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RESEARCH ARTICLE

Dust affects chewing efficiency and tooth wear in forest dwelling Western chimpanzees (*Pan troglodytes verus*)

Ellen Schulz-Kornas[1] | Julia Stuhlträger[1] | Marcus Clauss[2] | Roman M. Wittig[3,4] | Kornelius Kupczik[1]

[1]Max Planck Institute for Evolutionary Anthropology, Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Leipzig, Germany
[2]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zuerich, Zürich, Switzerland
[3]Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[4]Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, Abidjan, Côte d'Ivoire

Correspondence
Ellen Schulz-Kornas, Max Planck Institute for Evolutionary Anthropology, Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Leipzig, Germany.
Email: ellen_schulz@eva.mpg.de

Abstract

Objectives: In humans it has been shown that abrasive particles in the diet result in increased tooth wear and less intense chewing behavior, both of which decrease chewing efficiency. This behavioral response may also exist in non-human primates as a means to reduce the wear effect of dust-laden food. Here we tested whether the periodical occurrence of abrasive dust particles in the diet of Western chimpanzees affects tooth wear and reduces chewing efficiency.

Materials and methods: We measured fecal particle size of undigested food matter as an indicator of chewing efficiency in 13 Western chimpanzees of the Taï National Park (Ivory Coast) before (wet), after (wet) and during a dust-rich (dry) period. Moreover, feeding data were compiled for a further 12 chimpanzees and matched to three-dimensional surface texture data measured on two molar facets of 26 skulls of the same population.

Results: Fecal particles were larger during the dry period, indicating a reduced chewing efficiency compared to wet periods; age and sex did not have an effect. Concomitantly, dust led to an increase of abrasive wear evidenced by smaller texture features and higher density of fine furrows on wear facets.

Discussion: Our findings show that a periodical increase in dust loads on foods places a dietary-physiological stress on the digestive system in chimpanzees. We suggest that the impact of extrinsic abrasive particles from globally acting periodical dust-laden winds may affect evolutionary fitness. Further studies are required to elucidate this relationship in other non-human primates and fossil hominins.

KEYWORDS
abrasive particles, fecal particle size, mastication, Taï, texture

1 | INTRODUCTION

In herbivorous mammals such as primates, chewing efficiency is defined as the rate at which a defined amount of food is reduced to a certain mean ingesta particle size (Boesch & Boesch-Achermann, 2000; N'guessan, Ortmann, & Boesch, 2009; Perez-Barberia & Gordon, 1998). Chewing efficiency is one determinant of energy acquisition; it is influenced by the material properties of food (Dominy, Vogel, Yeakel, Constantino, & Lucas, 2008; Lucas, 2004), oral anatomy (Bates, Stafford, & Harrison, 1976; Kay, 1975), number, direction and intensity of masticatory movements (Hiiemae, 1978) as well as the force applied during chewing (Carlsson, 1973). Fecal particle size (FPS) has been used as a proxy for ingesta particle size reduction and thus chewing efficiency in placental (Clauss et al., 2015; Fritz et al., 2009; Steuer et al., 2010) and marsupial mammals (Lanyon & Sanson, 1986, 2002). There are various adaptive responses to offset the effects of reduced chewing efficiency (Perez-Barberia & Gordon, 1998). In primates, Dunbar and Bose (1991) found that baboons (*Papio anubis*) did not achieve the fine FPS as geladas (*Theropithecus gelada*). Also in geladas, Venkatamaran et al. (2014) observed that older individuals had larger FPS indicating lower chewing efficiency than younger individuals, particularly during the dry season. Moreover, Weary, Wrangham, and Clauss (2017) found an effect of seasonality (dry vs. wet), though not of age, on FPS in frugivorous Eastern chimpanzees (*Pan troglodytes schweinfurthii*). These authors hypothesized that the mainly frugivorous diet may be mechanically less challenging compared to the more folivorous diet of geladas. Likewise, Milette, Sauther, Cuozzo, and Ness (2012) suggested for ring-tailed lemurs (*Lemur catta*) that fruits are easier to process and digest than leaves, and Thiry et al. (2018) found that proboscis monkeys (*Nasalis larvatus*) had smaller FPS during the wet season when their feces contained higher amounts of seeds, indicating frugivory.

Food processing generates considerable mechanical stress on teeth and thus modifies the occlusal surface during an individual's life, leading to so-called wear facets. These facets develop during mastication either as the result of tooth-tooth contacts (attrition) or through tooth-substrate-tooth contacts (abrasion; for a review of terminology see Schultz et al. (2017)). Abrasives that are intrinsic to the food (e.g., phytoliths) and those that are extrinsic (e.g., grit, dust) have both been discussed as causes for tooth wear (Calandra, Schulz, Pinnow, Krohn, & Kaiser, 2012; Lucas et al., 2013, 2014; Massey, Ennos, & Hartley, 2006; Sanson, Kerr, & Gross, 2007).

The diet of chimpanzees includes a variety of foods which include different amounts of intrinsic abrasive particles. Chimpanzees consume a large proportion of ripe fruit, but often also ingest the potentially abrasive seeds at the same time (Boesch & Boesch-Achermann, 2000; Fahy, Richards, Riedel, Hublin, & Boesch, 2013; N'guessan et al., 2009). In addition, they forage on considerable amounts of foliage and to a lesser degree on animal matter such as vertebrate meat and insects (Boesch & Boesch-Achermann, 2000; N'guessan et al., 2009). Moreover, some populations of chimpanzees (e.g., *P. t. verus* in the Taï forest National Park, Ivory Coast) are known for tool-using behavior and nut-cracking during the dry period, mainly on *Coula* and *Parinari* (Boesch & Boesch, 1981; Boesch & Boesch-Achermann, 2000; Doran, 1997). Some authors consider such food items (fruits, seeds, and nuts) as abrasive hard food items inducing microscopic wear features in the form of pit-like damage on the surface of the facet (Percher et al., 2017; Scott et al., 2009). Also, sclerotized insect cuticles may result in micro-pitting on the tooth surface (Strait, 2014).

In addition to the intrinsic abrasives, wind-borne dust particles such as fine sand, silt and clay (see Enete, Obienusi, Igu, and Ayadiulo (2012); Stoorvogel, Van Breemen, and Jassen (1997)), which adhere to plant surfaces in high quantities during dry seasons, may contribute to wear (Lucas et al., 2014; Ungar, Teaford, Glander, & Pastor, 1995). While the presence of volcanic ash dust does only significantly affects premolar but not molar wear rates among populations of howling monkeys (*Alouatta palliata*; Spradley, Glander, & Kay, 2016), in humans it has been observed that extrinsic abrasive particles result in less intense chewing with a lower frequency and less mixing of the bolus (Prinz, 2004). The latter author concluded that there is a trade-off between short-term reductions in chewing efficiency against the deleterious long-term effects of the loss of tooth substance. Such a behavioral response to extrinsic abrasive particles in the diet may also exist in other non-human primates such as chimpanzees, but this remains to be investigated. In a broader evolutionary perspective, such a behavioral response may have important adaptive consequences like maintaining fitness by minimizing tooth wear (King et al., 2005).

