




# Dental microwear textural analysis as an analytical tool to depict individual traits and reconstruct the diet of a primate

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## Abstract

**Objectives:** Dental microwear is a promising tool to reconstruct animals' diet because it reflects the interplay between the enamel surface and the food items recently consumed. This study examines the sources of inter-individual variations in dietary habits in a free-ranging population of mandrills (*Mandrillus sphinx*) using a combination of feeding monitoring and in vivo dental microwear textural analysis (DMTA).

**Methods:** We investigated the impact of seasonality and individual traits on four DMTA parameters. In parallel, we further studied the influence of the physical properties of the food items consumed on these four parameters, using three proxies (mechanical properties, estimates of phytolith and external grit contents).

**Results:** We found that seasonality, age, and sex all impact DMTA parameters but those results differ depending on the facet analyzed (crushing vs. shearing facets). Three DMTA parameters (anisotropy, complexity, and heterogeneity of complexity) appear sensitive to seasonal variations and anisotropy also differs between the sexes while textural fill volume tends to vary with age. Moreover, the physical properties of the food items consumed vary seasonally and also differ depending on individual sex and age.

**Conclusion:** Considering the interplay between the tested variables and both dental microwear and diet, we reaffirm that food physical properties play a major role in microwear variations. These results suggest that DMTA parameters may provide valuable hints for paleoecological reconstruction using fragmentary fossil dental remains.

## KEYWORDS

DMTA, feeding ecology, *Mandrillus sphinx*, seasonality

## 1 | INTRODUCTION

Understanding the interplay between morphology and ecology is crucial when considering, for example, ecological reconstructions based on biological material such as bones or teeth. While phenotypes may constrain an organism to specific ecological niches, environmental conditions may also shape an individual's phenotype. Biotic and abiotic interactions, as well as individual life history traits, may all influence morphology and the developmental trajectory of an organism (Day & McPhail, 1996; Griffen & Mosblack, 2011; Lozovina, Pavicic, Pavicic, & Pavicic, 2004; Moermond & Denslow, 1983; Relyea, 2001). In turn,

inferring environmental characteristics where individuals live from morphological data alone appears possible. For example, the presence of linear enamel hypoplasias, resulting from punctual disturbances of tooth enamel secretion related to physiological stress such as malnutrition, has been observed in a population of rhesus macaques living on the island of Cayo Santiago, aiding in the reconstruction of the environmental context (Guatelli-Steinberg & Benderlioglu, 2006). By assuming that biological and physical laws are comparable across time, space and species, inferring some individual traits appears possible when the ecological context is unknown. In particular, the principle of actualism is widely used by paleontologists to reconstruct past environments and

species paleoecology based on the fossil record. For example, pre-mortem damages on bones or teeth can be used to identify the causes of death or individual paleopathologies (Njau & Blumenshine, 2006; Rühli, Chhem, & Böni, 2004). Among available fossil remains, teeth represent an ideal ecological proxy because their high mineralization (72–96% of apatite in humans; Williams & Elliott, 1979) favors survival in the postdepositional environment. Teeth further constitute a direct interface between an organism and its environment (Cuozzo, Ungar, & Sauter, 2012). In this context, dental microwear analysis appears as a relevant tool to reconstruct an animal's feeding ecology and environment (Puech, Prone, & Kraatz, 1980; Rensberger, 1978; Teaford & Glander, 1991; Walker, Hoeck, & Perez, 1978). The number of teeth, oral health and bite force - in relation to masticatory muscles mass—all influence the chewing strategies used by animals to reduce the alimentary bolus and may, in turn, impact dental microwear (Bakke et al., 1992; Charles, Jaeger, Michaux, & Viriot, 2007; de Souza Barbosa, de Morais Tureli, Nobre-dos-Santos, Puppim-Rontani, & Gavião, 2013; Diraçoglu et al., 2011; Gavião, Serra-Vicentin, & Gambarelli, 2011; Jain, Mathur, & Kumar, 2012; Morel, Albuissou, & Woda, 1991; Terhune, Hylander, Vinyard, & Taylor, 2015). In addition, different dental wear facets are variably involved during mastication as a function of two main phases: a shearing phase ("Phase I") and a crushing phase ("Phase II") (Fortelius, 1985; Kay, 1981; Krueger, Scott, Kay, & Ungar, 2008). During the shearing phase of mastication, the opposing crests slide against each other, with jaw movements being more or less parallel to the shearing facets. During the crushing phase, cusps are pressed into tooth basins through jaw movements more or less orthogonal to the dental wear facets (see Ungar, 2015 for a review). Dental microwear observed on these dental wear facets results from the local removal of dental tissue debris (enamel or dentin) caused either by tooth-tooth contacts (attrition) or by ingested particles that contact tooth surfaces (abrasion) under certain chewing forces (Kay & Hiemae, 1974; Maas, 1991; Stones, 1948; Teaford & Runestad, 1992; Xia et al., 2015). Although microwear signatures recorded on the enamel surface have sometimes been proposed to be produced by external grit alone (Covert & Kay, 1981; Lucas et al., 2013; Sanson, Kerr, & Gross, 2007), it is now generally accepted that food greatly influences dental microwear formation processes (Daegling, Hua, & Ungar, 2016; Hoffman, Fraser, & Clementz, 2015; Merceron et al., 2016; Spradley, Glander, & Kay, 2016; Xia et al., 2015). Consequently, dental microwear undergoes a permanent turnover, at a rate that depends on the food ingested, and reflects the individual's diet over weeks to months (Kay & Covert, 1983; Romero, Galbany, De Juan, & Pérez-Pérez, 2012; Teaford & Lytle, 1996). As such, dental microwear analysis allows the detection of short-term variations in animal feeding habits and gives a snapshot of an individual's diet, characterizing some environmental conditions that may change over a lifetime or even across seasons (Teaford & Glander, 1991; Teaford & Oyen, 1989). Feeding selectivity depends on the available resources that locally vary in their diversity and abundance depending on humidity, sunshine intensity, altitude, or soil composition (Denslow, 1987; Hooper & Vitousek, 1997; Wilson et al., 2005), and it may therefore impact the tooth surfaces in a variety of ways. In paleontological studies, dental microwear analyses have been frequently used

to reconstruct the diet of extinct species including dinosaurs, cynodonts, marsupials, ungulates, carnivores, rodents, and primates (Fiorillo, 1998; Fortelius, 1985; Merceron, de Bonis, Viriot, & Blondel, 2005; Peigné et al., 2009; Prédau et al., 2009; Puech, Albertini, & Serratrice, 1983; Rodrigues, Merceron, & Viriot, 2009; Shearer et al., 2015; Ungar, Grine, & Teaford, 2008).

Contrary to fragmentary, isolated and rare fossil remains, populations of living species constitute ideal models to understand the interplay between dental microwear and feeding ecology because the ecological context is generally known. The rare studies based on wild species have shown that dental microwear may reflect inter-individual variations in diet (Jablonski & Crompton, 1994; Nystrom, Phillips-Conroy, & Jolly, 2004; Romero, Ramírez-Rozzi, De Juan, & Pérez-Pérez, 2013; Teaford & Glander, 1991; Teaford & Oyen, 1989). In this context, using *in vivo* dental molds provides a unique overview of the feeding ecology of the studied species that may, in turn, allow useful inferences about extinct close species.

