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Mechanical food properties and dental topography differentiate three populations of *Lemur catta* in southwest Madagascar

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ABSTRACT

Determining the proximate causes of tooth wear remains a major focus of dental study. Here we compare the diets of three ring-tailed lemur (*Lemur catta*) populations and examine how different dietary components may contribute to patterns of wear-related tooth shape. Casts were made from dental impressions collected between 2003 and 2010 from lemurs in the gallery and spiny/mixed forests of the Bezá Mahafaly Special Reserve (BMSR; Parcels 1 and 2) and the spiny/mixed forests of Tsimanampesotse National Park (TNP), Madagascar. Tooth shape variables (occlusal relief and slope, angularity) were analyzed using dental topographic analysis. Focal observations and food mechanical properties (FMPs: toughness, hardness, elastic modulus) were conducted and tested, respectively, during wet and dry seasons from 2008 to 2012. We found that FMPs correlate with patterns of dental topography in these three populations. Specifically, food toughness and elastic modulus correlate with the dental variables, but hardness does not. Average food toughness and elastic modulus, but not hardness, are highest in BMSR Parcel 2, followed by BMSR Parcel 1 and TNP. Occlusal relief and slope, which serve as proxies for tooth wear, show the greatest wear in Parcel 2 and the least in TNP. Angularity is also more pronounced in TNP. Further, dental topographic patterns correspond to reliance on *Tamarindus indica* (tamarind) fruit. Both BMSR populations consume tamarind at high frequencies in the dry season, but the fruits are rare at TNP and only occasionally consumed. Thus, high seasonal tamarind consumption and its mechanical values help explain the low dental relief and slope among BMSR lemurs. By investigating the ecology of a single widespread species across a variety of habitats, we have been able to link specific components of diet to patterns of dental topography in this species. This provides a context for interpreting wear-related tooth shape changes more generally, illustrating that populations can develop different dental wear patterns resulting from a mix of intrinsic factors (thin enamel) and local conditions (food properties, frequency of consumption).

1. Introduction

Understanding the process of how mammalian teeth wear has garnered considerable attention (e.g., Baker et al., 1959; Kay and Covert, 1983; Teaford and Tylenda, 1991; Ungar et al., 1995; Ungar, 1998; Teaford, 2000; Dennis et al., 2004; Lucas, 2004; Nystrom et al., 2004; Cuozzo and Sauther, 2006; Sanson et al., 2007; Galbany et al., 2011; Rabenold and Pearson, 2011, 2014; Lucas et al., 2013; Pampush et al., 2013). These studies have identified numerous potential causal variables that include food mechanical properties, biogenic silica, exogenous grit, chemical properties of food, and food processing (e.g., Ungar et al., 1995; Sanson et al., 2007; Cuozzo et al., 2008; Rabenold and Pearson, 2011, 2014; Yamashita et al., 2012a; Lucas et al., 2013, 2014). However, to date, there remains a lack of consensus on which of these variables, or combination of variables, are the proximate

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causes of mammalian tooth wear (e.g., Lucas et al., 2013, 2014; Rabenold and Pearson, 2014).

Since 2006 we have been investigating the degree to which food mechanical properties (FMPs) contribute to differences in tooth shape in populations of ring-tailed lemurs (*Lemur catta*) from southwestern Madagascar. One of the benefits of studying dental topography in wild ring-tailed lemurs is the large body of ecological and behavioral information available for this species (e.g., Gould et al., 2003; Jolly et al., 2006; Sauther et al., 2015; and see below). Accordingly, ring-tailed lemurs are an ideal study species for dental ecology, which combines examination of dentition with detailed ecological information (Cuozzo and Sauther, 2012).

L. catta populations inhabit environments in southern Madagascar ranging from gallery forest to desert scrub (Goodman and Langrand, 1996; Sauther et al., 1999; Kelley, 2013; LaFleur et al., 2014). Until recently, they were primarily studied in gallery forest habitats (e.g., Jolly, 1966; Sauther et al., 1999), although current research outside these areas has expanded our knowledge of the ecological flexibility of these animals (e.g., Kelley, 2013; LaFleur et al., 2014; Sauther et al., 2015). The riverine gallery forests of Bezá Mahafaly Special Reserve (BMSR) and Berenty reserve, where ring-tailed lemurs have been studied for more than 25 years, are dominated by *Tamarindus indica* trees (e.g., Jolly, 1966; Sussman and Rakotozafy, 1994; Blumenfeld-Jones et al., 2006). The fruits of this tree are the dominant food in the diets of the ring-tailed lemurs in these forests (e.g., Sauther, 1998; Yamashita, 2002; Blumenfeld-Jones et al., 2006; Gould, 2006). Our earlier work has established that dependence on the fruit of *T. indica* is related to the degree of postcanine dental wear in the BMSR populations (Cuozzo and Sauther, 2006; Cuozzo and Sauther, 2008; Yamashita et al., 2012a). This fruit, particularly the outer shell of the ripe fruit, is the most mechanically challenging food (e.g., toughest, hardest, stiffest) in the ring-tailed lemur diet at this site (Yamashita et al., 2012a). The mechanical properties and the methods used by the lemurs to orally process the fruit contribute to the patterns of extreme wear and tooth loss observed in these populations (Yamashita et al., 2012a). The lemurs insert the long tamarind pod into the side of the mouth and bite repeatedly to crack the stiff outer shell. It is in precisely this location where we observe the heaviest wear. Furthermore, ring-tailed lemurs have thin dental enamel and the repeated stresses incurred from feeding on a relatively large fruit most likely contribute to producing microcracks in the enamel that radiate out from the enamel-dentine junction (Lucas et al., 2008; Constantino et al., 2009). Such cracks have been observed in ring-tailed lemur teeth (Campbell et al., 2012).

In this paper, we extend our analyses of diet and dental topography (i.e., dental ecology) to include a population of ring-tailed lemurs in the spiny and mixed forests of Tsimanampesotse National Park (TNP), which lies 135 km southwest of BMSR, and lemurs from the drier spiny and mixed forest in the western section of BMSR. Though tamarind is present in all three sites, it differs in abundance, thus allowing us to refine our hypothesis that consumption of the fruit is a primary cause of tooth wear in ring-tailed lemurs. Tamarind trees are common in the BMSR gallery forest, less common in the BMSR spiny and mixed forests 5 km to the west, and restricted to the base of a plateau and in limestone depressions at TNP (Sussman and Rakotozafy, 1994; Axel and Maurer, 2010; LaFleur, 2012). In our analyses, we compare three dental topographic variables with food mechanical properties, diet, and habitat across three populations of ring-tailed lemurs. Our primary goals in this paper are to determine if 1) dental topographic variables and 2) food mechanical properties differ by site and 3) if the dental and food properties variables are correlated among sites (definitions for dental terms are below).

