis comparing Liberian chimpanzees to Tai chimpanzees from dry and rainy period.

Data set	Test	Mean Difference	Lower CL*	Upper CL*	p-value
upper facet 9	Tai dry (8) vs. Liberia (36)	0.01	-1.24	1.27	1.000
	Tai wet (18) vs. Liberia (36)	-1.26	-2.19	-0.34	0.005
	Tai wet (18) vs. Tai dry (8)	-1.28	-2.64	0.09	0.071
lower facet 9	Tai dry (6) vs. Liberia (31)	-0.30	-1.74	1.13	0.865
	Tai wet (11) vs. Liberia (31)	-1.50	-2.62	-0.37	0.007
	Tai wet (11) vs. Tai dry (6)	-1.19	-2.82	0.44	0.190

*95% family-wise confidence level (CL), values in brackets indicate the sample size.

<https://doi.org/10.1371/journal.pone.0251309.t002>

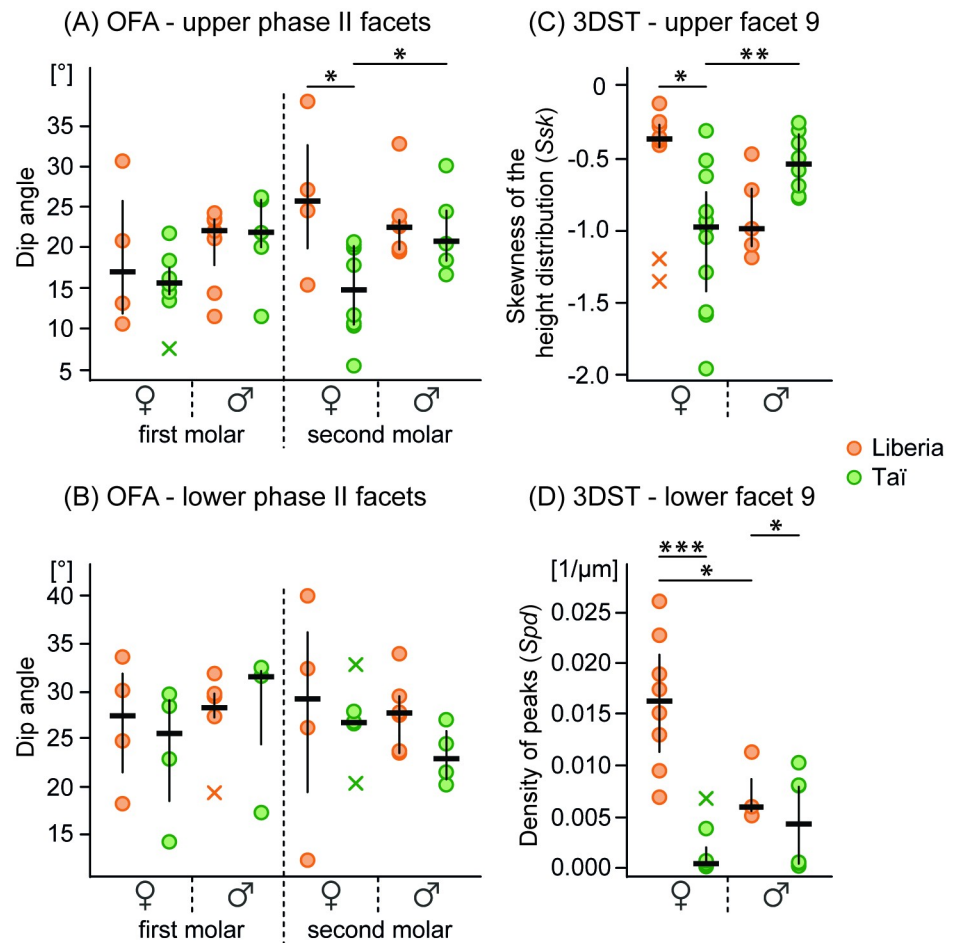


Fig 4. Variation between sexes and populations shown for phase II dip angles and selected 3DST parameters. Dip angle calculation on (A) upper and (B) lower phase II wear facets; (C) skewness of the height distribution (*Ssk*) on the upper facet 9; (D) density of peaks (*Spd*) on the lower facet 9. Strip charts indicate data median = horizontal line, interquartile range (IQR) = vertical line, and outlier ($> 1.5 \times \text{IQR}$) = x, significance levels are indicated by asterisks (* ≤ 0.05 , ** < 0.01 , *** < 0.001).

<https://doi.org/10.1371/journal.pone.0251309.g004>

chimpanzees (5 males for upper facet 9, 3 males for lower facet 9). Most interestingly, however, is the finding that the 3DST analysis groups the Liberian chimpanzees with those chimpanzees from the Taï population that knowingly died during dry periods, while they significantly differ from those Taï chimpanzees that died during rainy periods (see Table 2).