Here, we studied the seasonal and inter-individual variations of four dental microwear textural parameters (DMTA parameters) obtained *in vivo* on a large, free-ranging population of mandrills (*Mandrillus sphinx*). Mandrills have a highly diversified diet, largely composed of fruits, but also leaves, stems, roots, seeds, barks, mushrooms, invertebrates, and small vertebrates (Gautier-Hion, Colyn, Gautier, Dewynter, & Bouchain, 1999; Lahm, 1986). The studied individuals feed on about 150 different plant species representing 449 food items (Nsi Akoué et al., 2017). Their feeding strategies are, however, conditioned by seasonal variations that constrain food availability, but also by the age and sex of the individual. Additionally, in other primate species, social rank has been found to impact animals' feeding ecology (Post, Hausfater, & McCuskey, 1980; Whitten, 1983), although such an effect was not reported in the studied mandrills (Nsi Akoué et al., 2017).

We combined dental microwear and feeding ecology analyses by exploring the effects of the season of sampling together with individual age, sex, and social rank, on DMTA parameters, and on mandrills' diet. Based on previous findings on mandrills or other primates (Gordon, 1982; Jablonski & Crompton, 1994; Teaford & Glander, 1991), we expected that seasonality and individual traits all influence DMTA parameters and feeding habits. If so, these will provide insights on relationships between dental and feeding ecology. We then studied the relationship between DMTA parameters and the size of masticatory muscles and salivary glands. Indeed, we assumed that bite force depends on the thickness of masticatory muscles, as demonstrated in humans (Bakke et al., 1992; Gavião et al., 2011; Sasaki, Hannam, & Wood, 1989). Bite force should, in turn, influence mandrills' chewing strategies (Bakke, Holm, Jensen, Michler, & Möller, 1990; Ross et al., 2007) and therefore dental microwear patterns (Charles et al., 2007; McAfee and Green, 2015; Morel et al., 1991). We further hypothesized that larger salivary glands produce more saliva, as found again in humans (Inoue et al., 2006), limiting the formation of dental microwear by minimizing contacts between food items and tooth surfaces. We conducted all these analyses on four DMTA parameters collected on two different tooth surfaces, derived from the crushing and the shearing facets (Dahlberg & Kinzey, 1962; Kay, 1977). We expected these

dental wear facets to provide contrasting information because they are used differently during mastication as shown, for example, in chimpanzees, where the crushing facets present more and larger pits than the shearing facets (Gordon, 1982).

## 2 | MATERIALS AND METHODS

### 2.1 | Studied population and study area

This study was conducted on a natural population of ~130 mandrills living in the Lékédi park (140 km<sup>2</sup>) and surroundings, in southern Gabon. The study group originated from 65 individuals that initially lived in a semi-free ranging population housed at the CIRMF (Centre International de Recherches Médicales de Franceville, Gabon) and that were released on two occasions in the park (2002 and 2006; see for details: [Peignot et al., 2008]). Captive-born females reproduced with wild immigrant males from the first year post-release. In 2014, wild-born individuals represented more than 85% of the population (Brockmeyer et al., 2015). From October 2002 to April 2012, the mandrills were supplemented with bananas and home-made cake in decreasing quantities (Peignot et al., 2008). In the year following each release event, food supplementation occurred about three to five times a week, but did not provide full caloric requirements in order to incite spontaneous foraging behaviors. Consumption of food items found by natural foraging increased with time so that individuals were supplemented only once to twice a week in early 2012 and food supplementation completely ceased in April 2012 when the project started (Brockmeyer et al., 2015). The non-natural supplementation provided until this date probably did not impact DMTA parameters of the studied mandrills because bananas and home-made cake are very soft and were provided in small quantities. In addition, only three molds (see below) were obtained in April 2012 (removing them from the analyses did not change the results; not shown).

The Lékédi Park is mainly composed of closed canopy forests interspersed with some patches of humid savannas and grasslands (Peignot et al., 2008). Sediments of the soil collected in the Lékédi Park are composed of an assembly of quartz, kaolinite, gibbsite and undetermined clay (Galbany et al., 2014). The local climate is equatorial and is divided into two seasons over the year: a long rainy season (Feb–May), a long dry season (Jun–Sep) as well as two intermediary seasons: a short rainy season (Oct–Nov) and a short dry season (Dec–Jan).

### 2.2 | Dental molding and facial morphology

In total, we collected 169 in vivo dental molds from 92 individuals trapped randomly during five capture events that occurred between April 2012 and December 2015. During captures, mandrills were baited with bananas and anesthetized using blowpipe intramuscular injection of ketamine (Imalgène 1000®; 7 mg/kg body weight for adults and 5 mg/kg body weight for juveniles) mixed with xylazine (Rompun®; 3 mg/kg body weight for adults and 5 mg/kg body weight for juveniles; [Brockmeyer et al., 2015]). The individuals were awakened with the

help of atipamezole (Antisedan ND, 0.5 mg/ml) after anesthesia of about 35 min.

We removed remains of food lures from the mouth of anesthetized animals and washed their teeth using a water-pump, a toothbrush and a dryer (air pump and/or paper towel). The washing/drying manipulation did not take more than five minutes. We molded post-canine teeth with polyvinylsiloxane dental impression materials (PresidentJet regular body, Coltène®) following previous in vivo molding protocols (Romero et al., 2013).

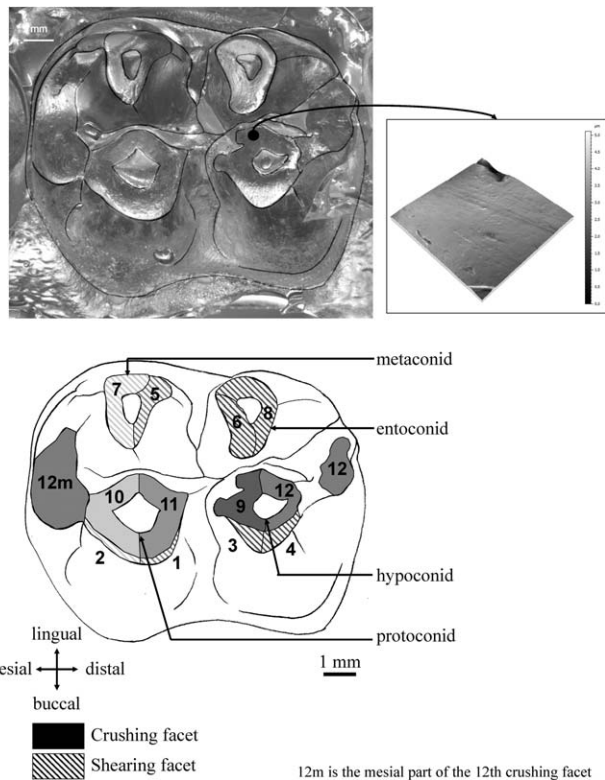
During one capture (Dec 2015), thickness measurements of the masseter muscle and the size of the parotid salivary gland were measured on 29 anesthetized individuals (among which 14 yielded suitable dental molds) using facial ultrasound scanning (MyLabOne Vet, frequency = 6–13 MHz linear probe). Anesthetized animals were positioned in dorsal recumbency with the head tilted to the right or to the left to expose the muscle and the gland and facilitate the placement of the ultrasound probe. The probe was orientated in a superior/inferior axis. Masseter thickness (different from a classical physiological cross-sectional area) was measured on a still image of the three muscle bellies acquired in the longitudinal plan with nicely elongated muscle fibers and linear appearance of the facial plan between the three bellies (See Appendix S1 in the Supporting Information). The probe was located ventrally and perpendicularly to the zygomatic arch (as the muscle inserts into this arch), laterally to the labial commissure where the muscle can be easily palpated and cranially to the mandibular ramus. Maximal length—in the superior/inferior direction—and maximal thickness of the parotid salivary gland were obtained using the same orientation, with a sliding of the probe caudally to the mandible and ventrally to the ear. The parotid gland can be recognized from the surrounding tissue because of a mildly heterogeneous parenchyma with poorly defined margins and a typical approximately oblong shape.

