

# Effects of Dietary Fracture Toughness and Dental Wear on Chewing Efficiency in Geladas (*Theropithecus gelada*)

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**ABSTRACT** Chewing efficiency has been associated with fitness in mammals, yet little is known about the behavioral, ecological, and morphological factors that influence chewing efficiency in wild animals. Although research has established that dental wear and food material properties independently affect chewing efficiency, few studies have addressed the interaction among these factors. We examined chewing efficiency, measured as mean fecal particle size, as a function of seasonal shifts in diet (and corresponding changes in food fracture toughness) in a single breeding population of a grazing primate, the gelada monkey, at Guassa, Ethiopia. We also measured dental topographic traits (slope, angularity, and relief index) and relative two- and three-dimensional shearing crest lengths in a cross-sectional wear series of gelada molars. Chewing efficiency decreased during the dry season, a pattern corre-

sponding to the consumption of foods with higher fracture toughness. Older individuals experienced the most pronounced decreases in chewing efficiency between seasons, implicating dental wear as a causal factor. This pattern is consistent with our finding that dental topographic metrics and three-dimensional relative shearing crest lengths were lowest at the last stage of wear. Integrating these lines of behavioral, ecological, and morphological evidence provides some of the first empirical support for the hypothesis that food fracture toughness and dental wear together contribute to chewing efficiency. Geladas have the highest chewing efficiencies measured thus far in primates, and may be analogous to equids in their emphasis on dental design as a means of particle size reduction in the absence of highly specialized digestive physiology. *Am J Phys Anthropol* 155:17–32, 2014. © 2014 Wiley Periodicals, Inc.

The central function of the mammalian dentition is to fracture and fragment food particles during chewing to reduce their size. Smaller particles in the mammalian gut are fermented at a higher rate and more thoroughly compared to larger particles because the increased surface area of damaged cell walls promotes microbial attachment (Pearce and Moir, 1964; McLeod and Minson, 1969; Latham et al., 1978). By facilitating nutritional input and energy uptake (Dean et al., 1980), the ability to chew efficiently is fundamental for both foregut and hindgut fermenters, since other digestive processes have little effect on the subsequent breakdown of particles after swallowing (Poppi et al., 1980; Murphy and Nicoletti, 1984; McLeod and Minson, 1988; Spalinger and Robbins, 1992; van Soest, 1994). Thus, the average size of particles in fecal matter directly reflects chewing efficiency and has served as a convenient and accurate noninvasive tool for studying dental ecology in wild animals as well as broad morphological trends in phylogenetic contexts (Hummel et al., 2008; Fritz et al., 2009). Studies suggest the main factors by which herbivore species evolve differences in chewing efficiency are dental design and/or mechanisms that allow repeated chewing of regurgitated ingesta (rumination) (Fritz et al., 2009; Matsuda et al., 2011).

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Chewing efficiency can vary among individuals in a population and even within individuals over time. Reduced chewing efficiency can occur through the consumption of nonpreferred foods (sensu Marshall and Wrangham, 2007) or mastication with senesced or impaired teeth, and has the effect of reducing nutritional and energetic input with potentially deleterious impacts upon survival and reproduction (Pahl, 1987; Skogland, 1988; King et al., 2005; Nussey et al., 2007). Moreover, reduced dental function associated with advanced stages of wear provides a plausible proximate mechanism for the decline in body weight, survival, fecundity, and reproductive performance observed during senescence in wild herbivores (cervids: Tyler, 1987; Gaillard et al., 1993; Ericsson and Wallin, 2001; Nussey et al., 2007; lemurs: King et al., 2005).

Dietary shifts often follow seasonal change, and some studies have noted that animals with compromised chewing efficiency are particularly susceptible to reduced energy intake and starvation during the dormant season. For example, lemurs experiencing dental senescence exhibited reduced chewing efficiency, rendering infants of older mothers more susceptible to seasonal mortality (King et al., 2005). Studies of other mammal groups have noted seasonal deterioration of body condition with dental wear due to reduced fat storage (in ungulates: Veiberg et al., 2007a, 2009). In primates, the deleterious effects of seasonality are thought to stem from the consumption of non-preferred resources, which tend to be more mechanically resistant than preferred foods (Kinzey, 1974; Lambert et al., 2004; Wright, 2005; Vogel et al., 2008; Wright et al., 2009). Animals with impaired teeth are expected to fracture mechanically resistant foods less efficiently, thereby reducing nutritional and energetic input.

Fragmentation of food depends on fracture toughness (the energy required to propagate a crack), or the combination of elastic modulus (the stress, or force per unit area, required to produce a proportional change in the strain) and fracture toughness of the plant tissue (Agrawal et al., 1997; Lucas et al., 2002; Williams et al., 2005; Wright et al., 2008). Fracture toughness can be rapidly assessed prior to ingestion and is among the primary sensory cues dictating food selection by herbivores (Dominy et al., 2001; Lucas, 2004; Sanson, 2006). Fracture toughness is correlated with fiber content (Choong et al., 1992; Hill and Lucas, 1996; Lucas et al., 2000, 2012; Lucas, 2004), and because fiber is difficult to digest, it is avoided by many herbivores when possible (Milton, 1979; Waterman et al., 1988; Rogers et al., 1990; Fashing et al., 2007). Seasonal increases in dietary fracture toughness have been documented for several primate species (Wright, 2005; Vogel et al., 2008, 2009) and such increases are expected to compromise an individual's ability to comminute food items and assimilate nutrients. To date, however, measures of the mechanical properties of food are seldom linked with chewing efficiency in primate field studies.

While food selection reflects the nutritional value of foods, it also reflects the animal's chewing capability, which is largely determined by the morphology of the masticatory apparatus (e.g., tooth shape, masticatory muscle size). For example, there is a strong relationship between dental morphology and the mechanical properties of food (Kay, 1975, 1978; Lucas, 1979, 2004; Bunn and Ungar, 2009). The morphology of the occlusal surface changes as teeth wear with the gradual removal of

enamel and dentine. Studies suggest that such changes, prior to the onset of dental senescence, maintain, or enhance tooth functionality (Rensberger, 1973; Fortelius, 1985; Luke and Lucas, 1985; Lanyon and Sanson, 1986b; King et al., 2005). For animals consuming tough diets, functionality is maintained by the appearance of compensatory shearing surfaces formed by newly exposed cutting edges surrounding islands of dentine (Rensberger, 1973; Luke and Lucas, 1985; Janis and Fortelius, 1988; Ungar and M'Kirera, 2003; Lucas, 2004; King et al., 2005). When teeth become heavily worn, however, reduced functional capabilities are almost certainly detrimental, particularly during seasons of resource scarcity. Some animals have been observed to alter their chewing behavior to counterbalance the effects of tooth wear by increasing the time spent chewing or chewing rate (Gross et al., 1995; Pérez-Barberia and Gordon, 1998a; Logan, 2003), but such behavioral compensation may not be sufficient to entirely counteract these effects.