Inferring environmental abrasives and seasonality from tooth wear

The macroscopic tooth wear patterns of both populations are similar. However, there seems to be a trend towards steeper and smaller wear facets in Liberian chimpanzees compared to Taï chimpanzees, with an exception of the upper M2s where Liberian chimpanzee wear facets are significantly steeper and smaller. Since we exclusively used teeth with similar tooth wear stages (for details see Occlusal fingerprint analysis (OFA) in Materials and Methods) for the macroscopic tooth wear analyses, we do not think that the steeper and smaller phase II wear facets of Liberian chimpanzees can be explained by age differences among individuals of both populations. We rather suggest that steeper and smaller wear facets point to a lower rate of tissue loss

in the Liberian chimpanzees, probably as a cumulative result of varying dietary properties dominated by low abrasive (a)biotic particles in a long-term perspective [19]. In contrast, more planar and larger wear facets, which are related to a higher rate of tissue loss, point toward a high abrasive diet. Previous studies on the feeding ecology of chimpanzees from regions around the Nimba Mountains, which are close to the reported distribution area of the Liberian chimpanzees studied here, reported intense consumption of different species of ants [72–74], which are considered as large abrasive dietary particles causing tooth wear [e.g. 25, 75]. In contrast, the Taï chimpanzees are well-known for their use of a hammer (e.g. branches or stones) and an anvil (e.g. root, stone) to access the soft endosperm (low abrasive) of nuts without chewing on the harder nut shells (for details see Supplement 5 in [13]). These particular and detailed dietary behaviors are not reflected in our macroscopic tooth wear results. However, it needs to be considered that first our sample size is quite small for the OFA data, and second the steeper and smaller wear facets in Liberian chimpanzees compared to Taï chimpanzees are statistically non-significant (with an exception of the upper M2) and therefore can only be treated as a trend. Hence, at this stage, it is too early to draw definite conclusions from the OFA, and it needs to be investigated further.

In contrast, the microscopic tooth wear results support the findings of previous studies that the Liberian chimpanzees, as a whole population (both sexes), presumably have fed more on insects (high density of microscopically small hill- and dale-like features) when compared to the Taï population (both sexes), who focused more on the consumption of nut endosperm. The Liberian chimpanzees in our sample show microscopically smoother wear facet surfaces with a higher density of narrow features than the Taï chimpanzees (pooled data set including dry and rainy period). A high density of microscopically small hill- and dale-like features (high values for *Spd*, small values for *Sha*, *Sda*) is indicative for chewing on large and hard dietary items, such as sclerotized insect exoskeletons or seeds [25]. Large hard food items fracture tooth enamel more heavily, and therefore microscopic hill- and dale-like features tend to be smaller since it is unlikely that large ones persist [25].

In addition to the inferences about the feeding preferences of Liberian chimpanzees, we found that the Liberian chimpanzees, with their many small and narrow microscopic wear features, cluster in the Factor Analysis (FA) with the Taï chimpanzees that died during dry periods (see Fig 3) (for details on the 3DST results of the Taï chimpanzees see [13]). Some of the former even have higher values on factor 2 than any of the Taï chimpanzees, implying that these Liberian individuals have the smallest and narrowest microscopic wear features of the whole data set. The habitats of both chimpanzee populations are characterized by a yearly occurring major dry period, approximately lasting from December until February [1, 41]. This dry period is accompanied by a dust-laden trade wind, the Harmattan, blowing from the Sahara Desert over West Africa into the Gulf of Guinea [43]. In fact, we know that the Harmattan reaches the Taï National Park for up to two weeks in this particular dry period, and that the forest is covered with dust particles until they are washed down by the rain at the beginning of the rainy period [1]. Despite the fact that the Liberian chimpanzees cluster with the majority of the Taï chimpanzees from Harmattan dry periods while differing from most of the Taï chimpanzees from rainy periods, both Taï chimpanzees from dry and rainy periods show some overlap in the FA, which may be accounted for as follows: Firstly, some of the Taï chimpanzee specimens died at the very beginning or end of a dry and/or rainy period. Even though the 3DST parameters reveal short-term tooth wear signals, the accumulation of new wear signals may take several days or a few weeks depending on the dietary particles [34–36]. For example, an individual that died at the beginning of the rainy period may still show microscopic wear features related to the prior period, the Harmattan dry period. Secondly, the overlap of Taï chimpanzees from dry and rainy periods might be explained by the fact that the

exact arrival of the Harmattan wind in the Taï forest, which we assume as one of the major causes of the microscopic wear signals, might have varied between years (e.g. few days to one week earlier or later). Due to the lack of information of the exact arrival and duration of the Harmattan wind in each year, we used all months of the dry period (December to February) [1] and assigned them to the Harmattan dry period in our analyses.