### 2.3 | Dental microwear acquisition

Tooth replicas were produced in the lab from the silicon-based molds using transparent epoxy resin (Araldite® 2020, Hunstman®) and previously validated techniques (Galbany et al., 2014; Romero et al., 2012; Scott, Teaford, & Ungar, 2012). We analyzed DMTA parameters on both shearing and crushing dental wear facets of the first and second lower molars, M<sub>1</sub> and M<sub>2</sub>. For each studied animal in a given trapping season, dental microwear analyses were performed on the molar that produced the best replica (see DMTA section below). We scanned the crushing and shearing facets numbered 9, 10, 11, 12 and 5, 6, 7, 8, respectively (Figure 1; Kay & Hiiemae, 1974; Maier, 1977). For the sake of homogeneity, we prioritized facets 9 and 11 for the crushing facets and facets 5 and 6 for the shearing ones because of their central position on the occlusal surface.

### 2.4 | Tooth surfaces scanning

Studied dental wear facets were placed under a Leica DCM8 confocal profilometer using white light confocal technology with a Leica 100× lens (Numerical aperture = 0.90; working distance = 0.9 mm). Surface



**FIGURE 1** Second molar ( $M_2$ ) of a male mandrill and its dental wear facets

elevations for each studied sample were collected at a lateral ( $x$ ,  $y$ ) interval of  $0.129 \mu\text{m}$  (against  $0.18 \mu\text{m}$  in Scott et al., 2006) with a vertical numerical step of  $1 \text{ nm}$ . A  $320 \times 280 \mu\text{m}$  area was scanned for each studied sample (against  $276 \times 204 \mu\text{m}$  in Scott et al., 2006). Some scans presented a few missing points ( $<3\%$ ), due to steep slopes on the surface relief, that were replaced with a smooth shape calculated from neighboring points (LeicaMap v.7.3). From the original scan, a  $200 \times 200 \mu\text{m}$  surface was extracted. Artifacts such as aberrant peaks (due to light interferences), traces of adhering food remains, saliva or dust were removed manually using a  $3 \mu\text{m}$ -diameter eraser (or a user-defined contour eraser in case of larger artifacts) and then replaced with a smooth shape also calculated from the neighboring points. A final leveling function (implemented in LeicaMap and Toothfrax softwares) was then applied on the resulting surfaces (Merceron et al., 2016). Two-dimensional photosimulations of the studied tooth surfaces are presented in Appendix S2 in the Supporting Information.

## 2.5 | Dental microwear textural analyses

Dental microwear textural analyses on the selected 3D tooth surfaces were performed using a scale-sensitive fractal analysis (SSFA; Scott, Ungar, Bergstrom & Brown, 2005; Scott et al., 2006; Toothfrax and Sfrax softwares). Four textural parameters were considered: anisotropy ( $epLsar$ ), complexity ( $Asfc$ ), heterogeneity of complexity ( $Hasfc$ ), and textural fill volume ( $Tfv$ ). Anisotropy (exact proportion of length scale anisotropy of relief) quantifies the directionality of microwear textures and is calculated at a given scale ( $1.8 \mu\text{m}$ ). Tooth surfaces presenting

high values of anisotropy display scratches oriented in the same direction. Complexity (area scale of fractal complexity) indicates the amount of changes on the surface's relief at different scales. High complexity increases with the local diversity of different microwear features (scratches and pits), characterized by their shape and their size. Heterogeneity of complexity (heterogeneity of the area scale of fractal complexity for a given surface) reflects variation in complexity of relief patches from the whole surface. Patches are obtained by dividing the whole surface studied into sub-surfaces. Here, we tested different sub-surface meshes via a Principal Component Analysis performed on the entire dataset. The different contributions of heterogeneity of complexity to the variance between studied samples using different settings (4, 9, 16, 25, 36, 49, 64, 81, 100, and 121 cells) were then compared. Heterogeneity of complexity considered for sub-regions of 36 cells contributed the most to the variance for the crushing facets and sub-regions of 64 cells contributed the most to the variance for the shearing facets. We therefore considered these to be the two best settings for all the analyses performed thereafter. Finally, textural fill volume, equating the volume of microwear features of the tooth surface, was calculated as the fill volume generated by cubes with  $0.2 \mu\text{m}$  edge minus the structural volume calculated with  $10 \mu\text{m}$ -face cuboids.

From the 169 dental molds initially available, we removed the ones that did not meet the required criteria of the different steps of the analysis. We first dismissed juvenile individuals without  $M_1$  or with unworn  $M_1$  and old individuals with an advanced stage of tooth wear with dentin replacing enamel on the studied dental wear facets (Figure 1). We then excluded dental molds producing scans of bad quality (containing artifacts or reproducing a thin layer of saliva). We therefore retained scans from 71 crushing and 46 shearing facets of  $M_1$  and  $M_2$  (see Appendix S2 in Supporting information), collected from a total of 48 individuals in the studied population (22 females and 26 males, aged 1.9–14.8; 1–3 molds/individuals).

## 2.6 | Diet and food categorization

Individuals' feeding strategies were collected on a daily basis for 17 months (May 2013–October 2014) using 5-min focal sampling (Altmann, 1974) of 57 individually-recognized mandrills (Nsi Akoué et al., 2017). Among these 57 individuals, 29 yielded suitable dental molds but direct correlation analyses between diet and DMTA were not possible because time overlap between these two data sets was negligible. We restricted our analyses to focal individuals observed for more than 1 hr during the different study periods considered ( $N = 57$  for the entire period of behavioral observations;  $N = 46$  for the pooled long dry seasons pooled together,  $N = 38$  for the pooled long rainy seasons, and  $N = 14$  for the pooled short rainy seasons). During the study period, mandrills consumed a total of 147 different plant species: 140 were identified by their species name, their type (tree, bush, grass, liana) and their organ (leaf, stem, root, flower, fruit, seed, bark, resin) seen eaten by the studied focal individuals. From this dataset, we classified a total of 333 consumed food items according to three broad categories. We first estimated (and not directly measured) the mechanical properties of the food items consumed based on the observation and