Although researchers recognize that seasonal dietary change and dental wear affect chewing efficiency, these three variables have not been measured simultaneously in wild animals. Instead, studies have examined either: a) seasonal dietary change and chewing efficiency (e.g., Millette et al., 2012) or chewing efficiency of animals on different diets (Hummel et al., 2008); b) seasonal dietary change and dietary fracture toughness and/or habitat quality (e.g., Kojola et al., 1998; Nussey et al., 2007; Veiberg et al., 2007b; Vogel et al., 2008, 2009; Sauther and Cuzzo, 2009; Wright et al., 2009); or c) dental wear/impairment and chewing efficiency (e.g., King et al., 2005; Millette et al., 2012). The study of these three variables simultaneously may provide a better understanding of the proximate mechanisms underlying both chewing efficiency and senescence in herbivores, particularly with reference to seasonality.

This article explores how seasonal dietary change (and the corresponding shift in dietary fracture mechanics) and dental wear impact chewing efficiency (measured by mean fecal particle size) in a wild population of a graminivorous cercopithecoid primate, *Theropithecus gelada*. This species, endemic to the Afroalpine grasslands of the Ethiopian highlands, feeds mostly on graminoid\* leaves, with moderate to strong seasonal shifts to forb leaves and underground storage organs (USOs; includes tubers, corms, and roots) in the dry season (Iwamoto, 1993; Fashing et al., in press). The gelada has a range of morphological adaptations that reflect its grazing habit. These include a high opposability index to enable precise manual grasping of grass blades (Jolly, 1970; Jablonski, 1993) and large, thickly enameled, high-crowned molars with an occlusal topography that wears to reveal curved enamel crests that aid in the comminution of tough foods (Jolly, 1970, 1972; Jablonski, 1993, 1994; Shellis et al., 1998). Among primates, this degree of hypsodonty and molar complexity is rivaled only by extinct Plio-Pleistocene theropithecines (Jablonski, 1993) and is considered an adaption to resist silica and/or grit-induced wear (Fortelius, 1985; Janis, 1986; Fortelius et al., 2002; Damuth and Janis, 2011; Hummel et al., 2011; Kaiser et al., 2013). Aspects of the digestive physiology of geladas are further suited to a graminoid-based diet,

\*Graminoids include grasses, sedges, and rushes (though the latter are not known to be present at Guassa).

including the absence of proline-rich proteins with tannin-binding capacity (in captive geladas: Mau et al., 2009), in addition to the ability to ferment the cell wall material of graminoids through a distinct sacculated large intestine for hindgut fermentation (Mau et al., 2011).

In this study, we evaluated how seasonal (wet vs. dry) dietary change, the corresponding change in dietary fracture mechanics, and dental wear affect chewing efficiency in wild geladas. We integrated several aspects of the feeding ecology of geladas at the Guassa Plateau in the Menz Highlands of north-central Ethiopia. First, we measured the fracture toughness of graminoid and forb species consumed by geladas. We then used 15 months of feeding records on the geladas at this site to calculate the monthly cumulative weighted mean and maximum fracture toughness (Vogel et al., 2008) of the diet of adults and juveniles.

Second, we measured the chewing efficiency, as reflected by mean fecal particle size, of wild geladas during the wet and dry seasons at Guassa, in addition to captive geladas from Zurich Zoo, thereby adding to the growing data available on the chewing efficiency of wild and captive primates (Dunbar and Bose, 1991; King et al., 2005; Fritz et al., 2009; Millette et al., 2012; Matsuda et al., 2014). Together, our data sources represent chewing efficiencies from a wide range of diets and a cross-sectional sample of ages, and consequently, when analyzed in relation to body mass (Fritz et al., 2009), have the potential to offer insight into the adaptive morphology of gelada molars in relation to diet.

We used dental topographic analysis (M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003) to characterize how the slope, angularity, and relief index (RFI) of the occlusal surfaces of gelada second mandibular molars ( $M_{2S}$ ) change with wear. Further, to investigate whether gelada molars retain shearing capacity (i.e., total shearing crest length) throughout life, we examined how relative two- and three-dimensional shearing crest lengths (King et al., 2005) change throughout the gelada  $M_2$  wear series. It is important to point out that our dental samples, which were acquired from skeletal material, did not match the individuals used for the fecal particle size part of our study. Further, we assumed that heavily worn  $M_{2S}$  (i.e., those with extensive dentine exposure) corresponded to old individuals. This assumption is based on research demonstrating that dentine exposure increases with age in other papionins (Phillips-Conroy et al., 2001; Galbany et al., 2011, 2014).

Based on the hypothesis that seasonal dietary fracture toughness and tooth wear affect chewing efficiency, we made the following predictions regarding our gelada sample:

1. According to the Jarman-Bell principle (Bell, 1971; Jarman, 1974; Müller et al., 2013), larger individuals will ingest a diet of lower quality (e.g., higher fiber levels) than smaller individuals due to reduced ability and opportunity for selective feeding. Because fiber is correlated with fracture toughness (and can be considered as the inverse of quality: Lucas, 2004), we predict that the fracture toughness of consumed foods will increase with body size.
2. During periods of preferred food scarcity (dry season), mean and maximum cumulative weighted dietary fracture toughness will increase for all age-sex classes.
3. During the dry season, chewing efficiency will decrease for all age-sex classes due to consumption of tougher foods, and particularly for older individuals with worn teeth. Again, we note that a high degree of dental wear was not directly measured but assumed to be present among old adult geladas.
4. Metrics characterizing the occlusal topography and shearing capacity of gelada  $M_{2S}$  will decrease in more advanced stages of wear, suggesting a compromise of function.

## MATERIALS AND METHODS

### Dietary fracture toughness

**Study site, behavioral methods, and food item classification.** We conducted our study of geladas on the Guassa Plateau (hereafter referred to as Guassa), a large (111 km<sup>2</sup>) and unusually intact Afroalpine tall-grass ecosystem located along the western edge of the Great Rift Valley (10°15'–10°27'N; 39°45'–39°49'E) at elevations between 3,200 and 3,600 m above sea level (Ashenafi, 2001; Fashing et al., 2010). During 2007–2012, the average monthly temperature at Guassa was  $11.0 \pm 1.2$  (SD) °C (Fashing et al., in press). Mean monthly low and high temperatures were  $4.3 \pm 0.5$  (SE) and  $17.8 \pm 0.3$  (SE) °C, respectively. Rainfall averaged  $1650 \pm 243$  (SD) mm per year (Fashing et al., in press). Rainfall was strongly seasonal, exhibiting a unimodal peak during July and August when more than two-thirds of the annual rainfall occurred. Rainfall drives the temporal variation in graminoid availability at Guassa, and Fashing et al. (in press) found cumulative rainfall three months prior to the end of each study month to be the best indicator of monthly food availability. Based on the results presented in Fashing et al. (Fig. 2; in press), we used <400 mm of three-month cumulative rainfall as the cutoff to classify months into the “dry season” (November–June) whereas those months with >400 mm were classified into the “wet season” (July–October).