Despite the overlap of the Taï chimpanzees from the Harmattan dry period with those from the rainy period, the former show more complex 3DSTs with a higher density of furrows compared to those Taï chimpanzees that died during the rainy period. The same applies for the Liberian chimpanzees. This is in accordance with previous studies that showed that the ingestion of abrasive components (e.g. dust) creates complex microscopic tooth wear signals with many and fine furrows and dales [13, 76]. Additionally, tooth wear and fecal particle sizes in Taï chimpanzees showed that during the dry period dust particles are consumed with the food and that their presence is reflected by a specific 3DST pattern on their molars [13]. Based on the similarities in the microscopic tooth wear of the Liberian chimpanzees and Taï chimpanzees that died during Harmattan dry periods as well as the fact that the Harmattan wind has also been present in Liberia at least since the early 20th century [77] it is highly conceivable that the Liberian chimpanzees died during such a Harmattan dry period. The chimpanzees in northeastern Liberia were reported to be under intense human predation [78]. Historical accounts from the 1950s indicate that the Liberian specimens used in this study were poached and butchered by local tribes of farmers, called Dan and Kran, and the skulls were kept as trophies [46, 47]. Even nowadays, hunting for bush meat in Nimba County (Liberia) is still a common activity by local groups; 91% of the people hunt year-round, in dry and rainy periods, but 80% of those people reported to increase their hunting activity intensively during dry periods [79]. This, in turn, is in line with our interpretation that the chimpanzees studied here most likely perished during an annual dry period, which might have accompanied by the dust-laden Harmattan trade wind. However, additional historical or cultural evidence from that time period is needed to reinforce our suggestion.

Sex-specific feeding ecology in Liberian chimpanzees

It has been widely known that chimpanzees show sex-specific feeding preferences [e.g. 1, 16, 80–82]. The macroscopic tooth wear results suggest that female chimpanzees tend to engage in a different chewing behavior than males. This is more obvious in female Taï chimpanzees where more planar and less inclined phase II wear facet surfaces are indicative of vertical chewing movements. Such chewing kinematics are thought to be required when dietary items need to be crushed (e.g. hard exoskeletons of insects, seeds) [83]. This tooth wear pattern is more pronounced on the upper second molars of Taï chimpanzees where females have significantly smaller phase II dip angles than Taï males. However, the trend for less inclined phase II wear facets in Taï females compared to males is also seen on the other molars (see Table 1). Large and less inclined phase II wear facets of Taï females indicate a high degree of repetitive vertical crushing combined with horizontal grinding activity. This could be related to an intense comminution of items like insects with hard exoskeletons and seeds embedded in fruit pulp (< 1.2 cm), on a regular basis [13].

Recently, Schulz-Kornas et al. [13] showed for the Taï chimpanzee population that female/male-specific dietary differences are reflected in the 3DST pattern. It was found that both sexes within the Taï population consume mainly fruit pulp without any hard seeds, but they differ in their feeding time on other dietary items. Females who consume more fruit pulp including large amounts of small seeds, leaves and insects have microscopically flatter and less voluminous wear facet surfaces with many micrometer-sized plateau-like features [13]. In contrast,

males who feed more extensively on large seeds, vertebrate meat, and in contrast to other observations [1, 15], on a larger amount on nut endosperms, have wear facet surfaces dominated by larger dales and less plateaus [13]. However, for the comparison with our data it needs to be considered that the dietary observations of Taï male chimpanzees arise mainly from the Harmattan dry period, which may mean that the dietary and dust signal in their 3DST is mixed [13].

Our results show that Liberian females and males differ to some extent in their 3DSTs, but in a different way, than has been described for Taï females and males. Liberian females have significantly more microscopic peaks and smaller hill and dale areas as well as slightly rougher wear facet surfaces than the Liberian males, although both Liberian females and males have more peaks than Taï chimpanzees of both sexes (see Fig 4D, S6 Table). Since chewing on large and hard dietary items such as sclerotized insect exoskeletons can produce rougher wear facet surfaces and many of the microscopically small hill-like features [25], we conclude that Liberian females consumed more insects than Liberian males. This is in agreement with Smith et al. [80] who analyzed carbon signatures of the Ganta chimpanzees from northern Nimba County (Liberia). This analysis suggested a higher insect consumption in female chimpanzees and a higher meat consumption in male chimpanzees. Although the Taï females are also known to consume more insects than males [13]; the former may have consumed less insects and more softer dietary items (e.g. nut endosperm, fruit pulp) when compared to the Liberian females. Therefore, the 3DST results suggest that both populations have different feeding ecologies, at least on a short-term basis, and that this is mainly driven by the female chimpanzees of each group.