manipulation of these items. We classified as “hard”: seeds or fruits with hard exocarp; as “soft”: flowers, mushrooms and soft fruits; and as “tough”: leaves, stems and roots. Some other items with specific mechanical properties (e.g., “brittle” dead leaves, “fibrous” fruits, or “doughy” tree sap) were not analyzed because they constituted a negligible proportion of mandrills’ diet (less than 4% of all consumed items each). Tough food items are pliable plant parts that contain a lot of fibers (Hill & Lucas, 1996; Lucas, Turner, Dominy, & Yamashita, 2000) and are resistant to crack propagation (Lucas & Luke, 1984). Hard food items have a better ability to resist to material deformation by contrast with soft ones (Lucas & Luke, 1984). Detailed information about insects, meat or mushrooms consumed by the studied mandrills was unavailable. We therefore described them as “indeterminate” food items and did not analyze them because of their low frequency of consumption. This classification is probably a rough estimate of the actual mechanical properties of the food items consumed (that may also vary seasonally; e.g., Onoda et al., 2011) but it represents a necessary oversimplification of the extremely diversified mandrills’ diet. Second and alternatively to these mechanical properties, we classified the food items consumed into two categories corresponding to their plant clade. We distinguished monocotyledonous plants from dicotyledonous plants because monocotyledonous plants generally show higher phytolith contents than dicotyledonous plants (Hodson, White, Mead, & Broadley, 2005). Indeed, some studies showed that phytoliths might be responsible for dental microwear formation ([Fox, Pérez-Pérez, & Juan, 1994; Gügel, Grupe, & Kunzelmann, 2001; Rabenold & Pearson, 2011; Xia et al., 2015] but see discussion in: [Lucas et al., 2013, 2017; Sanson et al., 2007]). We excluded from this classification moss and fern because they represent a small part of the mandrill’s diet (0.33% of all consumed food items). Third, we classified food items according to their potential content in external, potentially abrasive grit, estimated on the basis of the spatial position of the consumed parts (aerial vs. underground). Plant roots and tubercles were classified as “underground” food items, all the other parts were considered as “aerial” and small food items collected on the ground (e.g., invertebrates, dead leaves) were considered as “indeterminate” food items and were not analysed further (see Table S1 in Supporting Information). With this third classification, we assumed that underground food items may be surrounded by a higher quantity of abrasive particles from external grit compared to aerial ones.

## 2.7 | Statistical analyses

### 2.7.1 | Seasonality and individual traits

We performed General Linear Mixed Models (LMM, nlme package v. 3.1–127 [Pinheiro et al., 2017], R v. 3.2.3) with Gaussian distributions to study the effect of variables related to the environment, individual traits and material information for each of the four DMTA parameters analyzed. Because some individuals were sampled more than once, we set the individual’s identity as a random factor variable to avoid pseudo-replication biases. Depending on the dataset used in the statistical models (social rank information was, for example, available for a subset of 21 individuals only) complexity, heterogeneity of complexity,

and textural fill volume were log-transformed to fit to Gaussian distributions (anisotropy was always normally distributed). We used both visual checking and Shapiro-Wilk test (stats package, R) to test for normality of the residuals and checked the plot of the fitted values as a function of the residuals of the models to assess Goodness-of-Fit. Finally, we used Tukey’s Honest Significant Difference tests (HSD, multcomp package v. 1.4–5 [Hothorn et al., 2008], R) as post-hoc contrast analyses to ordinate class variables that impact significantly ( $p < .05$ ) or marginally ( $p < .10$ ) DMTA parameters.

In a first set of LMMs (four DMTA parameters for both the crushing and the shearing facets), we considered the season as a class variable with three modalities (the three studied seasons; no data were available for the short dry season). Sex was considered as a class variable and individual age as a continuous variable retrieved from exact birth dates or dates estimated from general body condition and patterns of tooth eruption and wear (Galbany et al., 2014). Finally, we considered as class variables the studied tooth (two classes:  $M_1$  vs.  $M_2$ ) and the dental wear facet (four classes for the crushing facets:  $n^\circ$  9, 10, 11, 12; four classes for the shearing facets: 5, 6, 7, 8). We kept the full models as final models.

In a second set of LMMs (four DMTA parameters for the crushing facets only), we further investigated the effect of female’s social rank because we hypothesized that individuals’ access to food resources might differ according to their hierarchical status (Appleby, 1980; Denehy, 2001). Studied females were classified in three categories of equal size: high-, middle-, or low-ranking individuals based on the outcomes of approach-avoidance behaviors (see for details: [Poirotte et al., 2016]). From the model structure used in the first set of LMMs, we used model selection based on the second order Akaike information criterion (AICc, MuMIn package v. 1.15.6 [Barton, 2009], R; see [Burnham & Anderson, 2004; Mundry, 2011]) to select a simplified model on females. Indeed, a full model comprising female’s social rank and the other variables considered above was impossible to fit because of a limited sample size.

Males were then tested separately from females because the social rank is not comparable between sexes (Setchell & Dixson, 2002). In males, we studied individuals aged 8 years and older because younger males are always of low rank possibly confounding the effect of the age with the effect of the social rank. As for females, we considered three classes of social rank: the alpha male was considered as high-ranking, males of rank 2–5 were considered as middle-ranking males and males below were all considered as low-ranking individuals. We used Kruskal-Wallis tests (stats package, R) to investigate the relationship between the DMTA parameters and the social rank in males because of a limited sample size.

### 2.7.2 | Masticatory muscle thickness and parotid salivary gland dimensions

For each sex, we first used a locally weighted scatterplot smoothing regression (LOESS) to obtain the residuals of organ sizes not explained by age. We then used Spearman correlation tests to explore the relationships between the residuals of masseter thickness or of parotid width/length and DMTA parameters of the crushing facets ( $N = 12$

individuals for whom both sets of information were available) only, because of a limited data set available for the shearing facets.

### 2.7.3 | Diet composition

We investigated the influence of seasonality, sex and age on the percentages of hard, soft, tough and fibrous food items, as well as the percentage of monocotyledonous plants consumed by the studied mandrills across the three seasons using LMMs with the individual's identity as a random effect. The consumption of underground food items was tested as a binary variable (whether the individuals were seen consuming such items or not) because of an over-representation of "0" (no consumption of underground food items).

## 2.8 | Ethics

Protocols used for our research have been validated by the CENAREST institution (authorization numbers: ARO001/14 and ARO018/15). Concerning the ethical treatment of non-human primates, we followed the legal requirements of Gabon.

## 3 | RESULTS

### 3.1 | Dental microwear textural parameters, seasonality, and individual traits

Anisotropy, complexity, and heterogeneity of complexity all vary according to the season of sampling (Table 1). The shearing facets tend to be more complex during the long rainy season but less anisotropic than during any other season, especially compared to the long dry season where anisotropy is the highest and complexity the lowest (Tables 1 and 2; Figure 2a,c). Complexity and heterogeneity of complexity of the crushing facets are lower during the long dry season compared to the short rainy season (Figure 2b,d). Anisotropy of the crushing facets is significantly higher in females than in males (Tables 1 and 2; Figure 3a). Additionally, textural fill volume of these facets tends to increase with age but the relationship is only marginally significant (Table 1). The individual social rank does not impact DMTA parameters, neither in females nor in males (Table 1a,b).

### 3.2 | Masticatory muscles, salivary glands, and dental microwear textural parameters

Females have thinner masseter muscles (mean = 6.70 mm) and a thinner (17.06 mm) but longer (29.48 mm) parotid than males (mean masseter thickness = 8.52 mm; mean parotid width = 18.68 mm; mean parotid length = 29.12 mm). Older individual present thicker masseter muscles and longer and larger parotid glands than younger animals. Despite these age-related effects, we did not find any correlation between masseter's and parotid's size and the four DMTA parameters (see Table S2 in Supporting Information).