Here we investigated to what extent extrinsic abrasives from periodically occurring dust loads, and intrinsic abrasives from food particles impacted chewing efficiency and microscopic tooth wear in Western chimpanzees (*Pan troglodytes verus*) of the Taï National Park (Ivory Coast). To this end we made use of fecal samples from living individuals collected during dry and wet periods as well as macerated craniodental material from deceased individuals from the same population. This skeletal material has been collected continuously in the wild since 1984 (Boesch & Boesch-Achermann, 2000). The Taï chimpanzee population is exposed to a high amount of dust accumulating on plant foods once a year. The eolian dust is transmitted by a dry northeasterly surface wind (called the Harmattan) blowing from the Sahara Desert over West Africa into the Gulf of Guinea between December and February (Stoorvogel et al., 1997) following a distinct seasonal cycle (Engelstaedter & Washington, 2007). This dust-laden Harmattan wind reaches the region of the Taï National Park usually for a few weeks in January (Wittig, 2018) yielding a dust deposition of ~60–100 kg/ha in the canopy of the Taï forest ecosystem (Stoorvogel et al., 1997). Eolian sands are fine to medium, non-plastic and uniformly graded materials present in many sandy sites, mainly in desert areas (Elipe & Lopez-Querol, 2014). In general, the eolian dust carried by the Harmattan has particle sizes typical of fine sand (50–125 μm), silt (2–50 μm), and clay (below 2 μm), with the majority of the fraction (69%) present in the silt range (Enete et al., 2012). We specifically assessed the following two hypotheses with regard to seasonal changes in diet and dust loads using a combination of fecal particle analysis (particle sizes), feeding observations and three-dimensional (3D) surface texture analysis (e.g., facet surface complexity, anisotropy, plateau, and valley void geometry) on upper and lower molars:

Hypothesis 1 *Chewing efficiency and surface texture in chimpanzees are influenced by periodical dust loads.*

We predict that:

1.1 High dust loads reduce the chewing efficiency. We expect to find larger mean fecal particle sizes during dust-rich dry periods as compared to periods of lower dust loads (Figure 1a).

1.2 The abrasive dust loads on plants result in molar wear facets characterized by a more homogeneous (anisotropic) surface texture with many fine linear furrows and valleys (as shown for rabbits in Schulz, Piotrowski, et al., 2013).

Hypothesis 2 *Nut and seed consumption affects surface texture.*

We predict that:

2.1 The increased consumption of leaves and/or the soft endosperm of nuts as alternate states during the dry period results in increased complexity and isotropy of the surface texture, with lower texture void volume and more texture plateaus. Increased seed consumption results in larger and deeper surface texture pits on the tooth facets (Scott et al., 2005; Ungar, Grine, & Teaford, 2008) with large peak heights and pit volumes.

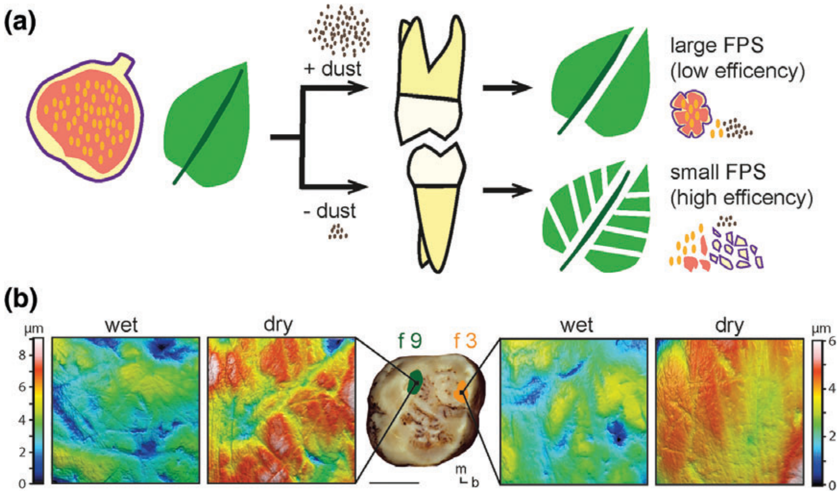

FIGURE 1 (a) Scheme illustrating the effect of dust on chewing efficiency as expressed by mean fecal particle size (FPS), (b) three-dimensional (3D) surface textures in two chimpanzee molar facets (f3 and f9) for the wet and dry period, respectively. 3D texture surfaces in top view (meshed axiomatic models, 160 × 160 μm, leveled and form filtered) of two specimens (upper first molar photography and texture of the wet period: ID 11903, texture of the dry period: ID 11800), m = mesial, b = buccal, scale = 5 mm

2 | MATERIAL AND METHODS

2.1 | Field site

The Taï-forest chimpanzee population in the southwest of Côte d'Ivoire has been studied continuously by the Taï-Chimpanzee-Project (TCP) since 1979 (Wittig, 2018). The site is located in the Taï National Park, one of the last primary rainforests in West Africa at an elevation between 80 and 396 m above sea level with sub-equatorial climatic conditions (Boesch & Boesch-Achermann, 2000) and with a mean annual rainfall (2013–2014) at Taï of 1,759 mm (Wessling et al., 2018).

2.2 | Fecal sampling and sieving analysis

The fecal sampling lasted for 19 weeks from November 23, 2014 to April 2, 2015. The sampling periods cover two wet periods, the first from 23 November to December 26, 2014 (5 weeks) and the second from 13 February to April 2, 2015 (7 weeks). These were interrupted by a dry period from December 27, 2014 to February 12, 2015 (7 weeks), accentuated briefly by the northern dust-laden Harmattan wind. The start of the dry period was defined by minimum temperatures below 20 °C and minimal rainfall (the first light rain, which was below 10 mm, was recorded on January 23, 2015). After the first rainfall the temperature increased gradually, indicating the end of the Harmattan. The first heavy rain that had more than 10 mm of precipitation was recorded on February 12, 2015 (55 mm). We use the term “Harmattan” to specifically refer to the period when the wind acts as transmitter of the dust.

During the 19 weeks of sampling trained field assistants collected 97 fecal samples systematically every second week from 13 selected animals (5 juveniles, 4 adolescents, and 4 adults; Supporting Information Supplement 1). The fecal samples were collected directly after defecation and placed in water-tight plastic bags in the field. Of the initial pile, a total of 30 g, split into two samples of 15 g each was used for further examination, stored in 50 ml Greiner tubes (if fine grained) or 60 ml Roth tubes (if coarse grained) and conserved in 96% ethanol.