2. Materials and methods

2.1. Study sites and species

Our study populations inhabit the riverine gallery forest (Parcel 1 [P1]) and degraded dry/spiny forest (Parcel 2 [P2]) of the Bezá Mahafaly Special Reserve (BMSR; 23°30′S, 44°40′E) and the mixed deciduous and spiny forest habitats of Tsimanampesotse National Park (TNP; 24° 07′S, 43°45′E). The two sites in BMSR are 5 km apart, with the gallery forest extending approximately 1 km west of the ephemeral Sakamena River. TNP is approximately 135 km southwest of BMSR and 7 km east of the Mozambique Channel (Fig. 1).

All three sites experience distinct wet and dry seasons, although the average durations vary by site. Generally, a warm, wet season occurs from November to March and a cool, dry season from April to October. Parcel 1 in BMSR comprises an 80 ha plot surrounded by a protective fence that serves to keep livestock out of the forest but does not prohibit lemur movement across the reserve boundary. A tamarind-dominated gallery forest forms the eastern boundary along the seasonal Sakamena River, and the forest becomes progressively drier to the west (Sussman and Rakotozafy, 1994; Sussman and Ratsirarson, 2006). Outside the fenced-in portion, the forest has been degraded by grazing livestock and other human actions (e.g., Cuozzo and Sauther, 2004; Sauther et al., 2006; Sauther and Cuozzo, 2009). Parcel 2 and the surrounding area are composed of a patchwork of dry, deciduous forest and spiny forest (Axel and Maurer, 2010). Our study groups are in Parcel 2 as well as to the north and west of this area. The ring-tailed lemur troops in this area primarily inhabit the dry forest, although groups also

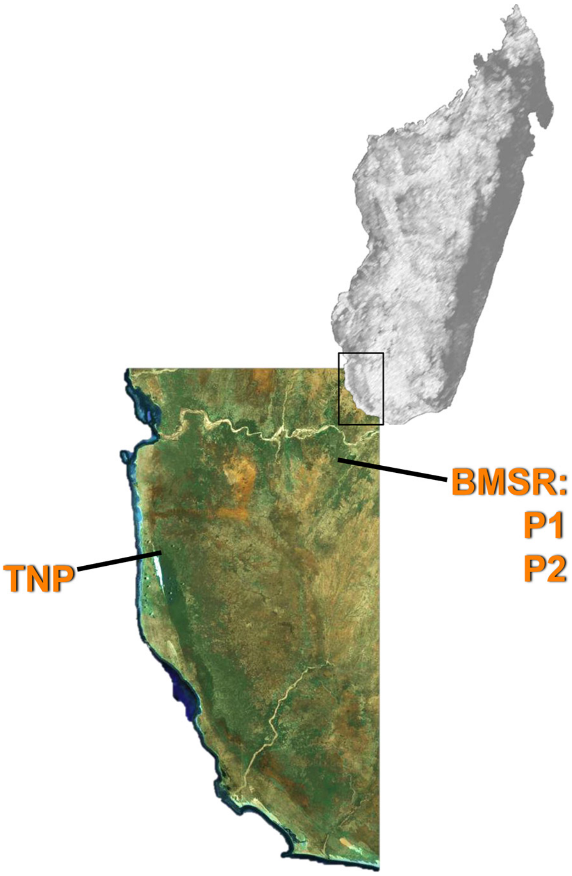

Figure 1. Location of the three study sites in southwest Madagascar (terrain map modified from Google maps, 2014).

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range to the top of an escarpment to the west, which is devoid of tamarind but contains characteristic spiny forest vegetation. The top and slopes of the escarpment represent a habitat type not found in P1 but instead is more similar to the plateau spiny forest at TNP.

Median rainfall in P1 is 620 mm, mostly falling in the wet season (Lawler et al., 2009). We note that rainfall amounts can oscillate widely over years. Average daily high temperatures have ranged from 34° to 38 °C in 1999–2000 in the dry and wet seasons, respectively (Yamashita, 2002), to 36° to 46 °C in 2009–2010 (O'Mara and Hickey, 2012). We do not have separate records for the P2 area.

The environment at TNP is arid and seasonal and is characterized as xerophytic spiny forest with few tall trees and little canopy (Sauther et al., 2013; LaFleur et al., 2014). The portion of the park located on the Mahafaly Plateau is dominated by xerophytic euphorbs, with areas below the plateau's western escarpment containing a mix of dry, seasonal, and xerophytic flora (Sauther et al., 2013; LaFleur et al., 2014). From September 2010 to April 2011, average daily temperatures ranged from 10° to 42 °C with highs >50 °C, and cumulative rainfall was 232 mm in the wet season from December to February (LaFleur et al., 2014).

2.2. Dietary data collection and mechanical tests

During 2008–2012, observations and mechanical food testing were conducted in the wet season in January–February and in the dry season in June–July (Table 1). The ring-tailed lemur troops in BMSR ranged from 5 to >15 individuals. We followed troops in P1 in different areas of the parcel to capture microhabitat differences. We primarily followed one semi-habituated group of ring-tailed lemurs in the P2 area. Observations at TNP were on two groups, which had approximately 10–14 adult individuals each. Most of the individuals in P1 and P2 at BMSR wore identifying collars and pendants, and at least two individuals in each group at TNP had collars.

Dietary data collection included focal animal observations with quantification of activity budgets followed by food collection and testing. Animals were observed with continuous bout focal observations. Data were taken on basic activities (e.g., feeding, movement) and time spent in each activity. During feeding, the precise plant part eaten (e.g., unripe fruit, mature leaves) and detailed feeding behaviors were noted. Foods were collected immediately after feeding, often from the same branch or vine from which the animals fed. In addition to the plant part that the animals were observed to eat, outer coverings that the animals processed orally and discarded were also tested. All collected plant parts were placed in sealed plastic bags with a small amount of water and brought back to the camp for mechanical testing (e.g., Yamashita et al., 2012a).