### 3.3 | Diet composition

The mechanical properties, the plant clade and the spatial position of the consumed items all vary across seasons (Table 3; and see Table S1 in Supporting Information for a full description of the consumed items). Mandrills feed significantly more on soft food items but less on tough food items during the long rainy season compared to the long dry season (Table 4; Figure 2e,f). During the long rainy season, monocotyledonous plants constitute a substantial part of the mandrills' diet compared to the other two seasons (Figure 2g). The studied individuals consume more underground food items during the long dry season than during the two rainy seasons (Figure 2h). Finally, males feed more on hard food items and less soft items than do females (Tables 3 and 4; Figure 3b) and older individuals also consume more hard food items compared to younger individuals (Table 3; Figure 3d). Moreover, the consumption of soft food items and monocotyledonous plants decreases with individual age (Table 3; Figure 3c).

## 4 | DISCUSSION

In this study, we investigated the effects of seasonality and individual traits on four DMTA parameters obtained in vivo from a large population of living non-human primates. We provided, as such, unique insights into the formation of dental microwear in natural conditions. In particular, we showed that the season of collection influences several DMTA parameters. In parallel, both the mandrill's diet (Nsi Akoué et al., 2017) and the estimated physical properties of the consumed food items also change seasonally. We further found that DMTA parameters vary with the individual's sex and age, possibly reflecting different feeding strategies. Finally, we reaffirmed that DMTA parameters vary by dental wear facet, highlighting the importance of considering the chewing phases (crushing vs. shearing) for a correct interpretation of the species' feeding ecology (Gordon, 1984; Krueger et al., 2008; Teaford & Walker, 1984).

Overall, mandrills of the studied population present relatively low anisotropy and low complexity of both the crushing and the shearing facets in that their average values are below a threshold proposed by Scott and colleagues (2012), respectively, set at 2 and  $5 \times 10^{-3}$ . This result is consistent with the omnivorous diet (but with a clear frugivorous tendency) of mandrills (Nsi Akoué et al., 2017). Following the concept of the feeding ecological space (Scott et al., 2012) and using anisotropy and complexity of the tooth surfaces as the two best diet proxies, we replaced mandrills among other Cercopithecidae species (Figure 4) for which DMTA parameters are available (Scott et al., 2012; Shapiro, 2015). Mandrills appear close to other generalist feeders such as *Lophocebus albigena* and *Cercopithecus mitis*. They are also close to folivorous species (eating tough food items; *Procolobus badius*, *Colobus guereza*, *Procolobus rufomitatus*) and to one species consuming important amounts of seeds (hard food items; *Colobus polykomos*). As expected, species that feed mainly on leaves show higher anisotropy than generalists, frugivorous or hard-item feeders (Merceron, Escarguel, Angibault, & Verheyden-Tixier, 2010; Scott, 2012; Shearer et al., 2015; Ungar, Merceron, & Scott, 2007). Additionally, these folivorous species

TABLE 1 Seasonal and individual effects on dental microwear textural parameters

(a) Results from the LMM are shown (degrees of freedom, *F* and *p*-values) for the two studied facets of *M*<sub>1</sub> and *M*<sub>2</sub>. The influence of female's social rank was further tested independently using the best model structure predicted by the second order Akaike information criterion (see Methods)

Dependent variable	Explanatory variable	Degree of freedom	Crushing facets			Shearing facets		
			Sample size	<i>F</i>	<i>p</i> -value	Sample size	<i>F</i>	<i>p</i> -value
<i>Anisotropy</i>	<b>Season</b>	2	71	1.96	.17	46	<b>7.14</b>	<b>.07</b>
	<b>Sex</b>	1		<b>7.06</b>	<b>.01</b>		0.64	.43
	Age	1		0.22	.65		1.10	.37
	Tooth	1		<0.01	.97		1.19	.36
	Facet	3		0.97	.43		1.42	.39
	Female's social rank	2	32		0.10	.91	-	-
<i>Complexity</i>	<b>Season</b>	2	71	<b>8.70</b>	<b>&lt;.01</b>	46	<b>8.79</b>	<b>.06</b>
	Sex	1		0.69	.41		0.49	.49
	Age	1		0.05	.82		1.72	.28
	Tooth	1		0.16	.69		<0.01	.95
	Facet	3		1.15	.36		0.75	.59
	Female's social rank		32		0.55	.60	-	-
<i>Heterogeneity of complexity</i>	<b>Season</b>	2	71	<b>2.83</b>	<b>.09</b>	46	1.49	.36
	Sex	1		0.70	.41		0.82	.37
	Age	1		0.51	.49		0.08	.79
	Tooth	1		0.21	.66		1.06	.38
	Facet	3		1.11	.37		0.81	.57
	Female's social rank		32		0.01	.99	-	-
<i>Textural fill volume</i>	Season	2	71	1.24	.32	46	1.29	.40
	Sex	1		1.92	.17		0.04	.84
	<b>Age</b>	1		<b>3.75</b>	<b>.07</b>		3.69	.15
	Tooth	1		0.85	.37		2.30	.23
	Facet	3		2.23	.12		0.57	.67
	Female's social rank		32		0.04	.875	-	-

Significant ( $p < .05$ ) effects or trends ( $p < .10$ ) are shown in bold.

(b) Effects of males' social rank on the four dental microwear textural parameters. Results from Kruskal-Wallis tests are shown ( $\chi^2$  and *p*-values). These analyses are based on males' crushing facets ( $N = 10$ ).

	$\chi^2$	<i>p</i> -value
<i>Anisotropy</i>	3.03	.22
<i>Complexity</i>	1.06	.59
<i>Heterogeneity of complexity</i>	1.86	.39
<i>Textural fill volume</i>	0.64	.73

present low mean complexity supporting the assumption that tough food items tend to be associated with a low complexity of the tooth surfaces (see discussion below). Generalist feeders, such as mandrills, are spread across the species' range and are characterized by a wide distribution of anisotropy and complexity. This latter observation suggests that the signals retrieved from DMTA parameters of generalist

feeders may be partly driven by the texture of the most frequent food item(s) consumed at the time of dental molding (or at the time of death in the case of post-mortem studies).

In the studied mandrills, anisotropy of the shearing facets and complexity of both facets vary seasonally while heterogeneity of complexity of the crushing facets yields similar results as complexity.

TABLE 2 Raw data of dental microwear textural parameters across seasons and sexes

	Anisotropy ( $\times 10^3$ )			Complexity		Heterogeneity of complexity		Textural fill volume ( $\times 10^{-3}$ )	
	N	m	sem	m	sem	m	sem	m	sem
<b>Crushing facets</b>									
Overall	71	4.28	0.26	1.73	0.09	0.45	0.03	68.75	1.34
Females	32	5.01	0.38	1.55	0.11	0.46	0.04	70.92	1.94
Males	39	3.66	0.32	1.87	0.14	0.44	0.04	66.97	1.82
Long rainy season	18	4.65	0.57	2.05	0.19	0.40	0.50	72.87	0.24
Long dry season	41	4.00	0.29	1.42	0.94	0.24	0.04	66.89	1.84
Short rainy season	12	4.61	0.80	2.28	0.28	0.598	0.09	68.91	3.09
<b>Shearing facets</b>									
Overall	46	4.39	0.27	1.55	0.12	0.43	0.03	68.19	1.57
Females	18	5.09	0.44	1.35	0.13	0.42	0.04	68.32	3.26
Males	28	3.93	0.33	1.68	0.18	0.43	0.04	68.11	1.55
Long rainy season	10	2.97	0.47	2.06	0.28	0.34	0.04	66.05	2.68
Long dry season	27	5.01	0.35	1.20	1.04	0.41	0.03	68.67	2.28
Short rainy season	9	4.08	0.51	2.03	0.33	0.58	0.09	69.13	3.13

Sample size (N), mean (m), and standard error of the mean (sem) for the four studied DMTA parameters of each studied facet are displayed.