We used the wet sieving method of Fritz, Streich, Schwarm, and Clauss (2012). The sieve cascade contained 11 sieves with pore sizes of 0.020, 0.040, 0.063, 0.125, 0.25, 0.5, 1, 2, 4, 8, and 16 mm. Sieving at MPI-EVA was conducted for 10 min in a sieving machine (AS 200 control, Retsch, Haan, Germany) using a vibration amplitude of 2 mm, and a water throughput of 2 L/min. The remains on each sieve were transferred onto pre-weighed petri dishes, deep-frozen at −20 °C for a minimum of 24 hr, freeze-dried in a vacuum chamber (1 mbar, Christ Alpha 1–4 LDplus, Osterode am Harz, Germany) for 24–72 hr, and weighed after adapting to room temperature using an analysis balance with measuring accuracy of 0.2 mg (Kern ABJ-NM/ABS-N, Kern, Balingen, Germany). Large seed sieving fractions (4/8/16 mm) were pre-dried at 40 °C in a drying oven (UN 55, Memmert, Schwabach, Germany). Mean FPS was calculated according to the dMEAN procedure (Fritz et al., 2012), as described in Weary et al. (2017). We also tested for the influence of individual age on FPS as suggested by Weary et al. (2017). Mean fecal particle size was calculated for two sieving cascade combinations: the first ranges in sieve pore sizes from 0.063 to 16 mm ($\mathrm{FPS}_{0.063\text{–}16\ \mathrm{mm}\ [\mathrm{no\ seeds}]}$) to be comparable to Fritz et al. (2012) and Matsuda et al. (2014). The second cascade ranges from 0.020 to 16 mm ($\mathrm{FPS}_{0.020\text{–}16\ \mathrm{mm}\ [\mathrm{no\ seeds}]}$) to be comparable to Weary et al. (2017). We quantified the amount of particles in the two smallest sieves (0.020 and 0.040 mm, silt range) as well as the amount of particles in the four largest sieves (2, 4, 8, and 16 mm, seed range) in percent of the dry matter retained on all sieves.

2.3 | Long term feeding observations

To explore the relationship between surface texture and dietary composition we used feeding observation data recorded in a long-term observation database on chimpanzee behavior (Wittig, 2018). We compiled observational data for 12 chimpanzees for the years 1992–2009 (Supporting Information Supplement 2), which coincided with the period when the cranial material was collected (see below). The database on chimpanzee behavior contains a diverse set of behavioral observations, including information on the genus or species of food source, plant part, and feeding duration, and gives an overview of intraspecific dietary variability (Supporting Information Supplements 3 and 4). We compiled both individual and group means (groups: adults, wet or dry period, and sexes) of the mean time spent on certain food items. Due to partial uncertainty of death dates of the individuals from which cranial material was collected, a time frame of 1–12 days in a period of 4 weeks before the individual's death date was used (Supporting Information Supplement 2). For living individuals the mean time spent on certain food items was calculated for the corresponding time period. We assumed similar precipitation and Harmattan influence for 1992–2009 (as described by (Boesch & Boesch-Achermann, 2000)) as for 2014–2015 and use the term "dry period" for the months December to February and "wet period" for the other months. Due to limited feeding observations, we pooled the data for three males and one female in the dry period and six females and one male in the wet period. To increase the quality of the given information, we added taxonomic information of the consumed food and classified the food types (e.g., various fruit types: nut, drupe, berry, and follicle). We considered nuts as a very soft, non-abrasive food category, because in the long-term observation database the category "nut" was used only if the soft endosperm of a nut was consumed after cracking the nut with a tool (Boesch & Boesch, 1981, 1984). For a complete description of the categories see Supporting Information Supplement 5.

2.4 | Craniodental material and texture sample collection

The crania of 26 individuals with an individual age of 5–40 years (Supporting Information Supplement 2) were chosen from the Taï chimpanzee osteological collection housed at MPI-EVA. The material had been collected between 1984 and 2016 in the framework of the TCP. We only selected individuals that had appropriate teeth for texture analysis (dataset t, Supporting Information Supplement 2) as well as available feeding observations from the long-term behavioral database of the MPI-EVA (dataset d, Supporting Information Supplement 2). We selected specimens with well-preserved occlusal surface of upper and lower first (M1) and second molars (M2). Molds of the molars on either the right or left side were taken with high resolution silicone (Provil novo Light C.D.2 regular set; Type 3; Heraeus Kulzer, Dormagen, Germany) using facet 3 (attrition-dominated) and 9 (abrasion-dominated) as measuring areas for 3D surface texture (Figure 1b). In previous microwear texture studies, only the Phase II facet 9 on upper and lower molars was considered (Scott et al., 2005). However, since the chewing mode in chimpanzees is supposed to consist of two phases (Kay, 1975; Kay & Hiiemae, 1974), we additionally included the attrition-dominated facet 3 as a facet of Phase I (Figure 1b) to control for functional differences. Further, we tested for tooth-specific functionality to control for differences between upper and lower teeth.

Surface texture measurements were conducted using the high-resolution confocal disc-scanning surface measuring system μsurf mobile (NanoFocus AG, Oberhausen, Germany) at the MPI-EVA. The surface texture analyses were performed in μsoft analysis premium software version 7.4.8076 (NanoFocus AG, Oberhausen, Germany; Digital Surf, Besançon, France) for a total of 45 parameters divided into five analysis types of which two followed ISO 25178 and ISO 12781 (International Organization for Standardization, 2012a; International Organization for Standardization, 2012b), and three that do not follow international standards namely texture direction, motif and furrow analyses (see Schulz, Calandra, & Kaiser, 2013; Schulz, Piotrowski, et al., 2013). Larger intrinsic abrasive particles increase the likelihood of large and deep texture valleys. These are detectable using a combination of several specific parameters (see Supporting Information Supplement 6 for exact parameters), including area (Sda_{ISO25178} and mea_{motif}), height (Sp_{ISO25178}, Sq_{ISO25178}, Sz_{ISO25178}, $S5v_{\mathrm{ISO25178}}$, $metf_{\mathrm{furrow}}$, and $madf_{\mathrm{furrow}}$), volume (e.g., *mev*, Vm_{ISO25178}, Vmc_{ISO25178}, Vmp_{ISO25178}, Vv_{ISO25178}, and Vvc_{ISO25178}), and plateau size ($FLTp_{\mathrm{ISO12781}}$, Smr_{ISO25178}, and Smc_{ISO25178}; Calandra et al., 2012; Kaiser, Clauss, & Schulz-Kornas, 2016; Schulz, Calandra, et al., 2013; Schulz, Piotrowski, et al., 2013). Smaller intrinsic abrasive particles are associated with smaller and shallower texture valleys. High homogeneity in occlusal movement pattern is detectable with large values of anisotropy ($Is_{\mathrm{texture\ direction}}$, $IS2R_{\mathrm{texture\ direction}}$, and Str_{ISO25178}) and density (Spd_{ISO25178}) parameters (Kaiser et al., 2016).