Our behavioral study focused on a ~220-member gelada band (Steelers Band) at Guassa. Methods of collecting behavioral data on gelada feeding ecology and details about plant classification are elaborated in Fashing et al. (in press). We collected feeding data (via activity scan sampling at 30-min intervals) on an average of  $15.9 \pm 3.5$  (SD) days for each month for members of the study herd, including adult males and females, and large, medium, and small juveniles during all-day follows from February 2007–April 2008. The juvenile size classes do not distinguish between males and females because instantaneous sex identification was sometimes difficult. During regular 30-min interval scan samples, if an individual was feeding we recorded the identity of the item being plucked, pulled toward its mouth, masticated, or swallowed. Initial designations of food items in the field included tall graminoid leaves, short graminoid leaves, graminoid seed heads, underground graminoid parts (corms, rhizomes, crowns), forb leaves, forb roots, forb pith, forb flowers, forb tubers, succulent forb leaves, unidentified underground items, unidentified above-ground items, and invertebrates. Following Fashing et al. (in press) “tall graminoid” included those taxa reaching  $\geq 10$  cm in height when fully grown, while “short graminoid” consisted of taxa <10 cm tall when fully grown. Thus, these data provide 15 months of



TABLE 1. Functional plant types consumed by geladas at Guassa, with mean and maximum fracture toughness values used in cumulative weighted fracture toughness analyses

Functional plant type	Mean fracture toughness ( $J m^{-2}$ )	Maximum fracture toughness ( $J m^{-2}$ )
Tall graminoid leaves	2,686	4,197
Graminoid crowns/ rhizomes	2,671	3,879
Forb roots	1,869	1,965
Short graminoid leaves	1,113	1,809
Forb leaves	762	2,089
Forb pith	533	767
Invertebrates	400 <sup>a</sup>	400 <sup>a</sup>
Graminoid corms	265 <sup>b</sup>	319 <sup>b</sup>
Succulent forb leaves	199	199
Forb tubers	198	232
Forb flowers	85	85

<sup>a</sup> Values from Strait and Vincent (1998) for locusts.

<sup>b</sup> Mean and maximum (upper 95% confidence interval) from Table 2 in Dominy et al. (2008).

feeding records ( $n = 9,994$ ) for five age-sex categories of geladas and contain monthly percentages of each food item in the diet (Fashing et al., in press).

The plant tissues consumed by geladas during these scan samples were classified into several functional plant types (Table 1) and by the frequency of consumption. Following Fashing et al. (in press), foods consumed “often” were those that formed a regular part of the diet year round, those consumed “sometimes” comprised a regular part of the diet on a seasonal basis or were consumed at low to moderate levels throughout the year, those consumed “rarely” corresponded to five or more recorded feeding incidents per year but were not commonly consumed, and those consumed “very rarely” corresponded to less than five feeding incidents per year. We examined plant species for which at least one functional plant type was consumed by the geladas, although some parts of such plants were never consumed. Due to the low number of food items in the “rarely” and “very rarely” categories, these items were pooled for analyses.

**Mechanical testing of plants.** We tested the fracture toughness of 50% (28/56) of the total plants listed in Table 2 of Fashing et al. (in press). Many of the remaining 50% are consumed very rarely (Fashing et al., in press). We tested 70% (16/23) of the species for which at least one part was consumed “often” or “sometimes.” As such, our mechanical data represent the bulk of foods consumed on a regular basis by geladas. The fracture properties of plant samples were assessed using a portable universal mechanical tester (Darvell et al., 1996; Lucas et al., 2001). Most gelada foods, such as graminoids and forbs, are rod- or sheet-like. Accordingly, we used the scissors test to measure the amount of energy in Joules (J) needed to propagate a crack along the tissue (Lucas and Pereira, 1990; Lucas et al., 2012). We then calculated fracture toughness (in units of  $J m^{-2}$ ) by dividing the area beneath the force-deformation curve by the dimension of the cut plant part. We used a wedge test to assess fracture toughness for larger and more irregularly shaped items such as pith and USOs (Lucas et al., 2012). Here, a 15° angle wedge was driven into a cubed specimen (Lucas et al., 2012). We tested several plant tissues, including

TABLE 2. Gelada specimens used for dental wear analyses

Specimen #	Sex	Museum (Locality in Ethiopia)
001 <sup>a</sup>	M	--- (Guassa)
004 <sup>a</sup>	F	--- (Guassa)
442	M	MCA (Guassa)
443	F	MCA (Guassa)
444	F	MCA (Guassa)
601	F	MCA (Guassa)
604	?	MCA (Guassa)
27039	M	FMNH (Ambo)
27184	M	FMNH (Gich)
27185	F	FMNH (Gich)
27233	M	FMNH (Salale)
27234	F	FMNH (Salale)

<sup>a</sup> Data for these specimens collected in the field at Guassa.

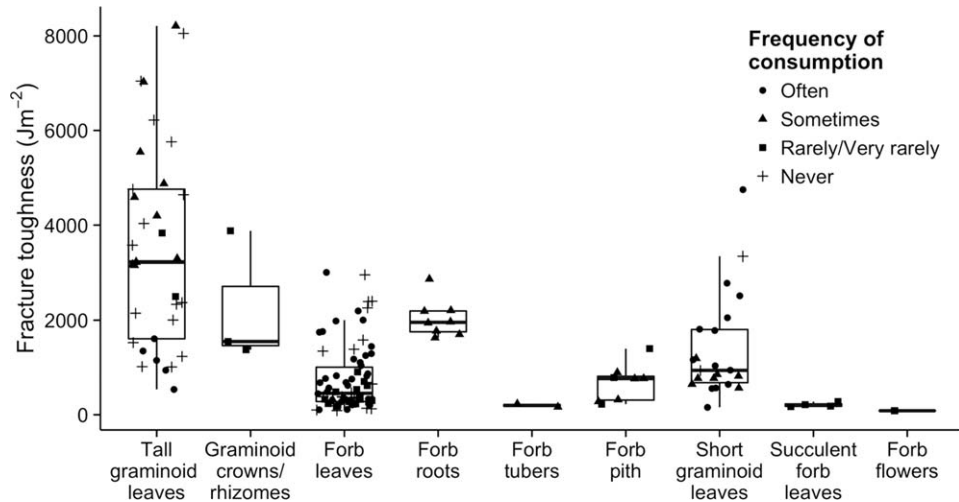
MCA: Museum of Comparative Anatomy, National Museum of Ethiopia; FMNH: Field Museum of Natural History.

blades (leaves), forb lamina (leaves), stems, pseudo-stems (stemlike structures composed of rolled graminoid blades and sheaths), and USOs. Samples were generally tested in the transverse direction. For graminoids, transverse fracture toughness is higher than longitudinal fracture toughness because of the longitudinally oriented woody sclerenchyma fibers that arrest lateral cracks (Vincent, 1982; Ennos, 2011). Both measures are relevant during chewing (Lucas, 2004). All mechanical testing occurred within three hours of specimen collection.

In two cases, we used published values for missing mechanical data (Table 1). Guassa geladas consume a wide variety of invertebrates, including earthworms, caterpillars, ants, grasshoppers/locusts, and crane flies (Fashing et al., in press). We did not test invertebrates in the field in this study and instead used the published value of  $400 J m^{-2}$  from Strait and Vincent (1998) for locust tissue. For graminoid corms, we used data from Dominy et al. (2008). We are not aware of any mechanical data for the fracture toughness of graminoid seeds, but they are unlikely to be tough (PW Lucas, pers. comm.) and account for only 2.2% of the annual gelada diet at Guassa (Fashing et al., in press).

**Data analysis.** We used analysis of variance (ANOVA) with Tukey’s post hoc tests to compare the fracture toughness of gelada foods according to i) frequency of consumption by geladas and ii) functional plant type. For statistical analyses, we excluded plant tissues listed as “never” (i.e., never consumed) because the extent to which these tissues randomly sample the mechanical environment is unclear (these tissues are, however, plotted in Fig. 1). The fracture toughness data were log-transformed to satisfy the assumption of normality for statistical tests.