Highest values of anisotropy were observed during the long dry season, also characterized by a diet composed of more tough and underground food items than other seasons. This is in agreement with other studies where anisotropy of the shearing facets was associated with elevated consumption of tough food items such as leaves, stems and roots (Hedberg & DeSantis, 2016; Merceron, Hofman-Kamińska, & Kowalczyk, 2014; Schulz, Calandra, & Kaiser, 2010; Ungar et al., 2008, 2007). In addition, the abrasive particles contained in the highly quartz-concentrated soils of the study place (Galbany et al., 2014), and probably covering underground food items, may contribute to increase anisotropy, as each single particle may scratch dental enamel. Underground food items constitute, however, only a minor part of mandrills' overall diet and dust deposits, reported in aerial food parts elsewhere (Ungar, Teaford, Glander, & Pastor, 1995), could also constitute an alternative and non-negligible source of abrasive particles. Abrasive particles may further explain why we observed a lower complexity of both studied facets during the long dry season compared to other seasons. Indeed, they may smooth the occlusal relief through hard rubbing resulting in a "polishing process" (for a related discussion on this process, see also: Puech, Cianfarani, & Albertini, 1986; Ryan, 1981). In addition, the plant parts included in the "tough" category contain silica phytoliths in varying concentrations that may also abrade dental enamel (Gügel et al., 2001; Rabenold & Pearson, 2011; Walker et al., 1978) and thus contribute to a low complexity observed during the long dry season. The low complexity of the crushing facets observed in anthropoid primates because of the grinding of (tough) leaves further supports the polishing process we suggest (Scott et al., 2012), although anisotropy seems unaffected by this process, perhaps because shallow scratches still accumulate on the tooth surface.

By contrast, the rainy seasons are characterized by more complex (but less anisotropic, especially true for the long rainy season) tooth surfaces. These observations are paralleled with an elevated consumption of soft food items, such as fruits, that season. Among browser ruminants, fruit eaters also present higher complexity of their tooth

surfaces than exclusive leaf consumers (Merceron et al., 2014). In anthropoid primates, however, higher complexity is the result of higher proportion of seeds (considered as hard food items) consumed (Scott et al., 2012). To solve these apparent discrepancies, we propose that the high complexity we observe in mandrills during the long rainy season may result from elevated consumption of small, but hard, fruit pips and seeds contained in some fruits that may indent tooth enamel (Lucas, Constantino, Wood, & Lawn, 2008; Teaford & Runestad, 1992). For example, pips consumed in large quantities impact dental microwear textural parameters in sheep (Ramdarshan et al., 2016). The studied mandrills also often consume pome fruits containing lots of pips, such as *Aframomum daniellii* or *Xylopiya aethiopica* (Nsi Akoué et al., 2017), reinforcing our hypothesis. Alternatively, fruits may contain more adhesive substances causing small pitting and thus increasing complexity (Teaford & Runestad, 1992). During the rainy seasons, the proportion of consumed monocotyledonous plants is also higher compared to the long dry season, paralleled with higher complexity of both facets and lower anisotropy of the shearing facets (especially during the long rainy season). However, we supposed that high concentrations in phytoliths, as expected in monocotyledonous plants compared to dicotyledonous plants, would rather decrease complexity through a polishing process and to increase anisotropy, as proposed above. As such, in ruminants, grazing diets (mainly composed of monocotyledonous plants) are generally associated with high anisotropy values (Merceron et al., 2014, 2016; Scott, 2012). Our counter-intuitive results in mandrills suggest that phytolith contents of the plants consumed probably impact the formation of dental microwear differently depending on the taxon considered and the surrounding environment.

In this study, we further found individual effects on DMTA parameters possibly reflecting different individual feeding strategies. The crushing facets appear less anisotropic in males than in females while males consume significantly more hard and less soft food items. These differences between sexes seem contradictory with the possible relationship we highlighted above between low anisotropy and high