2.5 | Statistical analyses

2.5.1 | Fecal particles

To test whether FPS, seed load (all seeds) or small particles (quantitative responses) were influenced by the absence or presence of dust carried by the Harmattan and/or the sampling week, we used a set of linear mixed models (Baayen, 2008). In these models, we included the predictors harm (representing the Harmattan, with the levels before, during and after the dry period) as a fixed effect and subject as a random effect. To check for the effect of age and *sex*, both were included as further covariates. Additionally we tested whether $\mathrm{FPS}_{0.020\text{–}16\ \mathrm{mm}}$ was influenced by the absence or presence of large (8–16 mm) or small seeds (2–4 mm) and/or the sampling week and included the predictor 8–16 seeds or 2–4 seeds and week as fixed effects. This is because the inclusion of seeds may lead to methodological complications, since they are often swallowed unchewed (Wrangham, Chapman, & Chapman, 1994) and therefore lead to an upward skew of the resulting measurement of FPS (Weary et al., 2017).

To keep Type I error rates at the nominal level of 5%, we included random slopes of week and age within subject but not into the correlation parameters between random intercepts and random slopes terms (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009). $\mathrm{FPS}_{0.063\text{–}16\ \mathrm{mm\ (no\ seeds)}}$ and $\mathrm{FPS}_{0.020\text{–}16\ \mathrm{mm\ (no\ seeds)}}$ were asymmetrically distributed and skewed, and we therefore log-transformed them. Age was distributed approximately symmetrically and z-transformed (to a mean of zero and a standard deviation of one). The models were fitted in R version 3.5.0 (RCoreTeam, 2018) using the lmer function of the R-package lme4 version 1.1-17 (Bates, Maechler, Bolker, & Walker, 2015). We checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. Both indicated no obvious deviations from these assumptions. The models were checked for stability by excluding subjects one at a time from the data and comparing the model estimates derived for these data subsets with those derived for the full data set. We found that there were no influential subjects. Variance inflation factors (VIF, Field, 2005) were derived using the VIF function of the R-package car (Fox & Weisberg, 2011) applied to a standard linear model excluding the random effects, and did not indicate collinearity to be an issue. The significance of the full model compared to the null model (comprising only age and the random effects) was established using a likelihood ratio test (R function ANOVA with argument test set to "Chisq", Dobson, 2002; Forstmeier & Schielzeth, 2011). To allow for a likelihood ratio test, we fitted the full model using maximum likelihood. We based *p* values for the individual effects on likelihood ratio tests, comparing the full with the respective reduced models (Barr et al., 2013). The sample size for the models (Table 1) was a total of 105 observations made on 13 individuals (Supporting Information Supplement 1).

2.5.2 | Surface texture

For surface texture analysis we followed the standard statistical procedure according to Calandra et al. (2012) applying the robust Welch–Yuen heteroscedastic omnibus test coupled with a heteroscedastic pairwise comparison test (analogously to Dunnett's T3 test) and a heteroscedastic rank based test according to Cliffs method to detect significant differences between trimmed (15%) means. The R packages xlsx version 0.4.2 (Dragulescu, 2012), doBy version 4.5.3 (Højsgaard & Halekoh, 2012), and R.utils version 1.12.1 (Bengtsson, 2012) were used. We conducted group-wise comparison testing for intra-specific variation in 45 surface texture parameters. Seven datasets were compiled testing for variation of sex (comparing female and male) and period (comparing the dry with the wet period, see Table 2). Upper and lower teeth and the two facets (f3 and f9) were analyzed separately. Age was not considered in a separate analysis, because it was not known for all specimen and ontogenetic changes in surface textures were not the focus of this study.

3 | RESULTS

3.1 | Fecal particle size

The full model for $\mathrm{FPS}_{0.063\text{–}16\ \mathrm{mm}\ (\text{no seeds})}$ was different and therefore more informative when compared to the null model (dry period as the variable harm; likelihood ratio test Chisq = 15.98, df = 5, *p* = .007). The Harmattan had a statistically significant effect on chewing efficiency leading to larger $\mathrm{FPS}_{0.063\text{–}16\ \mathrm{mm}\ (\text{no seeds})}$ during the dry period (Table 1). The interactions of age and sex did not have an obvious effect (likelihood ratio test $\mathrm{Chisq}_{\mathrm{age:sex}}$ = 1.94, df = 1, *p* = .164).

For the extended range of the sieving column, for $\mathrm{FPS}_{0.020\text{–}16\mathrm{mm}\ (\text{no seeds})}$, the full model was also more informative than the null model (likelihood ratio test, Chisq = 15.84, df = 5, *p* = .007) and independent of the interaction between age and sex (likelihood ratio test $\mathrm{Chisq}_{\mathrm{age:sex}}$ = 2.02, df = 1, *p* = .155). It also indicated that the dust of the Harmattan is leading to larger $\mathrm{FPS}_{0.020\text{–}16\ \mathrm{mm}\ (\text{no seeds})}$ during the dry period (Table 1, Figure 2a).

The particles on the four largest sieves represented un-damaged seeds (Supporting Information Supplement 7). The full-null model comparison for all seeds (the total dry matter retained in all sieves) yielded no difference (Chisq = 3.31, df = 5, *p* = .652) and was independent of interaction between age and sex (Table 1).

The full-null model comparison for the small particles indicated that during the dry period, lower amounts of small particles (dry matter on the 0.020–0.040 mm sieves in percentage of dry matter retained on all sieves) were found in the feces (likelihood ratio test Chisq = 12.53, df = 5, *p* = .028, Figure 2b). During the Harmattan the amount of small particles decreased (likelihood ratio test $\mathrm{Chisq}_{\mathrm{harm}}$ = 9.507, df = 2, *p* = .009). The interaction of age and sex did not have an effect on small particles (Table 1).

The full-null model comparison for large seeds indicated that consumption of large seeds did not affect chewing efficiency ($\mathrm{FPS}_{0.020\text{–}16\ \mathrm{mm}}$, likelihood ratio test: Chisq = 7.08, df = 4 *p* = .132), with no effect of the interaction of age and sex (Table 1). The same applies for the full-null model comparison for small seeds ($\mathrm{FPS}_{0.020\text{–}16\mathrm{mm}}$, likelihood ratio test Chisq = 5.401, df = 4 *p* = 0.249). Small seeds did not affect chewing efficiency either (Table 1). Estimated variances for the random effects and residuals for all models are given in Supporting Information Supplement 8 and descriptive statistics in Supporting Information Supplement 9.

3.2 | Feeding observations

Adult chimpanzees at the Taï forest fed on 48 plant genera and 7 animal sources (Supporting Information Supplement 3). The chimpanzees spent most of their feeding time on dicotyledons (dicots; Supporting Information Supplements 3 and 4, Figure 3b) including fruit pulp (42%), fruit pulp with seeds (21.2%), seeds (5.2%), nut endosperm (11.4%), leaves (6.1%), and unspecified parts of dicotyledonous plant genera (0.5%). Monocotyledonous (monocots) plant parts played a minor part in the diet (2.8% pith, 0.9% leaves, and 0.3% diverse parts). The amount of animal sources including insects (3.6%) and mammals (1.0%) was very low. There were few observations on taxa of unknown taxonomic assignation, and these consisted of feeding on diverse leaves (3.8%) and unknown taxa (1.0%).