Conclusions

In our chimpanzee example, the macroscopic tooth wear data (OFA) suggest a similar dietary ecology between both populations on a long-term basis. In contrast, microscopic tooth wear signals (3DST) were able to detect inferences about the season of death of the Liberian chimpanzees by using the Taï chimpanzee population as a reference data set. Furthermore, the 3DST results are robust in pointing out differences between the feeding habits of females and males and between populations, since it represents a direct signal of what the individuals consumed shortly before their death.

Our results therefore highlight that a combination of long-term and short-term dental wear analyses opens new options for uncovering details of ecological and dietary behaviors of chimpanzees, but also of other primates and other animal groups. Working on both scales should therefore be considered in future studies since it allows tracing changes in the long- and short-term dietary and environmental history of a single population.

Supporting information

S1 Text. Additional information about the conducted factor analysis and the R script. (PDF)

S1 Table. Specimens sampled for occlusal fingerprint analysis (OFA) and 3D surface texture (3DST) analysis. Wear facet 9 (for 3DST analysis) and phase II wear facets (for OFA) on deciduous fourth premolars (dp4), permanent first (M1) and second (M2) molars of the upper (U) and lower (L) jaw were sampled. (n.a.) no information is available. Taï chimpanzee data including their 3DST data are taken from Schulz-Kornas et al. [13] and Stuhlträger et al. [14].^a Taï chimpanzee project unpublished data. (XLSX)

S2 Table. Description of the 3D surface texture parameters (3DST) that were selected for this study.

(XLSX)

S3 Table. Descriptive and test statistics of significant 3D surface texture (3DST) parameters on facet 9 between Liberian and Tai chimpanzees. To test the level of significance a combination of the robust Welch–Yuen heteroscedastic omnibus test (WYT), heteroscedastic pairwise comparison test (Dunnett), heteroscedastic rank based test (Cliff) were used. Following Calandra et al. [25] values in bold indicate a significant differences ($p \leq p_c \leq 0.05$), no significant difference was detected in case of $p > 0.05$ and $p \geq p_c$. U = upper teeth, L = lower teeth, M1 = first molar, M2 = second molar, dp4 = fourth deciduous premolar, N = number of individuals, SD = standard deviation, Ft / ph = test statistics, p = level of significance, nu1 / nu2 / Df = degree of freedom, pl = lower 95% confidence interval, pu = upper 95% confidence interval, pc = critical significance level adjusted for family-wise error.

(XLSX)

S4 Table. Loadings of the factor analysis for the comparison of the Liberian and Tai chimpanzees from dry and rainy periods given for each 3DST parameter and factors with eigenvalues >1. First or second molars of 67 (upper facet 9) and 52 (lower facet 9) individuals were used for the factor analysis, respectively. Values in bold indicate interpretable loadings (≥ 0.7) [70].

(XLSX)

S5 Table. Test statistics for 3D surface texture (3DST) comparisons given for significant parameters and sorted according to data set. Following Calandra et al. [25] values in bold indicate a significant differences ($p \leq p_{crit} \leq 0.05$), no significant difference was detected in case of $p \geq p_c$. N = number of individuals, UM = upper molars, LM = lower molars, f = facet, Ft / ph = test statistics, p = level of significance, nu1 / nu2 / Df = degree of freedom, pl = lower 95% confidence interval, pu = upper 95% confidence interval, pc = critical significance level adjusted for family-wise error.

(XLSX)

S6 Table. Descriptive statistics for 3D surface texture parameters (3DST) of female and male Liberian chimpanzees. N = number of individuals, SD = standard deviation.

(XLSX)

Acknowledgments

We thank the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique and the Ministère des Eaux et Forêts in Côte d'Ivoire, and the Office Ivoirien des Parcs et Réserves for permitting the research at the Tai Chimpanzee Project. We are grateful to the staff of the Centre Suisse de Recherches Scientifiques en Côte d'Ivoire and the Tai Chimpanzee Project for their support.

We are indebted to Uta Olbrich-Schwarz (MPI-EVA, Leipzig, Germany), Christine Hemm and Janina Franz (Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany), and Matthias Krüger (Phyletic Museum Jena, Germany) for technical assistance in the osteological collections and 3D-surface scanning, as well as Adam van Casteren (MPI-EVA, Leipzig, Germany) for constructive comments and correction of English language.

Author Contributions

Conceptualization: Julia Stuhlträger, Ellen Schulz-Kornas, Ottmar Kullmer, Kornelius Kupczik.

Data curation: Julia Stuhlträger, Ellen Schulz-Kornas, Ottmar Kullmer.

Formal analysis: Julia Stuhlträger, Ellen Schulz-Kornas, Marcel M. Janocha.

Funding acquisition: Kornelius Kupczik.

Investigation: Julia Stuhlträger, Ellen Schulz-Kornas, Ottmar Kullmer, Marcel M. Janocha.

Methodology: Julia Stuhlträger, Ellen Schulz-Kornas, Ottmar Kullmer, Marcel M. Janocha.