Next, to determine how gelada dietary fracture toughness changes across the annual cycle, we calculated the fracture toughness of functional plant types in a second way that more fully accounts for the wide range of mechanical variation in plant tissues. Rather than using the raw data as described for the analyses in the previous paragraph, here we adopted an approach that weighted individual plant tissues (e.g., stem, leaf) and species more equally in calculating fracture toughness. For every plant tissue belonging to a species classified under the functional plant type of interest, we calculated the median fracture toughness for each plant tissue



**Fig. 1.** Fracture toughness of gelada foods according to functional plant type and frequency of consumption. The solid line within the boxplots represents the median. Lower and upper hinges correspond to first and third quartiles, respectively. Whiskers extend to the highest and lowest values within the interquartile range multiplied by 1.5.

belonging to a species, then averaged the median values from these tissues to arrive at a “species” value. We then averaged each of these “species” values to determine the mean value for the functional plant type (Table 1). As noted above, in some cases a given species contained tissues classified under different functional plant types. The maximum value for the functional plant type was determined as the highest median fracture toughness value for a tissue under that functional plant type (Table 1). We then calculated the cumulative weighted dietary fracture toughness (Vogel et al., 2008). According to this approach, the fracture toughness of each dietary item is weighted according to its frequency of consumption and these weighted products are summed. Here, we calculated mean cumulative fracture toughness by multiplying the percentage of scan samples on a monthly basis for each age-sex class devoted to each functional plant type by the mean fracture toughness of that functional plant type, as described above. We used an analogous procedure to calculate maximum dietary fracture toughness. Foods with corresponding mechanical properties accounted for most, but not all, of gelada diets every month (mean >92% for each age-sex class), and accordingly data were renormalized when necessary. We excluded data for September 2007 from the analysis due to a small number of scan samples for that month. To avoid over-representing rare food items in the cumulative toughness portion of the analysis, we excluded plant parts that were consumed “rarely,” “very rarely,” or “never.”

We examined seasonal variation in mean and maximum cumulative weighted dietary fracture toughness for all age-sex classes and used ANOVA with Tukey’s post hoc multiple comparisons tests to determine whether dietary fracture toughness increased with body size. We visually examined whether dietary fracture toughness increased during particular months.

### Fecal particle size

Fecal samples were collected during August–September 2011 (wet season) and March–April 2012 (dry season) from 11 individuals from the Steelers Band that

had no obvious dental or digestive pathologies. Samples were stored in alcohol prior to processing. Individuals were classified into standardized age-sex categories regularly used by the Guassa Gelada Research Project. We classified females and males that were in early to middle adulthood as prime adult females and prime adult males, respectively. We classified older individuals into the categories old adult females and old adult males. In comparison to prime individuals, old individuals had shaggier/rougher coats, sagging buttocks, and more wrinkled faces. In older females, the distributions of pinks and blacks in the paracollosal skin were patchier, and chest bead patterns more idiosyncratic. Two medium-sized juvenile males and a small-sized juvenile female in our study were classified as juveniles.

Feces from captive geladas were sampled at Zurich Zoo for the study of Fritz et al. (2009;  $n = 6$ ) and additionally for this study ( $n = 10$ ) in 2011. Feces were collected during summer on both occasions. Zurich Zoo keeps two harem groups of geladas, which consisted, at the time of sampling, of prime adults and juveniles. Feces could not be ascribed to individuals, but were collected from the enclosure during cleaning operations. The geladas at the zoo in Zurich are fed a diet of fresh grass in summer and hay complemented with apples, vegetables and soaked grain in the winter (Mau et al., 2009).

We needed to estimate gelada body masses to facilitate interspecific comparisons of mean fecal particle size. Based on data presented for geladas in Bergman and Beehner (2013) we used values of 19.0 kg ( $n = 5$ ) for adult males and 11.7 kg ( $n = 8$ ) for adult females.

Fecal particle size was determined by a standardized wet sieving method and the calculation of a discrete mean particle size following the method outlined in Fritz et al. (2012). Discrete mean fecal particle size (dMEAN) was measured in millimeters and reported with the standard deviation. We used matched-pairs  $t$ -tests to compare wet and dry season dMEAN values for each individual. We performed  $t$ -tests on dMEAN of old versus prime individuals of similar body sizes to examine whether age-class (and presumably dental wear, as these were not measured in the same individuals) was a

contributing factor to chewing efficiency (e.g., prime adult males vs. old adult males).

### Dental wear

Specimens of *Theropithecus gelada* are notoriously rare in museum collections (Eck, 1977; Teaford, 1993). Two collections of gelada teeth were used for our study of gelada dental wear (Table 2). These included five existing specimens housed at the Field Museum of Natural History (FMNH) in Chicago and seven new specimens from individuals that died of natural causes and were collected in the field at Guassa during 2007–2011 and deposited at the National Museum, Addis Ababa. Two of the specimens originating from Guassa were molded in the field while the other five were studied in the museum. The Guassa specimens are from the same breeding population as the one from which feeding and fecal data were collected.

Specimens at FMNH are wild-shot individuals of known proveniences from several regions of Ethiopia. Sex categories were based on museum records. Two specimens are from the Gich Plateau, Simien Mountains gelada population where a three-month study of diet was conducted in the 1970s (Iwamoto, 1979). Diets differ considerably between Guassa geladas and other geladas such as those in the Simien Mountains (Iwamoto, 1979; Hunter, 2001; Fashing et al., in press), but intraspecific variation in diet does not appear to generate significant differences in wear-related tooth shape in at least one other primate (chimpanzees: Klukkert et al., 2012). We therefore pooled gelada specimens from different localities for our analysis.

**Data collection.** Molds of  $M_2$ s were prepared using “President Jet” (Coltene-Whaledent, Mawah, NJ) polyvinylsiloxane dental impression material and casts were then prepared using dental stone (GC Fujirock EP; GC America, Alsip, IL). Casts were scanned at Arizona State University using a needle-point scanner (MDX-15, Roland) at a resolution of 50  $\mu$ m. Casts were positioned on the scanner such that the occlusal plane was parallel to the horizontal plane. Three-dimensional point-clouds were exported into GRASS GIS (GRASS Development Team., 2012). Digital elevation maps (DEMs) of the  $M_2$  occlusal table were defined by cropping scans at the deepest point on the occlusal surface.

We collected data on three variables that describe how the gross anatomy of the occlusal table changes with wear (Ungar and Williamson, 2000; M’Kirera and Ungar, 2003; Ungar and M’Kirera, 2003; King et al., 2005; Bunn and Ungar, 2009). The variable “slope” describes the average change in elevation between adjacent points on the occlusal table. The variable “angularity” represents the average change in slope between adjacent points on the occlusal table, such that high angularity indicates a “jagged” occlusal surface (Ungar and M’Kirera, 2003). The variable “RFI” describes the surface relief of the occlusal table and is calculated as the ratio of 2D and 3D surface area (King et al., 2005).

We measured shearing crest length in both two and three dimensions following the methodology of King et al. (2005). Aspect maps of occlusal tables, with minimum slope set to 5° and a 3 × 3 neighborhood around each cell, were reclassified so that raster cells that slope buccally and raster cells that slope lingually were set as

different colors. Reclassified aspect maps were smoothed using the neighborhood function with a 7 × 7 cell neighborhood around each cell. Shearing blades were identified and traced along the junctions of the two colors. Lengths identified as shearing blades by GRASS GIS were compared with the morphology of the tooth to avoid blade misidentification. Total blade length for each tooth was standardized by normalizing it to the mesiodistal length of the tooth, yielding the variables 2D and 3D relative shearing crest length.