Similar feeding times were found during the dry and wet period for monocots (leaves, pith, and diverse) and mammals (difference < 2%, Figure 3b, Supporting Information Supplement 4). However, during the dry period, chimpanzees spent more feeding time on nut endosperm (+15.6%) and seeds (+10.6%), but less on fruit pulp (with −13% and without seeds −2.2%) and insects (−4.8%). Feeding time of leaves (dicots as well as monocots) was lower during the dry period (−3.3%). Feeding duration for females (wet period only) and males (dry period only) was similar in the categories fruit pulp, dicots leaves, monocots leaves, and diverse plant parts (Supporting Information Supplement 4). Females spent more time feeding on insects (+5.8%), mono- or dicotyls leaves (+5.8%), fruits pulp with seeds (+13.4%), and monocot pith (+2.2%), but less on nut endosperm (−11.9%), seeds (−6.2%), and mammals (−2.9%).

3.3 | Surface textures

Individuals that had died during the dry period differed in 10 out of 45 surface texture parameters (Table 2, Supporting Information

TABLE 1 Model statistics given for mean fecal particle size (FPS), seeds and small-particles (bold values indicate sigificant levels $p<0.05$, fixed effects, random effects are given in Supporting Information Supplement 8)

Response	Term	Estimate	SE	$\mathrm{CI}_{\mathrm{lower}}$	$\mathrm{CI}_{\mathrm{upper}}$	Chisq	df	*p*
FPS $_{0.063\text{–}16\ \mathrm{mm}}$ (no seeds)	Intercept	1.392	0.096	1.196	1.594	[1]	[1]	[1]
	Age[3]	0.098	0.063	−0.037	0.234	[1]	[1]	[1]
	Sex	−0.240	0.124	−0.500	0.026	[1]	[1]	[1]
	Harm.before[2]	0.176	0.095	−0.029	0.385	10.54	2	**0.005**
	Harm.during[2]	0.419	0.093	0.211	0.621			
	Age[3]:Sex	−0.165	0.111	−0.405	0.076	1.94	1	0.164
FPS $_{0.020\text{–}16\ \mathrm{mm}}$ (no seeds)	Intercept	1.194	0.108	0.970	1.423	[1]	[1]	[1]
	Age[3]	0.110	0.070	−0.036	0.268	[1]	[1]	[1]
	Sex	−0.215	0.134	−0.497	0.070	[1]	[1]	[1]
	Harm.before[2]	0.209	0.113	−0.036	0.457	10.89	2	**0.004**
	Harm.during[2]	0.513	0.111	0.264	0.768			
	Age[3]:Sex	−0.121	0.110	−0.362	0.115	2.02	1	0.155
Small particles 0.020–0.040 mm	Intercept	0.221	0.033	1.196	1.593	[1]	[1]	[1]
	Age[3]	−0.017	0.012	−0.037	0.234	[1]	[1]	[1]
	Sex	0.007	0.017	−0.500	0.026	[1]	[1]	[1]
	Harm.before[2]	−0.042	0.037	−0.029	0.385	9.507	2	**0.009**
	Harm.during[2]	−0.117	0.036	0.211	0.621			
	Age[3]:Sex	0.025	0.019	−0.405	0.076	1.725	1	0.189
All seeds 2–16 mm	Intercept	0.504	0.103	0.287	0.713	[1]	[1]	[1]
	Age[3]	0.045	0.065	−0.090	0.179	[1]	[1]	[1]
	Sex	0.004	0.095	−0.198	0.219	[1]	[1]	[1]
	Harm.before[2]	0.200	0.118	−0.050	0.457	2.62	2	0.270
	Harm.during[2]	0.081	0.121	−0.173	0.343			
	Age[3]:Sex	−0.001	0.106	−0.229	0.226	0.0001	1	0.991
Large seeds 8–16 mm	Intercept	1.479	0.123	1.198	1.749	[1]	[1]	[1]
	Age[3]	0.111	0.061	−0.253	0.235	[1]	[1]	[1]
	Sex	−0.099	0.125	−0.371	0.208	[1]	[1]	[1]
	8-16.seeds[4]	−0.320	0.129	−0.601	−0.044	5.174	1	**0.023**
	Age[3]:Sex	−0.137	0.111	−0.368	0.111	1.295	1	0.255
Small seeds 2–4 mm	Intercept	1.448	0.119	1.203	1.609	[1]	[1]	[1]
	Age[3]	0.120	0.074	−0.034	0.279	[1]	[1]	[1]
	Sex	−0.213	0.139	−0.504	0.084	[1]	[1]	[1]
	2-4.seed[4]	−0.117	0.171	−0.463	0.226	0.465	1	0.495
	Age[3]:Sex	−0.208	0.124	−0.478	0.053	2.581	1	0.108

[1] Not shown because of having a very limited interpretation.
[2] Harm (Harmattan) was dummy coded with harm.before being the reference category; the indicated test was obtained from a likelihood ratio test comparing the full with a reduced model lacking the test variable Harmattan.
[3] z-tranformed.
[4] Seed was dummy coded (absence and presence) with absence being the reference category; showing estimated coefficients (Estimate), standard errors (SE), upper and lower confidence intervals ($\mathrm{CI}_{\mathrm{upper}}$ and $\mathrm{CI}_{\mathrm{lower}}$ and likelihood ratio tests (Chisq, *p*) of the individual effects.

Supplement 6). Upper and lower teeth appeared to be very similar (Figure 3a,c). We did not identify one specific parameter typical for period, sex, or tooth position (Table 2). In general, only minor differences between periods existed (Figure 1b), and were more prominent on the abrasion-dominated facet 9 than on the attrition-dominated facet 3 of both upper and lower teeth. Facet 9 had higher peaks and material volume (larger *S5p*, *Sp*, *Vm*, *Vmp*, *FLTp*; Table 2, Supporting Information Supplement 6) in the dry period, and facets 3 on the upper teeth had a higher density of furrows (*medf*) as well as smaller hills (smaller *mea*) and less voluminous hills (smaller *mev*) resulting in less plateau-like textures. Sexual differences were more prominent on the attrition dominated (shearing) facet 3 with 13 parameters compared to the (grinding) facet 9 with only 7 parameters (Table 2, Supporting Information Supplement 10). Females showed more anisotropic surfaces (lower *Is*, *Str* values) on the upper molar facet 3, their upper molar facet 9 was more plateau-like (smaller *Ssk* values), and they had less voluminous plateaus (*Vm*, *Vmp*) on facet 9 of the lower molars—all findings compatible with more attrition-dominated wear. In contrast, males had more peaks with smaller plateaus (larger *Ssk* values) in general, and rougher (larger *Sq*), deeper (larger *madf*, *metf*, *Sp*, *Sq*, *Sdq*) and more furrows (larger *Vv*, *Vvc*, *Smc*) and peaks (larger *Vmp*, *Vm*, *Smc*) on facet 3 of the lower molars—all findings were compatible with more abrasion-dominated wear.