Resources: Ellen Schulz-Kornas, Ottmar Kullmer, Roman M. Wittig, Kornelius Kupczik.

Supervision: Ellen Schulz-Kornas, Kornelius Kupczik.

Visualization: Julia Stuhlträger, Ellen Schulz-Kornas, Ottmar Kullmer, Marcel M. Janocha.

Writing – original draft: Julia Stuhlträger.

Writing – review & editing: Julia Stuhlträger, Ellen Schulz-Kornas, Ottmar Kullmer, Marcel M. Janocha, Roman M. Wittig, Kornelius Kupczik.

References

1. Boesch C, Boesch-Achermann H. The chimpanzees of the Taï forest: behavioural ecology and evolution. Oxford: Oxford University Press; 2000.
2. Tutin CEG, Fernandez M. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé reserve, Gabon. *Am J Primatol.* 1993; 30(3):195–211. <https://doi.org/10.1002/ajp.1350300305> PMID: 31937009
3. Pruett JD. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Feeding ecology in apes and other primates. Cambridge University Press; 2006. p. 161–82.
4. N'guessan AK, Ortmann S, Boesch C. Daily Energy Balance and Protein Gain Among *Pan troglodytes verus* in the Taï National Park, Côte d'Ivoire. *Int J Primatol.* 2009; 30(3):481–96. <https://doi.org/10.1007/s10764-009-9354-1>
5. McGrew WC, Baldwin PJ, Tutin CEG. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *Am J Primatol.* 1988; 16(3):213–26. <https://doi.org/10.1002/ajp.1350160304> PMID: 31968861
6. Doran D. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. *Int J Primatol.* 1997; 18(2):183–206.
7. Yamakoshi G. Dietary Responses to Fruit Scarcity of Wild Chimpanzees at Bossou, Guinea: Possible Implications for Ecological Importance of Tool Use. *Am J Phys Anthropol.* 1998; 106(3):283–95. [https://doi.org/10.1002/\(SICI\)1096-8644\(199807\)106:3<283::AID-AJPA2>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O) PMID: 9696145
8. Bogart SL, Pruett JD. Insectivory of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. *Am J Phys Anthropol.* 2011; 145(1):11–20. <https://doi.org/10.1002/ajpa.21452> PMID: 21484757
9. Morgan D, Sanz C. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press; 2006. p. 97–122.
10. Tutin CEG, Ham RM, White LJT, Harrison MJS. The primate community of the Lopé reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. *Am J Primatol.* 1997; 42(1):1–24. [https://doi.org/10.1002/\(SICI\)1098-2345\(1997\)42:1<1::AID-AJP1>3.0.CO;2-0](https://doi.org/10.1002/(SICI)1098-2345(1997)42:1<1::AID-AJP1>3.0.CO;2-0) PMID: 9108968
11. Tutin CEG, Fernandez M, Rogers ME, Williamson EA, McGrew WC. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philos Trans R Soc London Ser B Biol Sci.* 1991; 334(1270):179–86. <https://doi.org/10.1098/rstb.1991.0107> PMID: 1685576
12. Goné Bi ZB, Wittig R. Long-term diet of the chimpanzees (*Pan troglodytes verus*) in Taï National Park: interannual variations in consumption. In: The Chimpanzees of the Taï Forest. Cambridge University Press; 2019. p. 242–60.