Mechanical tests were performed with the Darvell mechanical tester and included toughness (scissors cutting test [R]), indentation (hardness [H)], and elastic modulus (in either compression or 3-point bending [E]). We tested all parts that we observed animals eating and any part that was stripped away orally prior to feeding.

Table 1
% Feeding time on *Tamarindus indica* fruits (within season %).[a]

Season	P1	P2	TNP
1999 dry	0.25		
2000 wet	0.27		
2008 dry	0.39		ND
2010 wet	0.36	0.14	
2010 dry	0.66	0.67	
2011 wet			0.00
2012 wet		0.01	

[a] Adapted from Yamashita et al. (2012a).

2.3. Dental topographic analysis

We define tooth wear as the removal of dental tissue through a combination of mechanical (food processing) and/or chemical (erosive) processes. Dental topographic analysis, a frequently used technique for assessing occlusal shape (Ungar and Williamson, 2000; Ungar and M'Kirera, 2003; Bunn and Ungar, 2009; Cuozzo et al., 2014), does not directly measure tissue removal but provides a set of proxy variables that reflect occlusal surface variation. Occlusal relief and slope reflect variation in height and shape of the occlusal surface; low relief and slope are interpreted as proxies for wear. This approach has the advantage of not requiring knowledge of unworn enamel tissue volume in order to assess degree of wear. This information is difficult to obtain for living primates and impossible for already worn fossil teeth. Both variables generally, and necessarily, show a relationship with age, although within population variation has been shown at young ages among wild ring-tailed lemurs (Cuozzo et al., 2014). Angularity measures the sharpness of the occlusal surface and has been shown to vary little within different primate taxa and across habitats (Ungar and M'Kirera, 2003), except at extreme stages of tooth wear as teeth approach functional senescence (see review in Cuozzo et al., 2014). Angularity is therefore a poor proxy for wear. Throughout the current study we use the term “wear” to reflect the proxy variables occlusal relief and slope and “topography” to denote all three dental variables assessed (relief, slope, and angularity).

Dental impressions were collected from wild lemurs captured from 2003 to 2010. Total sample numbers for P1, P2, and TNP were 45 (27 females, 18 males), 19 (9 F, 10 M), and 25 (10 F, 15 M) individuals, respectively. The P1 sample included repeat captures ($n = 30$) of some individuals over several years (2003–2010) for a total of 149 P1 samples. Parcel 2 dental impressions were collected in 2003 and 2010, while TNP impressions were collected in 2006. Individual lemurs in Parcel 2 and TNP were captured once each. Because of the tremendous variability in wear even among same-aged individuals (Cuozzo et al., 2010, 2014), we only had ages for individuals at the long-term field site of P1, where demographic records were used to assign age. Ages in P1 ranged from 1 to older than 10, with most of the individuals between the ages of 2–5 and greater than 10. We did not attempt to assess age or age grades at P2 or TNP other than “adult.” We would not expect age bias in any of the populations since most of the individuals in a troop (excluding infants and young juveniles) were captured for dental casting.

Dental impressions were collected using customized impression trays and President Plus Jet Regular Body polyvinylsiloxane impression material (Coltene®-Whaledent, Mawah, New Jersey, USA; Cuozzo and Sauther, 2006; Cuozzo et al., 2010). Procedures for animal capture are fully described in Cuozzo and Sauther (2006) and Cuozzo et al. (2010). All methods pertaining to animal handling and data collected from living lemurs in Madagascar received approval by and followed standard guidelines and protocols of the Institutional Animal Care and Use Committees of the University of North Dakota and/or the University of Colorado (most recent: University of North Dakota, IACUC #0802-2, approved 04/03/08). Data collection in Madagascar was conducted with approval by Madagascar National Parks, the body governing research in Madagascar's protected areas, and with CITES approval (05US040035/9).

High-resolution replicas of the first and second lower right molars were poured using Epotek 301 epoxy and hardener (Epoxy Technologies, Billerica, MA), centrifuged, allowed to harden, and then coated with Magnaflux Spotcheck (SKD-S2 Developer, Illinois Tools Works, Glenview, IL) to mitigate specimen translucency.

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Resulting replicas were mounted on an XSM multi-sensor scanner stage (Xystum, Turino, Italy) and oriented to maximize the buccolingual and mesiodistal dimensions of the occlusal surface in top view. Point clouds were generated using an integrated OTM3 laser head (Dr. Wolf & Beck GmbH, Wangen, Germany). Elevation data were collected using a lateral point spacing of 25 μm. This resulted in a matrix of 1600 z-values for each 1 mm^2 in the x-y plane. Point clouds were then rendered and processed as ASCII files using Digiline software (Xystum, Turino, Italy) and opened as tables in ArcView 3.2 with Spatial Analyst and 3D Analyst Extensions (ESRI, Redlands, CA). Finally, digital elevation models of the occlusal table were interpolated using inverse distance weighting and cropped to include only the surface above the lowest point on the central basin (for details see Bunn and Ungar, 2009; Cuozzo et al., 2014).

Slope, angularity, and relief values were calculated for each occlusal table model in ArcView. Slope is the average change in elevation between adjacent points on the surface (first derivative of elevation). Angularity, or surface jaggedness, is the average change in slope between adjacent points (second derivative of elevation). Finally, relief is the 2.5D surface area of the occlusal table, calculated in ArcView from a triangulated irregular network model, divided by the planimetric area as projected from above, multiplied by 100 (see M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003).

2.4. Statistical analyses

Data for the mechanical tests among sites were compared with nonparametric Mann–Whitney *U* and Kruskal–Wallis tests.

We first compared the individual dental variables (slope, relief, and angularity) between the M_1 and M_2 (combined sites and within sites) and then compared them among and between sites (see below). We checked for normality and homoscedasticity and used appropriate tests (parametric or nonparametric) depending on the results (see below).

Among the individual dental variables, slope and angularity were not normally distributed. Comparisons of the molar topography variables were therefore initially analyzed with nonparametric tests via three sets of analyses.

The first focused on comparisons between M_1 and M_2. Because the M_1s and M_2s were from the same individual, they were first compared with Wilcoxon signed ranks tests for paired individuals.

The second set of analyses looked at comparisons among and between sites. Given the non-normal distributions of the individual dental variables, we ran a nonparametric Kruskal–Wallis test to compare the dental topographic variables among sites and Mann–Whitney tests between sites. We used Mann–Whitney tests here because the individuals being compared between sites were not paired as they were for the comparisons of M_1 and M_2 above.