TABLE 2 Test statistics given for surface texture data sorted according to the two predictions

					Welch-Yuen				Dunnett		Cliff			
Prediction	**Data set**	**Specimen (n)**		**ST**	**Ft**	***p***	**nu1**	**nu2**	**Df**	***p***	**Ph**	**Pl**	**Pu**	***p***
Sex	Tx-f3	Female (11)	Male (7)	*Is*	7.49	**0.022**	1	9.58	9.58	**0.022**	0.86	0.56	0.97	**0.020**
				Str	7.49	**0.022**	1	9.58	9.58	**0.022**	0.86	0.56	0.97	**0.020**
	Tx-f9	Female (11)	Male (8)	*Ssk*	7.96	**0.015**	1	12.25	12.25	**0.015**	0.85	0.60	0.96	**0.008**
	Tm-f3	Female (4)	Male (6)	*Madf*	15.86	**0.008**	1	5.62	5.62	**0.008**	0.96	0.64	1.00	**0.007**
				Metf	14.11	**0.006**	1	7.64	7.64	**0.006**	0.96	0.64	1.00	**0.007**
				Sdq	6.44	**0.046**	1	5.69	5.69	**0.046**	1.00	0.61	1.00	**0.016**
				Smc	8.79	**0.020**	1	7.43	7.43	**0.020**	0.92	0.56	0.99	**0.025**
				Smr	7.30	**0.028**	1	7.71	7.71	**0.028**	0.08	0.01	0.44	**0.025**
				Sp	14.83	**0.005**	1	7.87	7.87	**0.005**	1.00	0.61	1.00	**0.016**
				Sq	5.83	**0.049**	1	6.51	6.51	**0.049**	0.92	0.56	0.99	**0.025**
				Vm	7.96	**0.036**	1	5.08	5.08	**0.036**	1.00	0.61	1.00	**0.016**
				Vmp	7.96	**0.036**	1	5.08	5.08	**0.036**	1.00	0.61	1.00	**0.016**
				Vv	8.97	**0.019**	1	7.34	7.34	**0.019**	0.92	0.56	0.99	**0.025**
				Vvc	10.23	**0.014**	1	7.49	7.49	**0.014**	0.92	0.56	0.99	**0.025**
	Tm-f9	Female (7)	Male (6)	*Vm*	6.71	**0.030**	1	8.51	8.51	**0.030**	0.83	0.51	0.96	**0.044**
				Vmp	6.71	**0.030**	1	8.51	8.51	**0.030**	0.83	0.51	0.96	**0.044**
Period	Tx-f3	Dry (10)	Wet (18)	*Is2R*[a]	12.50	**0.002**	1	19.86	19.86	**0.002**	0.14	0.05	0.33	**0.001**
				Mea	8.50	**0.009**	1	19.62	19.62	**0.009**	0.81	0.60	0.92	**0.005**
				Medf	8.57	**0.011**	1	13.43	13.43	**0.011**	0.18	0.07	0.39	**0.005**
				Mev	9.45	**0.007**	1	17.02	17.02	**0.007**	0.79	0.56	0.92	**0.014**
				Sal	5.81	**0.036**	1	10.21	10.21	**0.036**	0.77	0.51	0.92	**0.040**
	Tx-f9	Dry (10)	Wet(18)	*S5p*	5.88	**0.034**	1	10.79	10.79	**0.034**	0.21	0.08	0.46	**0.025**
				Sp	10.54	**0.004**	1	19.70	19.70	**0.004**	0.23	0.10	0.46	**0.022**
				Vm	6.81	**0.018**	1	18.15	18.15	**0.018**	0.26	0.11	0.48	**0.031**
				Vmp	6.81	**0.018**	1	18.15	18.15	**0.018**	0.26	0.11	0.48	**0.031**
	Tm-f9	Dry (7)	Wet (11)	*FLTp*	9.91	**0.010**	1	10.02	10.02	**0.010**	0.17	0.05	0.44	**0.020**
				Vm	12.18	**0.008**	1	8.30	8.30	**0.008**	0.06	0.01	0.32	**0.002**
				Vmp	12.18	**0.008**	1	8.30	8.30	**0.008**	0.06	0.01	0.32	**0.002**

Note. Chimpanzee data sets as presented in Supporting Information Supplement 6, Tx = tooth maxillary, Tm = tooth mandibulary, f = facet, ST = surface texture parameter, Ft / Ph = test statistics, *p* = level of significance (bold values indicate sigificant levels <0.05), nu1 / nu2 / Df = degree of freedom, Pl = lower 95% confidence interval, Pu = upper 95% confidence interval.

[a] Texture directionality (incl. *Is2R* values) can be studied only if the isotropy value is below 30%, otherwise the directions may not be sufficient significant.

4 | DISCUSSION

Previous studies in marsupial diprotodonts, placental ruminants, and strepsirrhine primates have indicated that there are three main adaptive responses to offset the effects of reduced chewing efficiency: (a) to increase chewing effort per unit food processed; (b) to alter the voluntary intake and passage rate; and (c) to select food items that are more easily processed (Perez-Barberia & Gordon, 1998). In folivorous koalas it was found that increased tooth wear eventually impinges on the digestive efficiency (Lanyon & Sanson, 1986), although animals with worn teeth respond with an increased food intake and increased chewing intensity (Logan & Sanson, 2002). Studies on gallery forest ring-tailed lemurs (*Lemur catta*) showed that dental abrasion reduced the efficiency with which food was processed and utilized; these lemurs were also observed to adjust their behavior to compensate for tooth loss (Milette et al., 2012). Furthermore, in rainforest lemurs (*Propithecus edwardsi*) increased tooth wear resulted in overall fitness decrease (King et al., 2005). Developmental defects in teeth (e.g., accentuated lines and hypoplasia) are a potential indicator of seasonal (heat or rain) stress events (Guatelli-Steinberg, 2003; Skinner, 1996; Skinner, Skinner, & Boesch, 2012). Such defects have been documented in tooth enamel of Taï chimpanzees (Smith & Boesch, 2015). Currently we do not have direct evidence from feeding observations on chimpanzees indicating such a behavioral compensatory mechanism for environmental stress, but studying tooth wear in combination with fecal particle size as a measure of chewing efficiency might be a new option of quantifying eco-physiological stressors.