For the analysis of dental wear, we followed the method of Bunn and Ungar (2009) for classifying each molar into a “wear stage.” Scott scores (Scott, 1979) were calculated by assigning each of the four molar cusps a value between zero and ten, with zero indicating no wear and ten indicating a completely worn cusp. Scores were summed for each tooth and specimens were arranged into five wear stage categories, with each category consisting of roughly the same number (2–3) of specimens.

We calculated the mean and standard error (SE) for slope, angularity, RFI, and 2D and 3D relative shearing crest length at each wear stage. Because of the small sample size for each wear stage, we did not perform statistical analyses. Instead, patterns were visually assessed.

Statistical data analyses for all portions of the study were performed in RStudio, version 0.95.263. We set the level of statistical significance at 0.05, and we interpret *P*-values between 0.05 and 0.10 as representing a trend in the data.

## RESULTS

### Food mechanics

**Gelada selection of plant tissues.** The fracture toughness of foods consumed at different frequencies by geladas were significantly different (Welch ANOVA for unequal variance,  $F_{2,113} = 8.2$ ,  $P < 0.001$ ). Foods eaten “often” tended to be less tough than those consumed “sometimes” (Tukey’s post hoc test:  $P = 0.10$ ). Foods consumed “rarely”/“very rarely” were less tough than foods consumed “sometimes” ( $P < 0.001$ ) or “often” ( $P = 0.04$ ).

**Fracture toughness of functional plant types.** Of the foods consumed “often,” “sometimes,” and “rarely”/“very rarely” by geladas, the fracture toughness differed according to functional plant type (Fig. 1; Welch ANOVA,  $F_{8,107} = 13.23$ ,  $P < 0.001$ ). Tukey’s post hoc tests (Table 3) showed that graminoids, particularly tall ones, were generally the toughest items in the gelada diet, while forb leaves, pith, tubers, and flowers were among the least tough. The rank order for the mean fracture toughness of the functional plant types was: Tall graminoid leaves > Graminoid crowns/rhizomes > Forb roots > Short graminoid leaves > Forb leaves > Forb pith > Invertebrates > Graminoid corms > Succulent forb leaves > Forb tubers > Forb flowers. This ranking is identical to that presented in Table 1, in which the fracture toughness values were calculated in a slightly different fashion (see Methods).

**Temporal trends in dietary fracture toughness across age-sex classes.** The overall fracture toughness of gelada diets (with all age-sex classes pooled) differed significantly across months (ANOVA,  $F_{10,59} = 3.9$ ,



TABLE 3. *P*-values for Tukey's post hoc multiple comparisons tests comparing log-transformed fracture toughness of functional plant types of gelada foods

	GT	FL	FR	FT	GU	FP	GS	SL	FF
GT	-	<b>&lt;0.001</b>	0.98	<b>&lt;0.001</b>	0.99	<b>&lt;0.001</b>	<b>&lt;0.002</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
FL	-	-	<b>&lt;0.003</b>	0.62	<b>0.05</b>	0.99	<b>&lt;0.02</b>	0.27	<b>0.02</b>
FR	-	-	-	<b>&lt;0.003</b>	1.0	<b>0.02</b>	0.39	<b>&lt;0.001</b>	<b>&lt;0.001</b>
FT	-	-	-	-	<b>0.016</b>	0.62	<b>0.06</b>	1.00	0.97
GU	-	-	-	-	-	0.21	0.84	<b>0.002</b>	<b>&lt;0.001</b>
FP	-	-	-	-	-	-	0.61	0.36	0.03
GS	-	-	-	-	-	-	-	<b>0.003</b>	<b>&lt;0.001</b>
SL	-	-	-	-	-	-	-	-	0.89
FF	-	-	-	-	-	-	-	-	-

Bolded values indicate significant pairwise differences at the  $\alpha = 0.05$  level.

Abbreviations: FF: forb flowers; FL: forb leaves; FP: forb pith; FR: forb roots; FT: forb tubers; GS: short graminoids; GT: tall graminoids; GU: graminoid crowns/rhizomes; SL: succulent forb leaves.

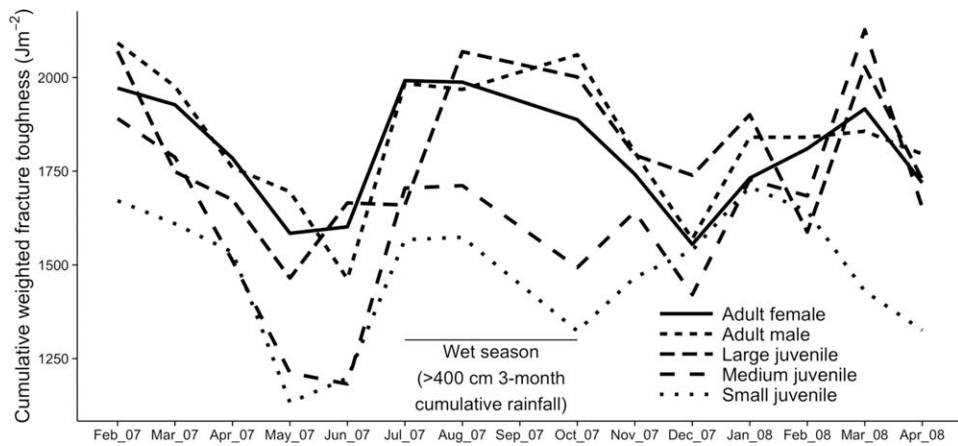


Fig. 2. Cumulative weighted fracture toughness of Guassa gelada diets during February 2007–April 2008 for five age-sex classes.

TABLE 4. Summary statistics for cumulative weighted fracture toughness analyses of gelada diets across the annual cycle

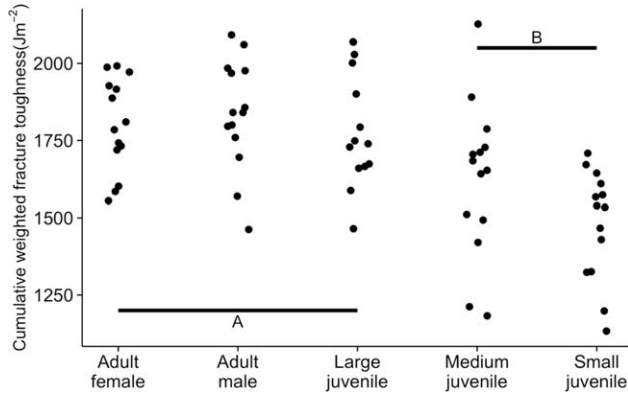
Age-sex class	Mean cumulative weighted fracture toughness (J m <sup>-2</sup> )				Maximum cumulative weighted fracture toughness (J m <sup>-2</sup> )			
	Mean	Min.	Max.	Range	Mean	Min.	Max.	Range
Adult male	1,836	1,463	2,092	630	2,987	2,648	3,340	692
Adult female	1,801	1,555	1,992	437	3,020	2,791	3,287	496
Large juvenile	1,795	1,465	2,070	605	2,925	2,453	3,431	979
Medium juvenile	1,625	1,183	2,128	945	2,769	2,300	3,351	1051
Small juvenile	1,480	1,133	1,708	575	2,579	2,265	2,843	578