13. Schulz-Kornas E, Stuhlträger J, Clauss M, Wittig RM, Kupczik K. Dust affects chewing efficiency and tooth wear in forest dwelling Western chimpanzees (*Pan troglodytes verus*). *Am J Phys Anthropol*. 2019; <https://doi.org/10.1002/ajpa.23808> PMID: 30821351
14. Stuhlträger J, Schulz-Kornas E, Wittig RM, Kupczik K. Ontogenetic Dietary Shifts and Microscopic Tooth Wear in Western Chimpanzees. *Front Ecol Evol*. 2019; 7:298. <https://doi.org/10.3389/fevo.2019.00298>
15. Boesch C, Boesch H. Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. *J Hum Evol*. 1981; 10(7):585–93. [https://doi.org/10.1016/S0047-2484\(81\)80049-8](https://doi.org/10.1016/S0047-2484(81)80049-8)
16. Boesch C, Boesch H. Tool Use and Tool Making in Wild Chimpanzees. *Folia Primatol*. 1990; 54(1–2):86–99. <https://doi.org/10.1159/000156428> PMID: 2157651
17. Walker A, Hoek H, Perez L. Microwear of mammalian teeth as an indicator of diet. *Science* (80-). 1978; 201(4359):908–10. <https://doi.org/10.1126/science.684415> PMID: 684415
18. Galbany J, Twahirwa JC, Baiges-Sotos L, Kane EE, Tuyisingize D, Kaleme P, et al. Dental macrowear in catarrhine primates: Variability across species. In: *Dental Wear in Evolutionary and Biocultural Contexts*. Elsevier; 2020. p. 11–37.
19. Martin LF, Krause L, Ulbricht A, Winkler DE, Codron D, Kaiser TM, et al. Dental wear at macro- and microscopic scale in rabbits fed diets of different abrasiveness: A pilot investigation. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2020;109886. <https://doi.org/10.1016/j.palaeo.2020.109886>
20. Lucas PW, van Casteren A, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, et al. The Role of Dust, Grit and Phytoliths in Tooth Wear. *Ann Zool Fennici*. 2014; 51(1–2):143–52. <https://doi.org/10.5735/086.051.0215>
21. Teaford MF, Runestad JA. Dental microwear and diet in Venezuelan primates. *Am J Phys Anthropol*. 1992; 88(3):347–64. <https://doi.org/10.1002/ajpa.1330880308> PMID: 1642321
22. Scott RS, Ungar PS, Bergstrom TS, Brown CA, Grine FE, Teaford MF, et al. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature*. 2005; 436(7051):693–5. <https://doi.org/10.1038/nature03822> PMID: 16079844
23. Kullmer O, Benazzi S, Fiorenza L, Schulz D, Bacso S, Winzen O. Technical note: Occlusal fingerprint analysis: Quantification of tooth wear pattern. *Am J Phys Anthropol*. 2009; 139(4):600–5. <https://doi.org/10.1002/ajpa.21086> PMID: 19425091
24. Fiorenza L, Benazzi S, Tausch J, Kullmer O, Bromage TG, Schrenk F. Molar Macrowear Reveals Neanderthal Eco-Geographic Dietary Variation. Rosenberg K, editor. *One PLoS*. 2011; 6(3):e14769. <https://doi.org/10.1371/journal.pone.0014769> PMID: 21445243
25. Calandra I, Schulz E, Pinnow M, Krohn S, Kaiser TM. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. *J Hum Evol*. 2012; 63(1):85–98. <https://doi.org/10.1016/j.jhevol.2012.05.001> PMID: 22705031
26. Lucas PW, Omar R, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, et al. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *J R Soc Interface*. 2013; 10(80):20120923–20120923. <https://doi.org/10.1098/rsif.2012.0923> PMID: 23303220
27. Kullmer O, Schulz D, Benazzi S. An Experimental Approach to Evaluate the Correspondence Between Wear Facet Position and Occlusal Movements. *Anat Rec Adv Integr Anat Evol Biol*. 2012; 295(5):846–52. <https://doi.org/10.1002/ar.22440> PMID: 22419654
28. Fiorenza L, Benazzi S, Kullmer O. Para-masticatory wear facets and their functional significance in hunter-gatherer maxillary molars. *J Archaeol Sci*. 2011; 38(9):2182–9. <https://doi.org/10.1016/j.jas.2011.03.012>
29. Kay RF, Hliemae KM. Jaw movement and tooth use in recent and fossil primates. *Am J Phys Anthropol*. 1974; 40(2):227–56. <https://doi.org/10.1002/ajpa.1330400210> PMID: 4815136
30. Ackermans NL, Winkler DE, Schulz-Kornas E, Kaiser TM, Müller DWH, Kircher PR, et al. Controlled feeding experiments with diets of different abrasiveness reveal slow development of mesowear signal in goats (*Capra aegagrus hircus*). *J Exp Biol*. 2018; 221(21). <https://doi.org/10.1242/jeb.186411> PMID: 30194251
31. Wood B, Schroer K. Reconstructing the Diet of an Extinct Hominin Taxon: The Role of Extant Primate Models. *Int J Primatol*. 2012; 33(3):716–42. <https://doi.org/10.1007/s10764-012-9602-7>
32. Fiorenza L, Benazzi S, Henry AG, Salazar-García DC, Blasco R, Picin A, et al. To meat or not to meat? New perspectives on neanderthal ecology. *Am J Phys Anthropol*. 2015; 156(S59):43–71. <https://doi.org/10.1002/ajpa.22659> PMID: 25407444
33. Schulz E, Calandra I, Kaiser TM. Applying tribology to teeth of hoofed mammals. *Scanning*. 2010; 32(4):162–82. <https://doi.org/10.1002/sca.20181> PMID: 20949615
34. Teaford MF, Oyen OJ. In vivo and in vitro turnover in dental microwear. *Am J Phys Anthropol*. 1989; 80(4):447–60. <https://doi.org/10.1002/ajpa.1330800405> PMID: 2513725