4.1 | Chewing efficiency and surface texture are influenced by periodical dust loads

The results revealed significantly larger mean fecal particle sizes and fewer smaller fecal particles (smallest sieving fractions $\text{particles}_{0.020\text{–}0.040\ \text{mm}}$) during the dry Harmattan period. Concomitantly, the molar surface texture contains fewer plateau-like features in the dust-rich dry period than in the wet period. Moreover, surface textures on the attrition-dominated facet 3 were less voluminous and had smaller surface texture features, while on

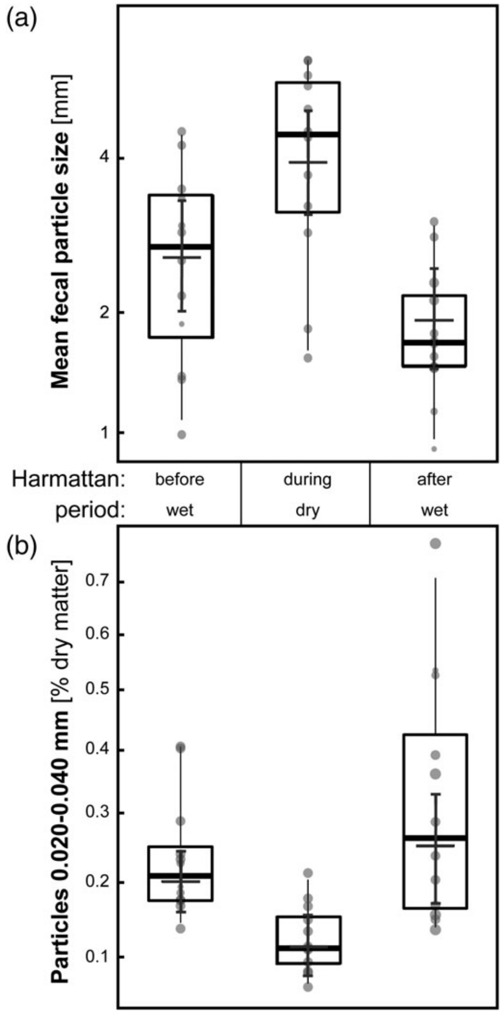

FIGURE 2 (a) Mean fecal particle size (sieve fractions 0.020–16 mm, Table 1, Supplement 9) and (b) amount of small particles 0.20–0.40 mm (total of all sieves) plotted for the two periods showing median, sample density (gray circles), upper and lower confidence intervals of the model (double T line in the boxplot)

the abrasion-dominated facet 9 higher peaks and larger material volume were found. These results are in line with Hypothesis 1, suggesting that extrinsic abrasives (dust loads) on the plant foods consumed by Western chimpanzees resulted in a periodical decrease in chewing efficiency (Prediction 1.1) and were detectable in the surface texture (Prediction 1.2). There is no evidence that the Taï chimpanzees have developed a washing behavior to avoid dust loads on foods during the dry period as has been observed in macaques (Kawai, 1965) or captive great apes (Allritz, Tennie, & Call, 2013). It would therefore be pertinent to investigate, through field observations and lab-based experiments, whether chimpanzees engage in fewer masticatory cycles or less intensely chewing when feeding on dust-laden food.

Our surface texture findings are in agreement with the description of the dental wear mechanism as proposed by Lucas, Constantino, Wood, and Lawn (2008) as well as with ingesta related hypotheses as proposed by Kaiser et al. (2016). Specifically, the latter suggested that a higher amount of dust particles increase the likelihood of abrasive contacts. These authors also argued that the extrinsic abrasives will create a high amount and deep small surface texture features during the food particle comminution process. Although dust has been contested as the primary cause for microwear (Merceron et al., 2016; Scott et al., 2005, 2009; Ungar et al., 2008), our data show the opposite. We therefore propose the following scenario for a dust-dependent wear mechanism: The consumption of dust covered foods creates micrometer-scale surface texture features (e.g., fine furrows and dales) while at the same time chewing is less intensive resulting in a lower amount of chews per ingesta and subsequently in larger mean fecal particle sizes. This proposed mechanism is in accordance with the findings of Prinz (2004), who showed in a lab-based study in humans that abrasives in food lead to reduced comminution, most likely involving the loss of tooth substance.

4.2 | The consumption of nut endosperm and seeds affect surface texture

During the wet period when the amount of extrinsic abrasives is low, the observed texture features are caused by the consumption of more dicotyledonous fruit pulp with seeds and insects (both reflected by few voluminous but flatter dales) as well as leaves (high anisotropy and more plateau-like hills) supporting Hypothesis 2 (Prediction 2.1). Moreover, and in line with previous observations in fossil hominins (see Peterson, Abella, Grine, Teaford, and Ungar (2018)), we did not find facet-specific functionalities; instead our data indicate very similar functions for both facets. Our findings thus suggest that surface texture, at least in chimpanzees, is only affected to a minor degree by tooth position. This has implications for future tooth wear studies, in particular those dealing with fossil teeth, as sample sizes can be increased by combining data from both upper and lower M1s and M2s.

While we did not find a sex-specific signal in the FPS data, there is some support for a separation of the sexes in the surface texture data. This may correspond to the fact that females engage more in nut cracking and feeding than males (Boesch & Boesch, 1981; Boesch & Boesch-Achermann, 2000; Doran, 1997). In contrast, in males the less frequent plateaus and larger dales are suggestive of feeding on a larger amount of dicotyledons seeds and lower amounts of leaves, creating larger dales in the nearly absence of insect feeding and high amount of nut endosperm (Supplement 10).

Previous studies have suggested that the consumption of hard particles (i.e., seeds and nuts) in primates results in a microwear texture pattern with large pits on the tooth facets (Scott et al., 2009; Ungar et al., 2008). Ragni, Teaford, and Ungar (2017) pointed out the challenge of discriminating seed-based diets in pitheciids, but found that volume and area parameters (*Sda*, *Sdv*) discriminate seed and non-seed eaters. In our sample, where seed and nut endosperm consumption was higher in the dry period, *Sda*, *Sdv* did not differ from the wet period; however other parameters describing area (*mea*), volume (*mev*, *Vm*, *Vmp*), height (*FLTp*, *S5p*, *Sp*, *Sz*), and density (*medf*) did. Our results also imply that seeds have an effect on the surface texture signature although we did not find that seed consumption per se affected chewing efficiency as indicated by fecal particle size.