$P < 0.001$ ). Dietary fracture toughness increased with body size, both for mean and maximum cumulative weighted fracture toughness when toughness is considered over the entire annual cycle (Fig. 2; Table 4). The difference in mean cumulative weighted dietary fracture toughness between age-sex classes was significant (ANOVA:  $F_{4,65} = 21.3$ ,  $P < 0.001$ ), as was the difference for maximum cumulative weighted fracture toughness (ANOVA:  $F_{4,65} = 8.4$ ,  $P < 0.001$ ). For both mean and maximum cumulative weighted dietary fracture toughness, adult males, and females and large juveniles were not significantly different from one another (Group A; Fig. 3), nor were medium and small juveniles (Group B; Fig. 3), but these two groups differed significantly (Tukey's post hoc,  $P < 0.05$ ). Moderate variation was apparent when the cumulative weighted fracture toughness of

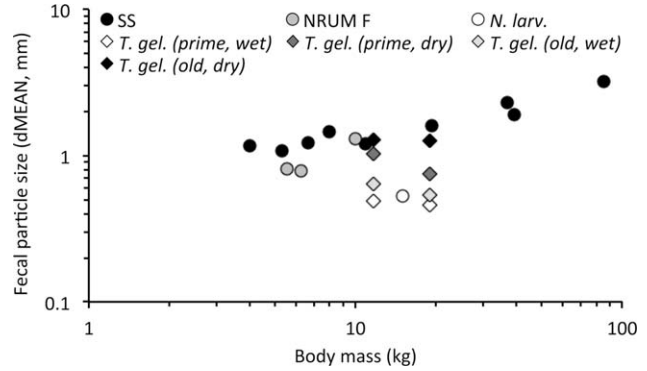
gelada diets was analyzed visually across the annual cycle and the shape of the curves were roughly similar for each age-sex class (Fig. 2). Mean cumulative weighted dietary fracture toughness was generally lowest in May and June 2007. The months of February, March, and April had different fracture toughness profiles in 2007 and 2008.

### Fecal particle size

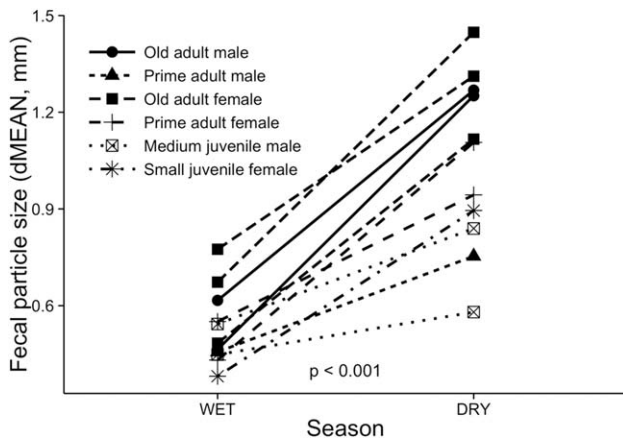
**Interseasonal comparison of dMEAN in Guassa geladas.** The mean fecal particle size (dMEAN) of the 11 studied gelada individuals was significantly higher in the dry season than in the wet season (dMEAN<sub>wet</sub> =  $0.53 \pm 0.04$  mm; dMEAN<sub>dry</sub> =  $1.05 \pm 0.08$  mm, matched-pairs *t*-test,  $t_{10} = -8.02$ ,  $P < 0.001$ ; Fig. 4), and this



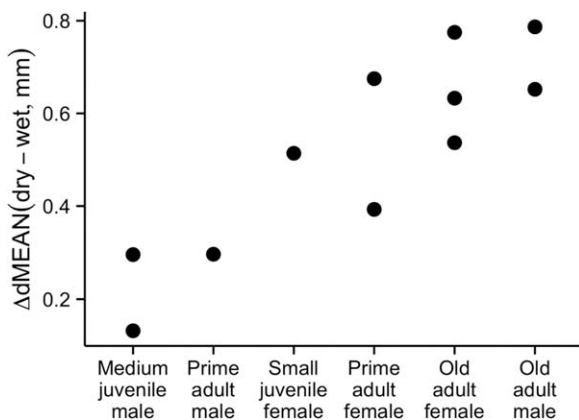
**Fig. 3.** Cumulative weighted fracture toughness values for the annual cycle plotted according to age-sex classes. Each point represents one month. Adults and large juveniles (A) consume significantly tougher diets compared with medium and small juveniles (B), Tukey's post hoc,  $P < 0.05$ . Data from September 2007 were excluded due to low sample size.



**Fig. 6.** Mean fecal particle size (dMEAN) of male (19.0 kg) and female (11.7 kg) adult geladas (*T. gel.*) labeled according to season of collection (wet, dry) and age of individual (old, prime). The other data points show dMEAN for 13 wild primate species, including nonruminant foregut fermenters (NRUM F), a putative ruminant foregut fermenter (*N. larvatus*), and those with simple stomachs (SS; see Matsuda et al., 2014).



**Fig. 4.** Mean fecal particle sizes (dMEAN) of geladas during the wet and dry seasons. Each data point represents an individual, and line segments connect the same individual across seasons. dMEAN is significantly higher during the dry season.



**Fig. 5.** Intraindividual differences between dry and wet seasons plotted against age-sex class. Older individuals generally show the largest differences in dMEAN between seasons.

increase was particularly marked for older individuals (Fig. 5). The near-doubling of dMEAN across a range of body sizes between seasons indicates that individuals comminute foods far less efficiently during the dry season. We also compared similar-sized old and prime adults to control for body size so that any differences in dMEAN may be attributed to differences in dental wear. Old ( $n = 5$ ) and prime similar-sized adults ( $n = 3$ ) had comparable dMEAN values during the wet season ( $dMEAN_{old-wet} = 0.60 \pm 0.13$  mm,  $dMEAN_{prime-wet} = 0.47 \pm 0.06$  mm, Welch  $t$ -test:  $t_{5,9} = 1.79$ , and  $P = 0.12$ ), but similar-sized old adults had significantly larger particle sizes than their prime adult counterparts during the dry season ( $dMEAN_{old-dry} = 1.28 \pm 0.12$  mm,  $dMEAN_{prime-dry} = 0.93 \pm 0.18$  mm, Welch  $t$ -test:  $t_{3,13} = 2.99$ , and  $P = 0.05$ ).