For the third set of analyses, due to the potential differences in the values of the dental variables between the M_1 and M_2 and the numbers of separate occlusal variables, we combined all the tooth variables in a principal components analysis (PCA). The resulting PCA factor scores, which represent linear combinations of differences, were then compared among and between sites. PCA factors 1 and 2 were not normally distributed (Shapiro–Wilk's test, factor 1: $W = 0.960$, $p < 0.001$, d.f. = 182; factor 2: $W = 0.957$, $p < 0.001$, d.f. = 182), so we compared the sites with nonparametric tests.

Finally, we compared the occlusal topographic data with the food properties dataset. Because mechanical dietary properties were collected per plant species at each site and dental topography was quantified per individual, we had to recode at least one set of variables. We expected that the dental variables would depend on the food properties, so we recoded the food property values (independent variable) as averages for each site and used the same value for all individuals in that site. The dental variables were the dependent variables in all of our models. We tested the dependent dental variables against the FMPs as independent variables using general linear models. We ran correlations with the dental variables separately against food property values, and we also used the component scores from the PCA to compare overall molar shape with food property values.

For the comparisons of the individual dental variables, some individual M_1 and M_2 values (i.e., slope and angularity) failed tests of normality (Shapiro–Wilk's tests, d.f. = 184 for all M_1 variables, relief M_1 $W = 0.989$, $p = 0.185$; slope M_1 $W = 0.962$, $p < 0.001$; angularity M_1 $W = 0.872$, $p < 0.001$; d.f. = 192 for all M_2 variables, relief M_2 $W = 0.973$, $p = 0.001$; slope M_2 $W = 0.954$, $p < 0.001$; angularity M_2 $W = 0.854$, $p < 0.001$) and had non-linear Q–Q plots. We attempted several transformations to normalize individual variables (e.g., log, square root, inverse, squared) but none yielded a satisfactory result (Sokal and Rohlf, 1995). Nevertheless, we used a linear model because we wanted to model the effect of food properties on tooth shape where the magnitude of the repeated FMP value was important. We report the results with the caveat that the data did not conform to assumptions of normality (though homogeneity of variances was generally supported). One of the three dental variables, relief on the M_1, was normally distributed and the Q–Q plot for relief on the M_2 was essentially linear, so we ran tests with just this dependent variable as a check on the larger model.

For the comparisons involving the PCA component scores, the factor scores from the PCA of tooth shape variables were not normally distributed, although variances were homogeneous. We wanted to treat differences in tooth shape as a continuous variable to investigate whether the actual FMP values were correlated with the degree of molar shape change. We note that the PCA factor scores do not necessarily capture molar shape change per se, but represent linear combinations of the dental topography dataset that summarize variation. We transformed factor 1 by first adding a constant to remove the negative values and tried a number of common transformations (e.g., log, square root, inverse; Sokal and Rohlf, 1995). The square transformation (x*x) resulted in normally distributed data (Shapiro–Wilk's test, $W = 0.989$, $p = 0.156$, d.f. = 182 and a linear Q–Q plot; Wilkinson et al., 1996). Subsequent models were tested with this newly transformed factor 1 with linear models. We could not normalize the distribution of the second component. As with the individual dental variables above, we ran a linear model to assess the effect of food property values on tooth shape with this caveat.

All individual dental variables and FMP tests were two-tailed with $\alpha = 0.05$. In cases of multiple tests, we applied a Bonferroni correction of α/number of tests (Sokal and Rohlf, 1995). SPSS 20 was used for statistical analyses (IBM Corp., 2011).

After testing, we ran permutations in the R statistical package using the packages lme4 (Bates et al., 2014) and lmerTest (Kuznetsova et al., 2014) to check the probability of obtaining an F-statistic greater than the observed value (R Core Team, 2014). We randomly assigned individuals with their associated dental variables to sites, which were already associated with a particular mechanical food value. Permuted values were either individual FMP variables (for models with more than one dependent variable) or individual PCA factor variables (for models with more than one independent variable) for simplicity. We permuted the individual models for k = 10,000 iterations to obtain a distribution of F-statistics that were then compared against the observed value.

3. Results

3.1. *Tamarindus indica* in the lemur diet

Tamarind fruits were eaten year-round in the gallery forest of P1, with consumption highly seasonal in P2 (Table 1). Data from a year-

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long study in P1 in 1999–2000 were included with the data from this study to demonstrate patterns among years in seasonal distribution and time spent feeding on this food.

We did not observe the TNP lemurs feeding on tamarind in the dry season of 2008. In the dry season of 2010, only a few plant species were eaten and most of these foods were leaves (Marni LaFleur, pers. comm.). Although not included in this study, we observed the TNP lemurs eating unripe tamarind fruits in the late dry season of 2013. In the wet season of 2011, the tamarind trees did not have fruit during the observation period.

3.2. *Food mechanical properties*

Mechanical properties of diets differed among sites (Fig. 2). All Kruskal–Wallis tests comparing the mechanical values of diets among sites were significant (Table 2). For individual FMPs, the patterns among sites showed differences depending on the variable. For toughness, P2 was significantly different from P1 and TNP; whereas for hardness, P1 was significantly different from P2 and TNP. For elastic modulus, TNP was significantly lower than the other two sites. Generally, TNP populations consistently had the lowest values for the variables assessed.

3.3. *Dental topography*

3.3.1. Comparisons of M$_1$ and M$_2$ The M$_1$ and M$_2$ topography variables were significantly different among sites and within P1 using the Wilcoxon signed ranks test for paired individuals (Table 3). In contrast, the animals in P2, and to some extent TNP, showed similar values for the dental variables on both molars.

3.3.2. Comparisons of individual dental topographic variables among and between sites Dental topography differed significantly among sites. Parcel 2 individuals in all cases had the lowest values for the dental shape variables. Similarly, all comparisons between sites were significant except for slope on M$_2$ between P1 and TNP (Table 4).

3.3.3. PCA results The dental topographic variables separated by site in the first two axes of the PCA. P1 overlapped broadly with the other two sites, and P2 and TNP were almost completely separated along the first axis. The first two PCA components explained 64% and 17.5% of the variation, respectively. Principle component 1 was driven by slope and relief, and principle component 2 by angularity (Fig. 3). The lemur population in P2 had the lowest values for the dental shape variables, followed by P1, then TNP (Fig. 4).