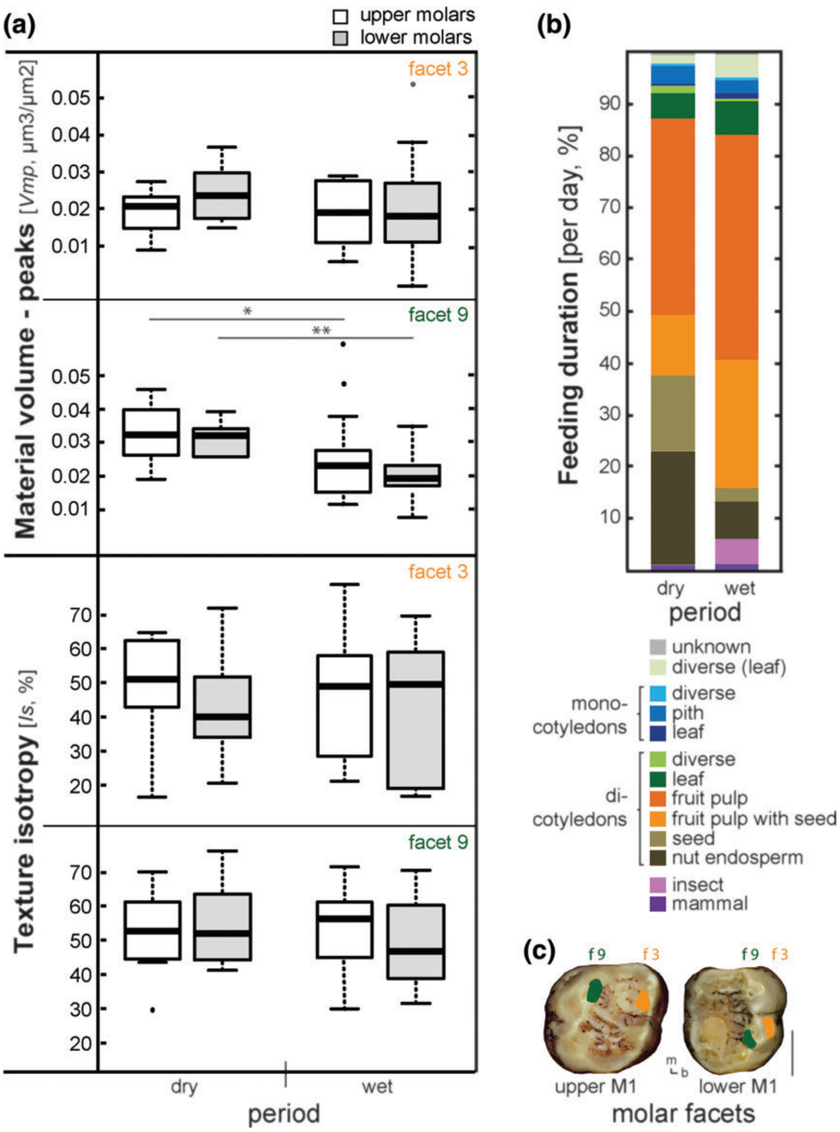

FIGURE 3 (a) Selected boxplots of surface texture parameters are given for facets 3 and 9 of upper and lower molars. (b) Long-term feeding observation data displayed as feeding duration per day, data sets as in Table 2 and Supplement 6, and (c) facet positions (f3 and f9) on occlusal surfaces of molars, m = mesial, b = buccal, scale = 5 mm

4.3 | Implications for dietary ecology and paleoecological reconstruction

Our study demonstrates that periodically increased dust loads result in decreased chewing efficiency in Western chimpanzees. Moreover, dust has a stronger impact on chewing efficiency reduction than do intrinsic dietary abrasive particles originating from hard seeds. This finding supports the notion that seed toughness and hardness are of minor importance in surface texture formation while embedded dust particulates abrade teeth even at low loads (Lucas et al., 2013; van Casteren et al., 2018). Although this hypothesis requires further research, we assume that other fruit-feeding mammal species inhabiting the Taï forest such as colobine monkeys (Cercopithecidae: *Cercopithecus diana*, *Piliocolobus badius*, *Colobus polykomos*) or duikers (Bovidae: *Cephalophus jentinki*, *C. sylvicultur*, *C. ogilbyi*, *C. dorsalis*, *C. zebra*) may also experience such dust driven ecological constraints. What is more, we found evidence that abrasive loads from regionally (the West African subcontinent) acting periodical dust winds represent an ecological constraint for a local environment (Taï forest). The chimpanzees from the Taï forest are therefore one of the rarely described examples in African terrestrial environments where dust loads can be quantified and directly related to tooth wear (see Madden (2014)).

Understanding intraspecific tooth wear patterns in chimpanzees is also a crucial first step for reconstructing the paleoecology of extinct hominins. Early South African fossil hominins lived in seasonally fluctuating environments (Reed, 1997; Reed & Fish, 2005; Vrba, 1975) and were probably exposed to high dust loads during dry periods (deMenocal, 2004). Considering the increasing bias toward dry climate phases in the South African early hominin record between 3.2 and 1.3 Ma (Pickering et al., 2018), we recommend that the impact of dust on tooth wear and chewing efficiency should be considered. Valle, Dupont, Leroy, Schefuß, and Wefer (2014) proposed that based on meridional sea surface temperature differences in the equatorial Pacific (Lawrence, Liu, & Herbert, 2006) the zonal and meridional atmospheric circulations, including African trade winds, started at

3 Ma (Feodorov et al., 2006; Wara, Ravelo, & Delaney, 2005) and intensified around 2 Ma (Marlow, Lange, & Rosell-Mele, 2000). We therefore hypothesize that seasonal dust impact from these trade winds might have been an important source for extrinsic dietary abrasives in hominin evolution.

There is also an ongoing debate about the dietary ecologies of Plio-Pleistocene hominin fossils from South Africa (Grine, Sponheimer, Ungar, Lee-Thorp, & Teaford, 2012; Kupczik, Torro-Ibacache, & Macho, 2018; Macho & Shimizu, 2009; Peterson et al., 2018; Sponheimer et al., 2013). Based on the fine furrowed microwear texture on its molar facets, *Australopithecus africanus* has been reconstructed as a soft fruit feeder which also fed on leaves (Grine, 1986; Peterson et al., 2018; Scott et al., 2005). When considering the findings of the present study, it is also conceivable that the fine furrowed microwear texture of *A. africanus* can be attributed to dust particles adhering to plant foods. Although one can only speculate, dust may have also triggered a decreased chewing efficiency, leading to dietary-physiological stress on the digestive system of this fossil species.

Another South African fossil hominin whose dietary ecology has been of recent interest is the Pleistocene *Homo naledi* from the Dinaledi Chamber; its molars facets are characterized by a highly complex and largely pitted microwear texture lacking fine furrows (Ungar & Berger, 2018). Again, in the light of our findings this would make a dust-loaded diet unlikely but rather suggests that this microwear signature was the result of small sized seeds. However, we cannot fully exclude the possibility that grit (sensu stricto—coarse sand with a grain size of 0.5–2 mm) caused these chips and was also involved in texture formation as suggested by Towle, Irish, and De Groote (2017) and Berthaume, Delezene, and Kupczik (2018). Both fossil hominin examples show that more field observations and feeding experiments under controlled conditions are needed to better understand texture formation. To differentiate more clearly between extrinsic and intrinsic abrasive particles of varying sizes in the surface texture signature, we recommend developing new statistical models and using pattern recognition algorithms (such as those applied to bone wear analysis Martisius et al., 2018).

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DATA ACCESSIBILITY

The data (fecal particle size, feeding observation and surface texture) supporting the findings of this study are accessible through the open access data repository of the Max Planck Society (via https://dx.doi.org/10.17617/3.20).

ORCID

Ellen Schulz-Kornas https://orcid.org/0000-0003-1657-8256
Marcus Clauss https://orcid.org/0000-0003-3841-6207
Roman M. Wittig https://orcid.org/0000-0001-6490-4031
Kornelius Kupczik https://orcid.org/0000-0003-1502-581X

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