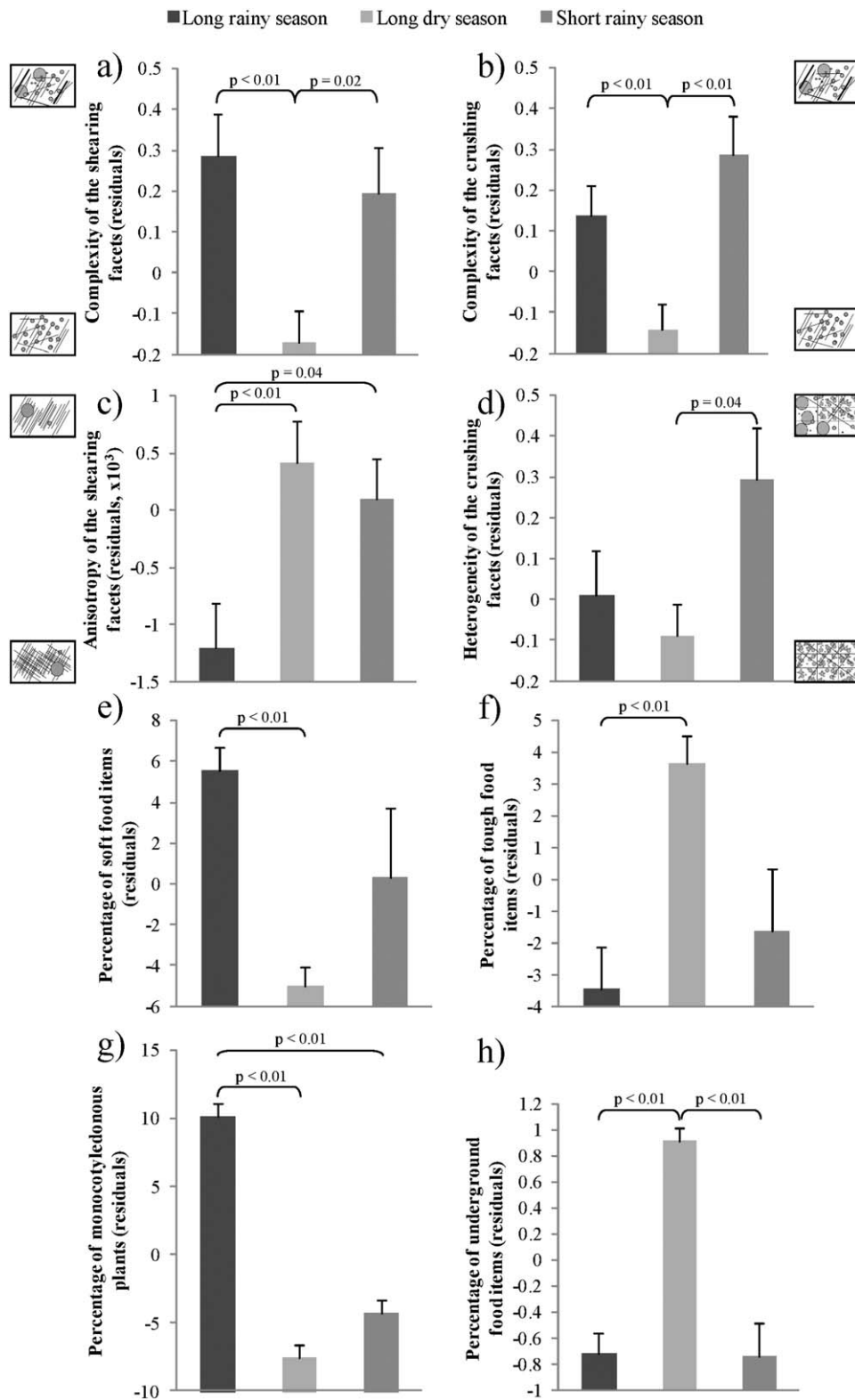


FIGURE 2 Effects of seasonality on DMTA parameters and on mandrills' diet. Small drawings of dental microwear were modified from Scott et al. (2006). Standard errors of the mean and Tukey's HSD *p*-values used for pairwise comparisons are displayed on each panel

consumption of soft items. Alternatively, differences of anisotropy between sexes may depend on sexual dimorphism in jaw kinematics (as per: Schmidt et al., 2016), although we currently have no

data to support this hypothesis and our limited sample size did not allow to bring out any effect of masseter thickness on DMTA parameters.

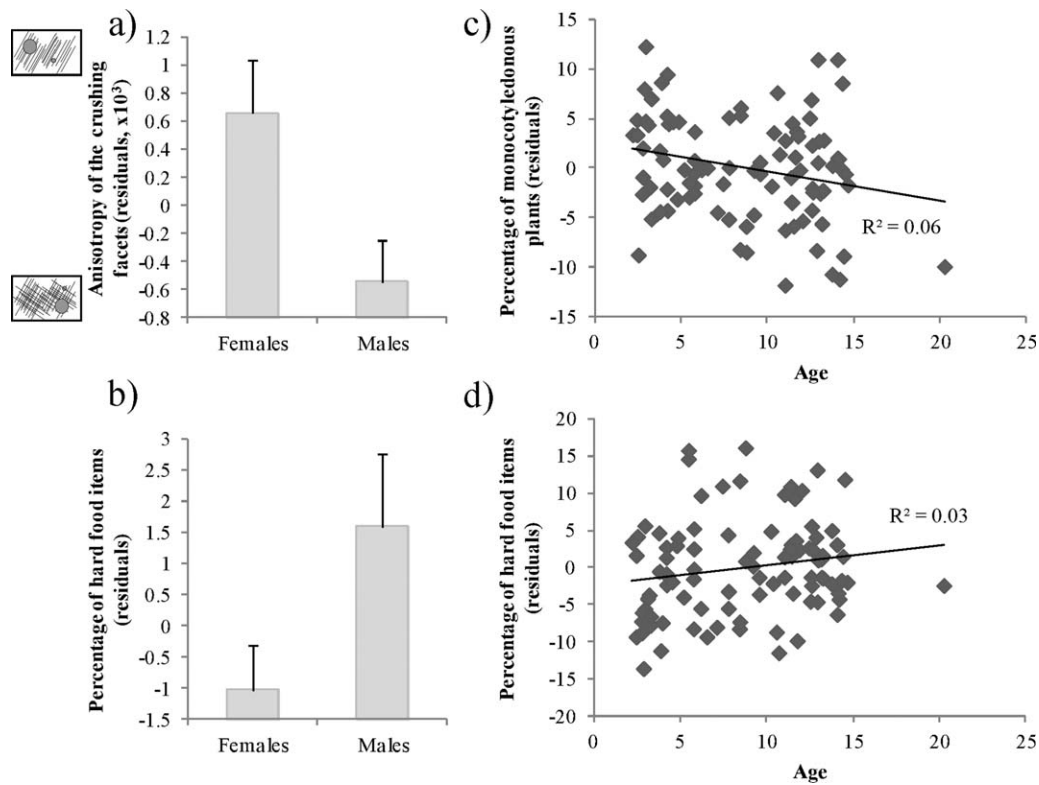


FIGURE 3 Effects of individual's sex and age on DMTA parameters and on mandrills' diet

TABLE 3 Seasonal and individual effects on the physical properties of the food items consumed by 45 individuals

Dependent variable	Explanatory variable	Degree of freedom	F	p-value
<i>Hard</i>	Season	2	2.32	.11
	Sex	1	5.96	.02
	Age	1	4.18	.05
<i>Soft</i>	Season	2	18.34	<.01
	Sex	1	6.05	.02
	Age	1	3.72	.06
<i>Tough</i>	Season	2	10.54	<.01
	Sex	1	0.53	.47
	Age	1	<0.01	.99
<i>Monocotyledonous</i>	Season	2	108.49	<.01
	Sex	1	2.00	.17
	Age	1	8.33	.01
<i>Underground<sup>a</sup></i>	Season	2	16.17	<.01
	Sex	1	0.03	.66
	Age	1	0.62	.43

Results of LMM are shown (degrees of freedom, *F* and *p*-values), with significant effects ( $p < .05$ ) and trends ( $p < .10$ ) in bold.

<sup>a</sup>The intake of underground food items was considered as a binary variable (see Methods section).