The variation among sites was significant for factor 1 but not factor 2 with nonparametric tests. Similarly, all comparisons between sites showed significant variation for factor 1 (Table 5).

3.4. *Comparisons of food mechanical properties and tooth shape*

3.4.1. Comparisons using individual tooth shape variables Though M$_1$ and M$_2$ slope and angularity values did not conform to assumptions of normality, we found that the results of the overall model were similar to comparisons with relief and PCA factor scores, both of which were normally distributed (see below). We therefore present these results in a parametric framework. Toughness (R), hardness (H), and elastic modulus (E) were generally correlated with M$_1$ and M$_2$ dental variables, although hardness (H) was not for the M$_2$ (Table 6). Individual tests between each dental variable and each FMP (e.g., relief M$_1$ × E, slope M$_2$ × R; calculated as between-subjects effects within the linear model) were all significant in comparisons with R and E and none were for H (Supplementary Online Material [SOM] Table 1).

Linear models of relief on the M$_1$ (which was normally distributed) and FMPs were similar to the full model; M$_1$ relief was significantly correlated with R ($F_{1,182} = 36.87$, $p < 0.001$) and E ($F_{1,182} = 23.07$, $p < 0.001$) but also to H ($F_{1,182} = 6.32$, $p = 0.013$). The linear model of M$_1$ relief with R + H + E was significant ($F_{2,181} = 21.76$, $p < 0.001$, adjusted $R^2 = 0.185$).

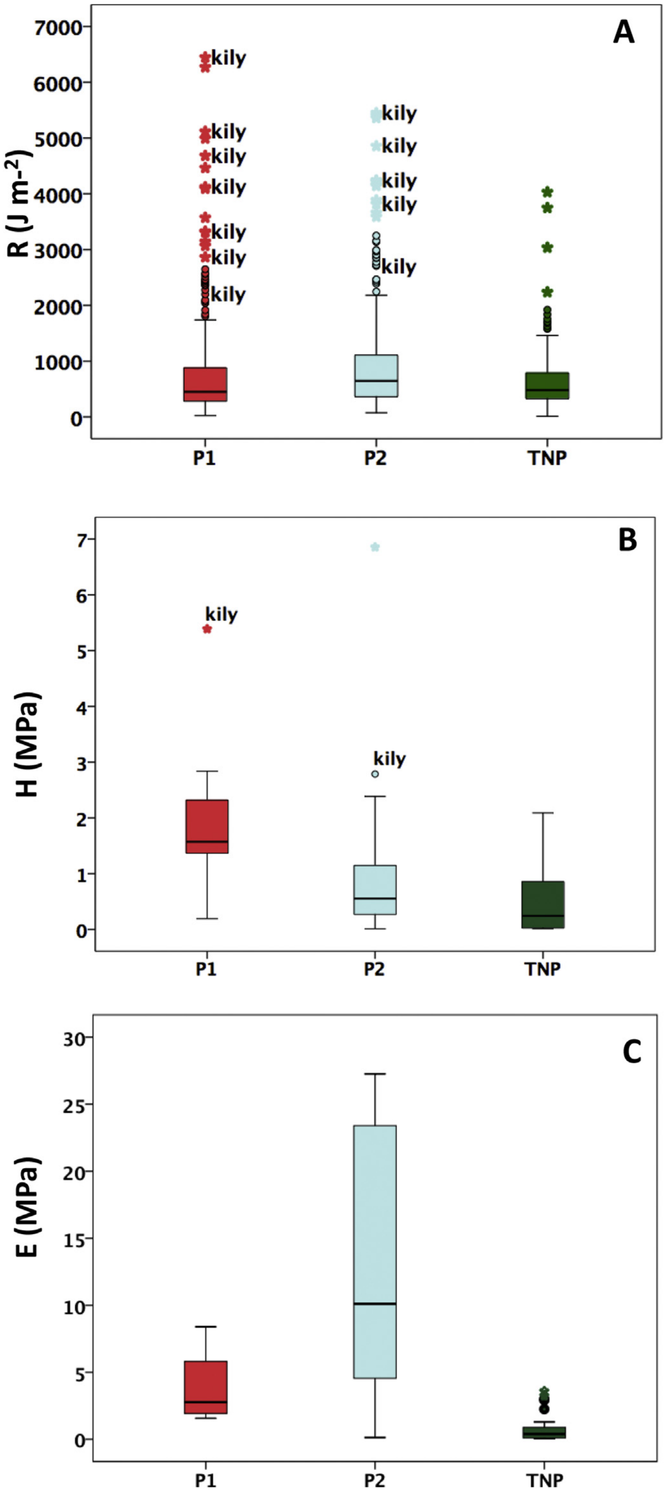

Figure 2. Food mechanical properties among sites for toughness (A), hardness (B), and elastic modulus (C). See Table 2 for statistical comparisons. Note that the scale for E has been truncated and that two extreme outliers (tamarind or *kily*) for P2 are not shown. Boxes enclose the central half of the data, the median is the line in the box, outlying data points are show as whiskers (1.5 times the data range of the box), circles (1.5–3 time the data range of the box), and asterisks (greater than 3 times the data range of the box).

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Table 2
Comparisons of mechanical properties among and between sites[a].

	All sites[b]	P1 × P2[c]	P1 × TNP	P2 × TNP
Toughness (R)	**13.992**	**−3.328**	−0.646	**−3.058**
	$p = 0.001$	$p = 0.001$	$p = 0.518$	$p = 0.002$
Hardness (H)	**17.038**	**−3.164**	**−3.752**	−1.891
	$p < 0.001$	$p = 0.002$	$p < 0.001$	$p = 0.059$
Elastic modulus (E)	**25.741**	−1.705	**−2.619**	**−4.747**
	$p < 0.001$	$p = 0.096$	$p = 0.005$	$p < 0.001$

[a] Results that were significant following Bonferroni correction are in bold.
[b] Comparisons among sites analyzed with Kruskal–Wallis.
[c] Comparisons between sites analyzed with Mann–Whitney *U* (Z-scores).