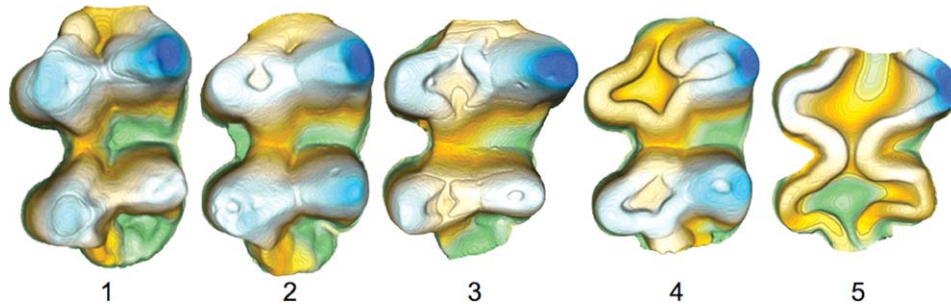
**Comparison to zoo animals and other primate species.** The dMEAN values for zoo geladas ( $dMEAN_{zoo} = 1.58 \pm 0.7$  mm;  $n = 16$ ) and wild adult geladas (both prime and old individuals:  $dMEAN_{wild-wet} = 0.56 \pm 0.12$  mm,  $dMEAN_{wild-dry} = 1.15 \pm 0.22$  mm;  $n = 8$ ) were significantly different. Zoo geladas had dMEAN values  $\sim 3\times$  higher than Guassa geladas in the wet season ( $t_{16,752} = -5.68$ ,  $P < 0.001$ ), and values  $\sim 1.4 \times$  higher than Guassa geladas in the dry season ( $t_{19,889} = -2.24$ ,  $P = 0.04$ ). In fact, the zoo geladas had dMEAN values no different from (but numerically higher than) the dry season values for old male and old female adult geladas at Guassa ( $t_{17,357} = -1.6436$ ,  $P = 0.12$ ).

Comparing the dMEAN for prime adult male and female geladas to measurements from other primate species (Fig. 6) indicated that among the free-ranging primate species measured so far, geladas during the wet season had the smallest recorded fecal particle size, at  $\sim 90\%$  of that reported for proboscis monkeys (Matsuda et al., 2014). During the dry season, the chewing efficiency of geladas (and particularly older individuals) approached what would be expected for a primate of their body size.

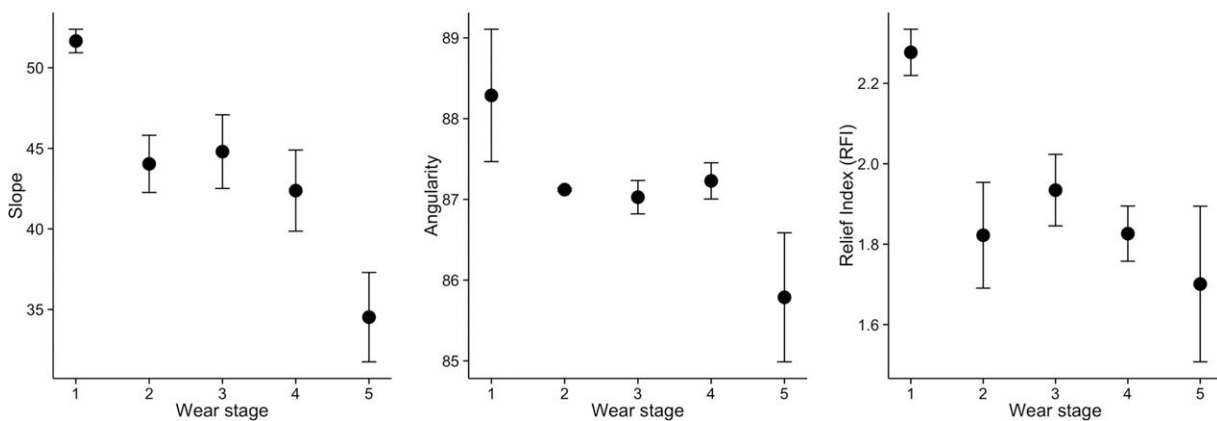
**Dental wear**

Representative specimens for each wear stage are shown in Figure 7. Slope, angularity, and RFI of gelada

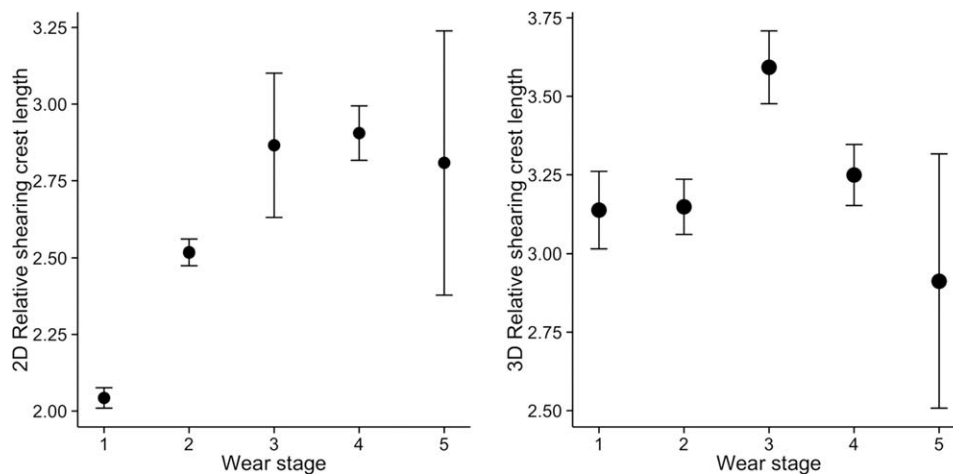




**Fig. 7.** DEMs of occlusal surfaces showing representative teeth for each wear stage (1–5). Note that compensatory shearing crests arise as dentine becomes exposed. The infolded nature of the gelada tooth crown produces C-shaped (wear stage 4) and S-shaped (wear stage 5) shearing crests at later wear stages. Teeth are scaled to the same distance between mesial and distal cusps.



**Fig. 8.** Slope, angularity, and RFI (mean  $\pm$  SE) throughout the gelada  $M_2$  wear series ( $n = 3, 2, 3, 2, 2$  for wear stages one through five, respectively). As wear progresses, all three measures of occlusal topography decrease and all are lowest in wear stage five.



**Fig. 9.** Two- and three-dimensional relative shearing crest lengths (mean  $\pm$  SE) throughout the gelada  $M_2$  wear series ( $n = 3, 2, 3, 2, 2$  for wear stages one through five, respectively). Mean 3D relative shearing crest length is lowest in wear stage five.

$M_2$ s illustrate a similar pattern of morphological change across wear stages. Individuals with unworn teeth (wear stage one) possessed  $M_2$ s with the steepest slopes, highest angularity values, and the greatest RFIs (Fig. 8). For all three variables, a sharp decrease occurred between wear stage one and two, followed by a plateau at wear stages two to four. The lowest values for slope, angular-

ity, and RFI occurred in those individuals with the most advanced dental wear (wear stage five; Fig. 8). Despite the sharp decrease in slope, angularity, and RFI between wear stage one and two, 2D relative shearing crest lengths increased between these two wear stages while 3D relative shearing crest lengths remained constant (Fig. 9). Compensatory shearing crest blades began to

appear as dentine became exposed with wear, which was reflected in the elongation of 2D shearing crests, until their decrease at wear stage five (Fig. 9). 3D relative shearing crest lengths peaked at wear stage three, subsequently decreased, and were lowest at wear stage five (Fig. 9). Hence, compensatory shearing crests disappeared in the last wear stage, resulting in the decrease of both 2D and 3D relative crest lengths. Variance in relative shearing crest length was highest in wear stage five, reflecting enhanced idiosyncratic variability in worn morphology.