**TABLE 4** Physical properties of the food items consumed by the studied individuals

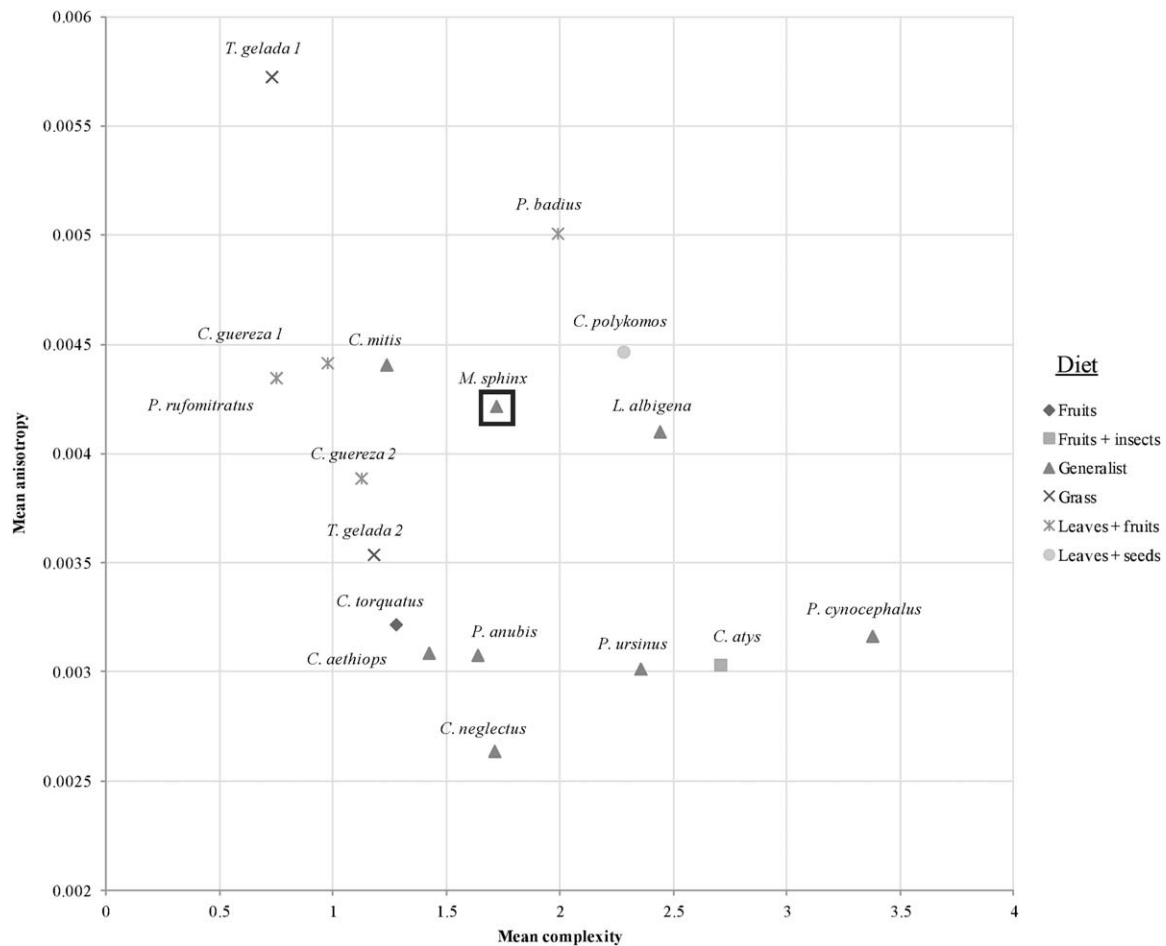
Physical properties	Overall	Long rainy season	Long dry season	Short rainy season
<b>Mechanical properties</b>				
Hard	28.47 Females: 28.88 Males: 30.80	27.88	31.29	33.50
Soft	40.21 Females: 39.98 Males: 38.13	44.85	33.77	37.45
Tough	26.97 Females: 26.68 Males: 26.93	22.91	30.65	24.81
<b>Spatial position</b>				
Aerial	97.30 Females: 97.56 Males: 97.28	99.48	95.30	99.03
Underground	2.70 Females: 2.44 Males: 2.72	0.52	4.70	0.97
<b>Plant clade</b>				
Dicotyledonous	79.77 Females: 78.53 Males: 78.93	67.26	85.78	84.36
Monocotyledonous	19.98 Females: 21.19 Males: 20.90	32.74	14.09	14.52

The table presents the percentages of consumption of food items according to their mechanical properties, their plant clade and their spatial position (averaged across studied animals). Indeterminate and rare food items (fibrous, doughy, moss, fern) are not presented in this table.

We also found that textural fill volume of the crushing facets tends to increase with age, suggesting that this textural parameter may reflect general tooth wear, higher in older mandrills (Galbany et al., 2014) and in other mammals (Lambrechts, Braem, Vuylsteke-Wauters, & Vanherle, 1989; Venkataraman et al., 2014; Wright, Viner-Daniels, Parker Pearson, & Albarella, 2014). In the studied population, juveniles spend more time feeding compared to adults and diet composition varies according to individual age (Nsi Akoué et al., 2017). Moreover, age slightly impacts the proportion of hard food items and monocotyledonous plants consumed. These food items may partly drive the variation observed of textural fill volume. Accordingly, some authors argued that hard food items processing may cause large pits on the enamel surface compared to superficial damages produced by softer food items thereby increasing textural fill volume (Calandra, Schulz, Pinnow, Krohn, & Kaiser, 2012; Daegling & Grine, 1999; El-Zaatari, Grine, Teaford, & Smith, 2005; Teaford & Oyen, 1989; Teaford & Runestad, 1992; Teaford & Walker, 1984). Overall, the four DMTA parameters studied all indicate inter-individual variations, with the crushing and the shearing facets yielding slightly different results that may be related to individual differences in feeding selectivity. The chewing strategy depends on morphological constraints imposed by jaws, teeth and muscles but also on the mechanical properties of the food items consumed that may all vary between individuals, between populations and even between species (Dumont, 1999; Iriarte-Díaz, Reed, & Ross, 2011; Kay, 1977; Kay & Hiiemae, 1974; Krueger et al., 2008; Van Valkenburgh, 1996; Venkataraman et al., 2014). The generalist diet characterizing mandrills implies diversified feeding habits

which result in a combination of the two chewing phases and, accordingly, in distinct signals on the dental wear facets involved. Our results should, however, be interpreted cautiously as dietary data and tooth replicas were not obtained at the same time on the study population. This may also explain some of the seemingly contradictory results we found between seasonal vs. individual effects and between our study and other studies on primates. In addition, the coarse-grained estimates of food physical properties we used may further complicate the signals we tentatively highlighted. We did not, for example, record which fruit tissue (endocarp, mesocarp, or exocarp) was consumed while these tissues are clearly characterized by different mechanical properties (Vogel et al., 2008).

To conclude, we reaffirm that dental microwear textural parameters, especially anisotropy and complexity, are promising estimates of both the local environment and individual traits and may further contain useful information to determine the physical properties of a species' preferred food items although our results need now to be confirmed using experimental approaches such as controlled diet. Microwear data obtained on this natural population of mandrills may be used in future paleontological studies, for example to infer some aspects of the paleoecology of extinct Old World monkeys such as *Soromandrillus* Gilbert et al. 2014 or *Procercocebus* Gilbert 2007 (Plio-Pleistocene, Olduvai Bed I, Tanzania), two extinct species phylogenetically close to mandrills (Gilbert, Frost, & Delson, 2016). Ultimately, understanding the relationships between morphology and diet in living species is essential to reconstruct the feeding ecology from isolated dental material belonging either to extinct species or to cryptic animals.



**FIGURE 4** Mandrills from the studied population (within the bold square) replaced in an ecological space with other cercopithecoid populations. This ecological space is defined by the anisotropy and the complexity of the tooth surfaces, averaged for each population. Species displayed on the graph are: *Cercocebus atys* (*C. atys*), *Cercocebus torquatus* (*C. torquatus*), *Cercopithecus mitis* (*C. mitis*), *Cercopithecus neglectus* (*C. neglectus*), *Chlorocebus aethiops* (*C. aethiops*), *Colobus guereza* (*C. guereza*), represented by two different populations (1 and 2), *Colobus polykomos* (*C. polykomos*), *Lophocebus albigena* (*L. albigena*), *Mandrillus sphinx* (*M. sphinx*), *Papio anubis* (*P. anubis*), *Papio cynocephalus* (*P. cynocephalus*), *Papio ursinus* (*P. ursinus*), *Procolobus badius* (*P. badius*), *Procolobus rufomitratus* (*P. rufomitratus*), and *Theropithecus gelada* (*T. gelada*), represented by two populations (1 and 2)

## AUTHOR'S CONTRIBUTIONS

AMP, MJEC, JG, AR, and GM conceived the ideas and designed the methodologies; AMP, GN, MJEC, and JG collected the data; AMP analyzed the data; AMP and MJEC led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Authors will make the data accessible in Dryad in case of acceptance of this manuscript.

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## SUPPORTING INFORMATION

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