Table 3
M_1 and M_2 comparisons among and between sites (Wilcoxon Signed Ranks test for paired individuals Z-scores).[a]

	Relief	Slope	Angularity
Combined parcel	**−7.702**	**−9.978**	**−6.031**
	$p < 0.001$	$p < 0.001$	$p < 0.001$
P1	**−7.260**	**−9.076**	**−5.625**
	$p < 0.001$	$p < 0.001$	$p < 0.001$
P2	−1.420	−1.988	−0.909
	$p = 0.156$	$p = 0.047$	$p = 0.363$
TNP	−2.139	**−3.646**	−2.031
	$p = 0.032$	$p = 0.0002$	$p = 0.042$

[a] Results that were significant following Bonferroni correction are in bold.

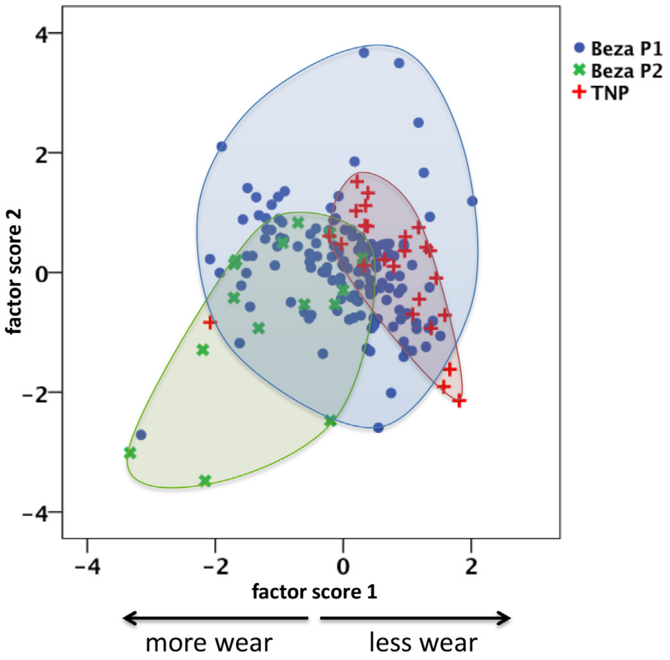

Figure 3. Plot of first two PCA factor scores of molar topographic variables. Ellipses are freeform shapes around the points for each site, not confidence intervals.

3.4.2. Comparisons using dental topography PCA factor scores For the first principle component, we first ran a linear model with transformed factor 1 against each FMP separately (Table 6). Comparisons with R and E were significant and H was not. The significant models showed only a weak positive correlation (adjusted R^2; Fig. 5). The linear model with factor 1 and all FMPs was significant ($F = 21.103$, $p < 0.001$, adjusted $R^2 = 0.182$).

As with factor 1, for the second principle component comparisons with R and E were significant and H was not (Table 6). The adjusted R^2 values generally showed no correlation. The linear model with factor 2 and all the FMPs as covariates was significant.

The results of the permutations agreed with the results above. Food toughness and elastic modulus were correlated with the three dental topographic variables and hardness was not (Table 6). This was also the case for the two PCA factor scores.

We summarize our results in Table 7.

4. Discussion

4.1. *Food mechanical properties and tooth wear are correlated*

Mammalian tooth wear is a complex process (e.g., Baker et al., 1959; Janis and Fortelius, 1988; Teaford and Tylenda, 1991; Ungar, 1998; Cuozzo and Sauther, 2006; Sanson et al., 2007; Galbany et al., 2011; Rabenold and Pearson, 2011; Lucas et al., 2013). In order to more completely assess the variables related to tooth wear, we investigated variation in tooth shape in a single species across different habitats with known feeding ecology. By looking at occlusal topography in a single species, we were able to broadly control for variables such as dental morphology and enamel thickness. Our data show that food properties differ significantly across the three sites studied as does tooth shape. Moreover, our various statistical models of food properties predicting degree of wear-related tooth shape by site are generally supported (Table 6). The models are significant when all food properties are included, whether input individually or “combined” as a PCA factor. However, although both models (individual tooth shape variables, transformed PCA factor 1) are significant, individual variables are not in both cases and the correlations are quite low. When considering the FMPs separately, toughness and elastic modulus are significantly correlated with tooth shape and hardness is not. These correlations are probably a consequence of the site with the lowest dental topographic values and highest average toughness and elastic modulus (P2) not having the hardest diet (Fig. 2). The low R^2 values

Table 4
Comparisons of individual dental topographic variables among and between sites[a].

	M_1			M_2		
	Relief	Slope	Angularity	Relief	Slope	Angularity
All sites[b]	**32.460**	**22.784**	**24.479**	**25.371**	**16.183**	**38.535**
	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
P1 × P2[c]	**−3.567**	**−3.263**	**−3.784**	**−3.783**	**−3.293**	**−4.425**
	$p = 0.0004$	$p = 0.001$	$p = 0.0002$	$p = 0.0002$	$p = 0.001$	$p < 0.001$
P1 × TNP	**−4.285**	**−3.260**	**−3.059**	**−3.160**	−1.933	**−4.309**
	$p < 0.0001$	$p = 0.001$	$p = 0.002$	$p = 0.002$	$p = 0.053$	$p < 0.001$
P2 × TNP	**−4.650**	**−4.169**	**−4.062**	**−4.210**	**−3.840**	**−4.776**
	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p = 0.001$	$p < 0.001$

[a] Results that were significant following Bonferroni correction are in bold.
[b] Comparisons among sites analyzed with Kruskal–Wallis.
[c] Comparisons between sites analyzed with Mann–Whitney *U* (Z-scores).

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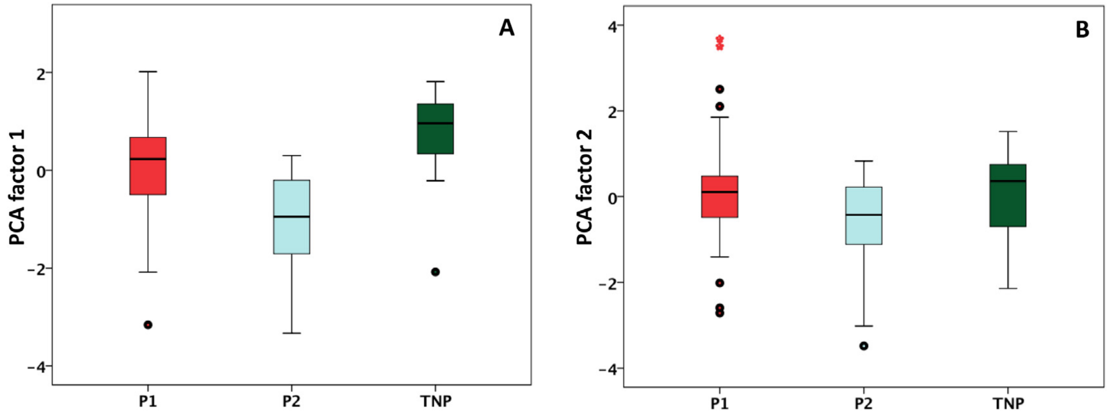

Figure 4. Boxplots of first two PCA factor loadings for dental topography by site. See Table 5 for results of statistical tests. Plot conventions are as in Figure 2.