35. Teaford MF, Ungar PS, Taylor AB, Ross CF, Vinyard CJ. In vivo rates of dental microwear formation in laboratory primates fed different food items. *Biosurface and Biotribology*. 2017; 3(4):166–73. <https://doi.org/10.1016/j.bsbt.2017.11.005>
36. Grine FE. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J Hum Evol*. 1986; 15(8):783–822. [https://doi.org/10.1016/S0047-2484\(86\)80010-0](https://doi.org/10.1016/S0047-2484(86)80010-0)
37. El Zaatari S, Grine FE, Ungar PS, Hublin J-J. Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis. *J Hum Evol*. 2011; 61(4):411–24. <https://doi.org/10.1016/j.jhevol.2011.05.004> PMID: 21719068
38. Schulz-Kornas E, Winkler DE, Clauss M, Carlsson J, Ackermans NL, Martin LF, et al. Everything matters: Molar microwear texture in goats (*Capra aegagrus hircus*) fed diets of different abrasiveness. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2020; 552:109783.
39. Winkler DE, Tütken T, Schulz-Kornas E, Kaiser TM, Müller J, Leichter J, et al. Shape, size, and quantity of ingested external abrasives influence dental microwear texture formation in guinea pigs. *Proc Natl Acad Sci*. 2020. <https://doi.org/10.1073/pnas.2008149117> PMID: 32839331
40. Steentoft M. Flowering plants in west Africa. Cambridge University Press; 1988.
41. Climatic Research Unit of University of East Anglia. No Title [Internet]. 2018.
42. Voorhoeve AG. Liberian high forest trees. Centre for Agricultural Publications and Documentation, Wageningen; 1965.
43. Stoorvogel JJ, Van Breemen N, Jassen BH. The nutrient input by Harmattan dust to a forest ecosystem in Cote d'Ivoire, Africa. *Biogeochemistry*. 1997; 37(2):145–57.
44. Adhvaryu A, Bharadwaj P, Fenske J, Nyshadham A, Stanley R. Dust and Death: Evidence from the West African Harmattan. Centre for the Study of African Economies, University of Oxford. 2016.
45. Lesschen JP, Stoorvogel JJ, Smaling EMA, Heuvelink GBM, Veldkamp A. A spatially explicit methodology to quantify soil nutrient balances and their uncertainties at the national level. *Nutr Cycl Agroecosystems*. 2007; 78(2):111–31. <https://doi.org/10.1007/s10705-006-9078-y>
46. Protsch von Zieten RR, Eckhardt RB. The Frankfurt Pan *trogodytes verus* collection: description and research agenda. *Lab Primate Newsl*. 1988; 27:13–5.
47. Himmelheber H, Himmelheber U. Die Dan: Ein Bauernvolk im westafrikanischen Urwald. W. Kohlhammer Verlag; 1958.
48. Dierbach A. Intraspecific variability and sexual dimorphism in the skulls of *Pan troglodytes verus*. *Hum Evol*. 1986; 1(1):41–50. <https://doi.org/10.1007/BF02437284>
49. Wittig RM. Tai Chimpanzees. In: *Encyclopedia of Animal Cognition and Behavior*. Cham: Springer International Publishing; 2018. p. 1–7.
50. Setvat E, Patnrel JE, Lubes H, Kouatme B, Ouedraogo M, Maason JM. Climatic variability in humid Africa along the Gulf of Guinea Part I: detailed analysis of the phenomenon in Cote d'Ivoire. *J Hydrol*. 1997; 191(1–4):1–15.
51. Kullmer O, Menz U, Fiorenza L. Occlusal Fingerprint Analysis (OFA) reveals dental occlusal behavior in primate molars. Martin T Koenigswald W v(eds) *Mamm Teeth—Form Funct Pfeil*, Munich. 2020;25–43.
52. Maier W, Schneck G. Konstruktionsmorphologische Untersuchungen am Gebiß der hominoiden Primaten. *Z Morphol Anthropol*. 1981; 72(2):127–69. PMID: 7314796
53. Grine FE. Trophic differences between “gracile” and “robust” Australopithecines: A scanning electron microscope analysis of occlusal events. *S Afr J Sci*. 1981; 77(5):203–30.
54. Smith BH. Patterns of molar wear in hunter-gatherers and agriculturalists. *Am J Phys Anthropol*. 1984; 63(1):39–56. <https://doi.org/10.1002/ajpa.1330630107> PMID: 6422767
55. Fiorenza L, Benazzi S, Kullmer O. Do it yourself: Morphology, wear and 3D digital surface models: Materials and techniques to create high-resolution replicas of teeth. *J Anthropol Sci*. 2009; 87:211–8.
56. Ulhaas L, Kullmer O, Schrenk F. Tooth wear and diversity in early hominid molars: A case study. In: *Tetrapod Paleobiology and Paleoanthropology*. Springer; 2007. p. 369–90.
57. Fiorenza L, Benazzi S, Tausch J, Kullmer O, Schrenk F. Brief communication: Identification reassessment of the isolated tooth Krapina D58 through occlusal fingerprint analysis. *Am J Phys Anthropol*. 2010; 143(2):306–12. <https://doi.org/10.1002/ajpa.21311> PMID: 20853483
58. Schulz E, Calandra I, Kaiser TM. Feeding ecology and chewing mechanics in hoofed mammals: 3D tribology of enamel wear. *Wear*. 2013; 300(1–2):169–79. <https://doi.org/10.1016/j.wear.2013.01.115>
59. International Organization for Standardization. ISO 25178–2—Geometrical product specifications (GPS)—Surface texture: Areal—Part 2: Terms, definitions and surface texture parameters. ISO. 2012;