Table 5
Dental topography attribute comparisons among and between sites using PCA component scores[a].

	Factor 1	Factor 2
All sites[b]	**32.848**	4.015
	$p < 0.001$	$p = 0.134$
P1 × P2[c]	**−4.061**	−1.875
	$p < 0.001$	$p = 0.061$
P1 × TNP	**−3.911**	−0.597
	$p < 0.001$	$p = 0.551$
P2 × TNP	**−4.652**	−1.718
	$p < 0.001$	$p = 0.088$

[a] Significant results are in bold.
[b] Comparisons among sites analyzed with Kruskal–Wallis.
[c] Comparisons between sites analyzed with Mann–Whitney *U* (Z-scores).

most likely result from repeating average FMP values for each individual at each site (Fig. 5). However, we did not quantify some variables for our analysis that have been shown to contribute to tooth wear, such as grit (see below). Exogenous abrasives could explain some more of the variation in dental topography.

We obtained similar results with different dependent variables and with our permutations (Table 6). This gives us confidence that although some variables are not normally distributed our findings of correlations between food properties and dental topography are generally robust.

4.2. Role of tamarind

We confirm in this study that ripe tamarind fruit shell is the most mechanically challenging item that the ring-tailed lemurs process, and the presence of the fruit in the diet increases the average FMP values for each site in which it is eaten (Fig. 2). Furthermore, patterns of consumption are seasonal and site-specific (Table 1). In contrast to the wet season diets (Yamashita et al., 2012b), the majority of the mechanically extreme foods were being eaten in the dry season. At the height of the wet season in 2012, the most commonly eaten food in BMSR P2 (the site with the lowest dental topographic values) was *Talinella grevei* (*dango*) fruits that had an average toughness of 756 J m^{-2} (tamarind shell in comparison is > 3000 J m^{-2}; Yamashita et al., 2012b). Tamarind plant parts were not eaten in quantity during this season, which is

Table 6
Comparisons of dental topography and food mechanical properties (FMPs)[a].

Dependent variable(s)	Independent variable(s)	*F*[b]	d.f.	*p*-value	Adjusted R^2	*p*-value from permutation[c]
Relief M_1, slope M_1, angular M_1[d]	R	**21.114**	1,182	<0.001		0
	H	**3.672**	1,182	0.013		0.013
	E	**15.987**	1,182	<0.001		0
Relief M_2, slope M_2, angular M_2[d]	R	**15.342**	1,189	<0.001		0
	H	0.961	1,189	0.412		0.420
	E	**13.771**	1,189	<0.001		0
PCA factor 1 (transformed)	R	**39.359**	1,180	<0.001	0.175	0
	H	3.630	1,180	0.058	0.014	0.054
	E	**27.345**	1,180	<0.001	0.127	0
	R + H + E	**21.103**	2,179	<0.001	0.182	0
PCA factor 2 (untransformed)	R	**6.549**	1,180	0.011	0.030	0.012
	H	1.295	1,180	0.257	0.002	0.257
	E	**8.310**	1,180	0.004	0.039	0.004
	R + H + E	**4.228**	2,179	0.016	0.034	0.025

[a] Significant results are in bold.
[b] *F*-values reported for tests with multiple dependent variables are Wilk's Lambda.
[c] We permuted the models for k = 10,000 iterations to obtain a distribution of *F*-statistics that were then used to calculate the probability of obtaining an *F*-statistic greater than the observed *F*-statistic. Permuted values were either individual FMP variables (for models with more than one dependent variable) or individual PCA factor variables (for models with more than one independent variable).
[d] Because we could not transform these variables to make them normally-distributed, we ran a linear model with only M_1 relief (M_1 relief was normal) and FMPs. The results were similar to the full model. See text for details.

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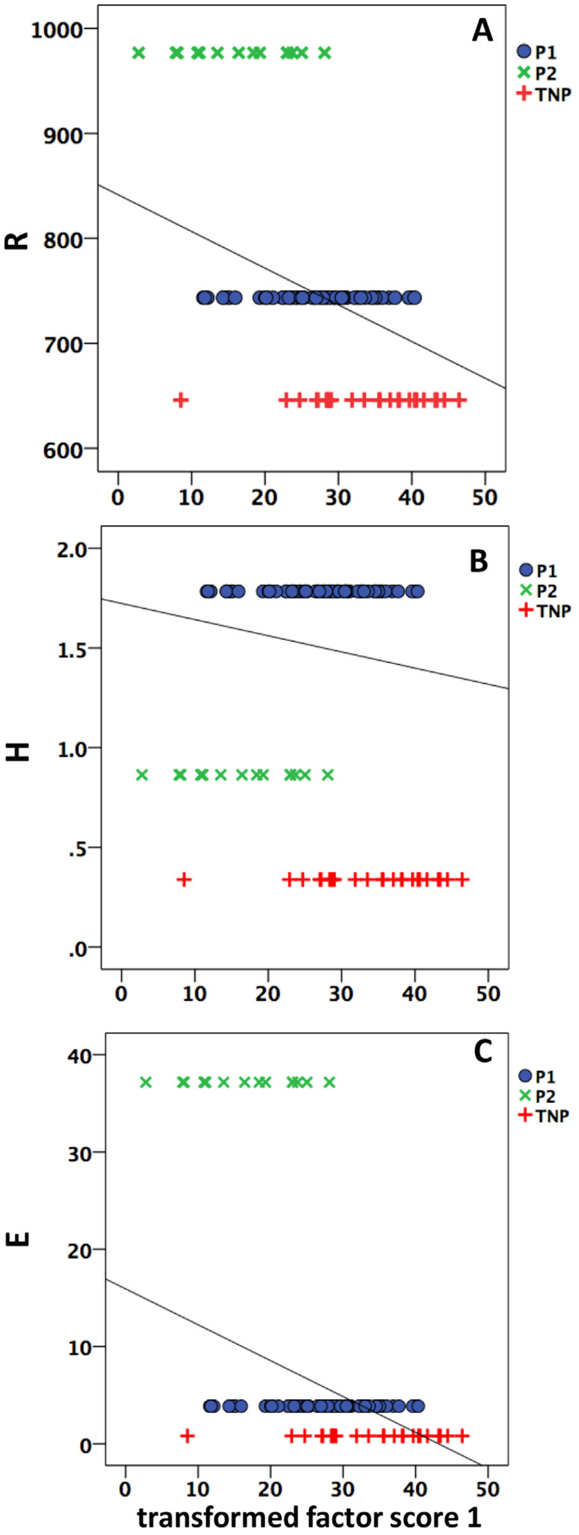