60. International Organization for Standardization. ISO 12781–1—Geometrical product specifications (GPS)—Flatness—Part 1: Vocabulary and parameters of flatness. ISO. 2011;
61. Fisher NI. Statistical analysis of circular data. Cambridge University Press; 1995. 277 p.
62. Batschelet E. Circular statistics in biology (Mathematics in biology) [Internet]. Academic Press; 1981. 372 p.
63. Mardia K V, Jupp PE. Statistics of directional data. 2. Edition. John Wiley & Sons, Ltd; 2000. 429 p.
64. Zar JH. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey. 1999. 663 p.
65. R Development Core Team. A language and environment for statistical computing. R Foundation for Statistical Computing [Internet]. 2017.
66. Dragulescu AA. xlsx: Read, write, format Excel 2007 and Excel 97. R package version 042. 2012.
67. Højsgaard S, Halekoh U, Robinson-Cox J, Wright K, Leidi A. doBy: Groupwise summary statistics, general linear contrasts, population means (least-square-means), and other utilities. R package version 4.5–3. 2012.
68. Bengtsson H. R. utils: Various programming utilities. R package, version 2.4. 0. 2015.
69. Calandra I. Tribology of dental enamel facets of Ungulates and Primates (Mammalia): Tracing tooth-food interaction through 3D enamel microtexture analyses. 2012;
70. Budaev S V. Using Principal Components and Factor Analysis in Animal Behaviour Research: Caveats and Guidelines. *Ethology*. 2010; 116(5):472–80. <https://doi.org/10.1111/j.1439-0310.2010.01758.x>
71. Chajewski M. rela: Scale item analysis. Vol. 4, R package version. 2009.
72. Humle T. Culture and variation in wild chimpanzee behaviour: a study of three communities in West Africa [Internet]. University of Stirling; 2003.
73. Humle T, Matsuzawa T. Behavioural Diversity among the Wild Chimpanzee Populations of Bossou and Neighbouring Areas, Guinea and Côte d'Ivoire, West Africa. *Folia Primatol*. 2001; 72(2):57–68. <https://doi.org/10.1159/000049924> PMID: 11490130
74. Humle T, Matsuzawa T. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am J Primatol*. 2002; 58(3):133–48. <https://doi.org/10.1002/ajp.10055> PMID: 12454957
75. Strait SG. Molar microwear in extant small-bodied faunivorous mammals: An analysis of feature density and pit frequency. *Am J Phys Anthropol*. 1993; 92(1):63–79. <https://doi.org/10.1002/ajpa.1330920106> PMID: 8238292
76. Kaiser TM, Clauss M, Schulz-Kornas E. A set of hypotheses on tribology of mammalian herbivore teeth. *Surf Topogr Metrol Prop*. 2015; 4(1):14003.
77. Ross E. The Climate of Liberia and Its Effect on Man. *Geogr Rev*. 1919; 7(6):387.
78. Eckhardt RB, von Zieten RP. Enamel hypoplasias as indicators of developmental stress in pongids and hominids. *Hum Evol*. 1993; 8(2):93–9. <https://doi.org/10.1007/BF02436608>
79. Bene J-CK, Gamys J, Dufour S. The hunting practice in northern Nimba County, Liberia. *Glob Adv Res J Environ Sci Toxicol*. 2013; 2(1):22–36.
80. Smith CC, Morgan ME, Pilbeam D. Isotopic ecology and dietary profiles of Liberian chimpanzees. *J Hum Evol*. 2010; 58(1):43–55. <https://doi.org/10.1016/j.jhevol.2009.08.001> PMID: 19796791
81. Fahy GE, Richards M, Riedel J, Hublin J-J, Boesch C. Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees. *Proc Natl Acad Sci*. 2013; 110(15):5829–33. <https://doi.org/10.1073/pnas.1221991110> PMID: 23530185
82. Lonsdorf E V. Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Anim Behav*. 2005; 70(3):673–83. <https://doi.org/10.1016/j.anbehav.2004.12.014>
83. Spears IR, Crompton RH. The mechanical significance of the occlusal geometry of great ape molars in food breakdown. *J Hum Evol*. 1996; 31(6):517–35. <https://doi.org/10.1006/jhev.1996.0077>