Figure 5. Scatterplots of transformed first PCA factor score and individual FMPs; A) dental topography × toughness, $R^2 = 0.179$; B) dental topography × hardness, $R^2 = 0.020$; C) dental topography × elastic modulus, $R^2 = 0.132$. Slopes are negative because dental shape differences run from greatest to least on the X-axis. Independent variables are on the Y-axis.

in stark contrast to the dry season when tamarind fruit formed the majority of the diet (Table 1; Yamashita et al., 2012a). For comparison, the toughest foods in the wet season were large fruits, such as *Strychnos madagascariensis* (*bakoa*; 1300 J m^{-2}) and *Gardenia suavissima* (*voafotake*; 1500 J m^{-2}), access to which was limited by the lemurs' gape as much as by food mechanical properties. Individuals had difficulty opening their mouths wide enough to bite into the fruit, judging by direct observations and marks left on intact fruit.

Table 7
Summary table of comparisons among the three sites.

Comparison	Directionality
Tooth wear	P2 > P1 > TNP
Toughness (R)	P2 > P1 ≈ TNP
Indentation (H)	P1 > P2 ≈ TNP
Elastic modulus (E)	P2 > P1 > TNP
tamarind freq consumption-dry	P2 > P1 > TNP
tamarind freq consumption-wet	P1 > P2 > TNP

When we compare the frequency of tamarind consumption with the dental variables and FMPs, we find a familiar pattern, that of the greatest dental wear (in the BMSR P2 animals) corresponding to the highest average R and E and the highest seasonal consumption of tamarind. Following Lucas et al. (2008) and Constantino et al. (2009), we had previously postulated (Yamashita et al., 2012a) that the thin enamel of ring-tailed lemur teeth (Campbell et al., 2012) often cracked under the repeated stresses incurred when feeding on a large, obdurate fruit. From such a perspective, a combination of variables would contribute to persistent, localized, and relatively high loads that eventually cause cracking of the enamel from the enamel-dentine junction to the outer surface. In addition, much of this fruit is eaten off the ground so added grit may also contribute to the heavy wear found in the BMSR P2 population. Thus, grit may be an additional variable that contributes to tooth wear in the P1 lemurs, especially those that inhabit areas along the river margin where exogenous materials are common on fruit surfaces (Cuozzo et al., in revision). These new data also support our hypothesis that tamarind fruit, when consumed at high frequencies such as at BMSR, is not a food for which ring-tailed lemurs are dentally adapted, thus indicating evolutionary disequilibrium (Cuozzo and Sauther, 2006, 2012; Millette et al., 2009; Sauther and Cuozzo, 2009).

Simply eating tamarind by itself does not explain our results as all three populations use this food at some point. However, the degree to which tamarind is consumed does vary, especially between TNP and the BMSR groups. This supports the idea that tamarind at TNP plays a limited role in patterns of overall tooth wear, which contrasts with the far greater role of tamarind in both of the BMSR samples. Comparing P2 with P1, BMSR lemurs indicates greater wear for P2 lemurs. Tamarind consumption by P1 lemurs does not vary dramatically from season to season for most years, but it appears to be higher than P2 lemurs during the wet season. In 2010, there was a significant drought and both P1 and P2 lemurs focused heavily on tamarind fruit at that time. For P1 this is quite different from other dry seasons (see Table 1). This suggests that we might also consider the role of such stochastic events in understanding how teeth wear, as challenging foods such as tamarind fruit can and do become central during periods of resource reduction (e.g., Sauther and Cuozzo, 2009).

An additional confounding factor for understanding the relative patterns of differences in dental topography between the BMSR groups is the dramatic anthropogenic degradation found in and around P2, which has led to numerous open areas with little to no ground cover. As the P2 lemurs frequently consume tamarind fruits found on the ground, the possibility of these fruits containing notable exogenous grit could be playing a role in the more dramatic pattern of tooth wear found among the P2 lemurs. Overall, other preliminary data suggest that interactions among FMPs, food

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processing, and exogenous materials likely underlie the patterns of wear seen among these lemur populations (Cuozzo et al., in revision). Our data on the role of FMPs and food processing add to the ever-evolving discussion on how teeth wear, which has recently focused on the function (or lack thereof) of either biogenic silica (i.e., phytoliths) or exogenous materials (e.g., Sanson et al., 2007; Hummel et al., 2011; Rabenold and Pearson, 2011, 2014; Schulz et al., 2013; Lucas et al., 2014). We would endorse investigating a broader model of the underlying causes of tooth wear that included identifying and quantifying exogenous abrasives in foods that could remove enamel. With respect to our results, we would additionally like to determine if tooth wear produced by exogenous materials differs from that produced by microcracking, and if enamel already weakened by microcracking is more susceptible to abrasive wear. Our data suggest that food mechanical properties, at least in specific circumstances, can also be relevant to the discussion of dental wear.

5. Conclusions

We found that dental topographic variables, including proxy variables for tooth wear such as occlusal relief and occlusal slope, are correlated with food mechanical properties (R, E, H) and frequency of consumption of key foods across our study populations. Thin dental enamel and exogenous grit from eating fallen fruit off the ground could also be contributing factors. Because we are studying extant taxa with known ecology and behavior, we view our findings as providing context for general studies of mammalian tooth wear. By comparing multiple sites in different seasons and including detailed feeding ecology data, we have been able to pinpoint how some of the different possible variables can interact to produce extreme wear patterns. A combination of intrinsic factors (thin enamel) and site-specific environmental variables (FMPs, feeding frequency, potentially exogenous materials) interact to produce a range of wear patterns in different populations of a single primate species.

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Supplementary Online Material

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