## DISCUSSION

We found that behavior, ecology, and morphology interact to influence chewing efficiency in geladas. The fracture toughness of gelada diets was consistently high across the annual cycle and increased with body size. Gelada chewing efficiency decreased during the dry season when preferred foods, which tend to be less tough, were scarce, and such decreases were greater in older individuals, which presumably had more worn teeth. We emphasize that post-masticatory digestive processes have little effect on food particle size reduction. As such, our analysis suggests a functional association between shearing capacity and tooth wear, with decreased shearing capacity resulting in decreased chewing efficiency. Although the fitness impacts of chewing efficiency have long been recognized, our study provides, to our knowledge, some of the first empirical support for the idea that chewing efficiency can itself be influenced by a combination of the mechanical properties of food and dental wear patterns in a wild animal population. Our research highlights the value of integrating behavioral, ecological, and morphological data in investigations of foraging ecology, particularly in species with highly specialized diets.

### Dietary fracture toughness

We found that dietary fracture toughness varied positively with body size in geladas at Guassa, a finding consistent with our prediction that larger individuals would consume poorer quality foods than smaller individuals. Large geladas ingest tough (i.e., potentially high-fiber) graminoid vegetation, while smaller geladas tend to focus on more brittle (and potentially more nutritious) forbs. These patterns conform to the Jarman-Bell principle on an intraspecific level (Fashing et al., in press), in which larger individuals consume more low quality foods, where quality is considered the inverse of fracture toughness (Lucas, 2004).

We also found that, in line with our prediction, gelada diets were consistently tough across the annual cycle and corresponded generally with rainfall-driven resource availability. Cumulative weighted dietary fracture toughness was variable throughout the annual cycle for each age-sex class, with local dips and peaks of moderate magnitude (Fig. 2). Clear and consistent differences in dietary fracture toughness across the annual cycle were apparent among five age-sex classes of geladas (Fig. 3; Table 4). Graminoids were the foods with the highest fracture toughness values in the gelada diet, so it is not surprising that increased consumption of graminoids during periods of resource scarcity were responsible for the observed trends. The ranges of cumulative weighted fracture toughness by month showed that no age-sex classes consumed a range of fracture toughness greater than  $1051 \text{ J m}^{-2}$  in the annual diet (Table 4). The range

for medium juveniles was the highest among the age-sex classes, perhaps indicating a wider sampling of the mechanical environment throughout the year. Whereas previous studies have found equivocal evidence for differences in dietary mechanics as a function of ontogeny (Raguet-Schofield, 2010; Chalk, 2011; McGraw et al., 2011), the consistent differences in dietary fracture toughness between age-sex classes across the annual cycle in geladas suggests that the mechanical demands of juvenile and adult diets differ fundamentally in this taxon.

### Chewing efficiency

We found that fecal particle size increased during the dry season in geladas at Guassa, a finding consistent with our prediction that the consumption of tougher foods (during periods of food scarcity) will lead to reduced chewing efficiency across all age-sex classes (Figs. 4 and 5). Our results therefore suggest that reduced food availability in the dry season necessitated a dietary switch to more widely available and tougher foods. The absence of hard material in the fecal matter, which mostly contained graminoids and forbs, indicates that tough (rather than hard) vegetation is likely responsible for the observed trend. This dietary shift necessarily reflects consumption of different functional plant types but it could also involve consuming tougher species (e.g., *Festuca macrophylla*) or more mature tissue within a functional plant type. Overall, our results provide strong evidence that food material properties influence chewing efficiency, a pattern widely discussed or assumed but not directly demonstrated in previous research (Pérez-Barbería and Gordon, 1998b). In further support of our third prediction, differences in chewing efficiency between wet and dry seasons were greatest in old adults, suggesting an interaction between tooth wear and consumption of tough graminoids in older individuals. These results are consistent with our findings on how the morphology of gelada molars changes with wear. However, because our dental samples were not matched with the living individuals from which fecal samples were collected, this last interpretation must be made with some caution. We suggest that future research on the interactions between dental wear and chewing efficiency focus on matched samples whenever possible. Lastly, chewing efficiency can be influenced by several behavioral factors that we did not measure. The amount of food chewed, the bite forces produced during chewing, chewing rates, and time spent chewing are all examples of behaviors that can influence chewing efficiency (Pérez-Barbería and Gordon, 1998a). More experimental and observational research is needed to fully appreciate the effect that these behaviors have on chewing efficiency and whether animals alter chewing behavior in accordance with body size, dental wear, and food type and size.

### Dental wear

We also found that measures of occlusal topography (mean slope, angularity, and RFI) decreased as dental wear progressed. These results are in general agreement with previous studies of topographic change with wear in other primate species (e.g., Ungar and Williamson, 2000; M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003; King et al., 2005; Bunn and Ungar, 2009; Klukkert et al., 2012). Relative 2D shearing crest length increased

with wear, while relative 3D shearing crest length remained relatively constant (with an increase in the third stage of wear), but both decreased in the last stage of wear, suggesting a compromise of function in the most advanced wear stage. Our shearing crest results mirror those of King et al. (2005), who also reported an increase in 2D shearing crest lengths, coupled with maintenance of 3D shearing crest lengths, and a decrease of both in old individuals. Our study did not directly match dental topography and shearing capacity with chewing behavior or diet at an individual level, but the majority (7/12) of specimens examined here were from the Guassa gelada population, for which the ecology and behavior are known; such correspondence is rare in primate studies. Here, we assumed that the last wear stage corresponded with the dental morphology of old individuals. As a test of this assumption, we examined the percentage of dentine exposure (PDE) of the two geladas included in the fifth wear stage of this study. The  $M_2$ s of these individuals retained enamel only around the buccal and lingual rims of the teeth (Fig. 7) and had PDE values of 55% and 37% when calculated using the method described in Galbany et al. (2011). We compared these values to PDE data from  $M_2$ s of known-age Amboseli baboons and Lékédi mandrills (Fig. 3b in Galbany et al., 2014). Of the large comparative sample in that study ( $n = 94$  for baboons and  $n = 37$  for mandrills), only two mandrills and three baboons exceed a value of 30% PDE, and these individuals were among the oldest in the samples. This post hoc analysis supports our assumption that wear stage five represents the dental morphology of old geladas.

Janis and Fortelius (1988) described the occlusal morphology of herbivorous mammals as “acquired,” such that compensatory cutting surfaces are exposed with wear. They hypothesized that acquired morphology is functionally optimal, implying that unworn teeth of herbivores are less functional than teeth that exhibit some degree of wear. Our results provide support for this claim. In geladas, the initial decrease in slope, angularity, and RFI between wear stages one and two indicates a general loss of crown volume and a reshaping of the occlusal surface (Fig. 8). These changes were associated with an increase in 2D, but not 3D relative shearing crest length (Figs. 7 and 9). In other words, because 3D relative shearing crest lengths did not change, the shearing functionality of an unworn gelada  $M_2$  does not differ from that of an  $M_2$  with some exposed dentine. However, during the third wear stage, 2D and 3D relative shearing crest lengths increased, indicating an increase in tooth functionality that may contribute to the ability of adult and large juveniles to masticate a tougher diet than medium and small juveniles (Figs. 2 and 3).

The concept that tooth functionality decreases with the onset of dental senescence is supported by our results, which showed that slope, angularity, RFI, and 3D relative shearing crest length were lowest in the last wear stage (Figs. 8 and 9). Our fecal particle size results indicated that old individuals experienced a decrease in chewing efficiency, particularly during the dry season (Figs. 4 and 5). If the last stage of dental wear reflects the occlusal morphology of old individuals, it is reasonable to assume that dental senescence is the proximate mechanism by which old geladas experience compromised chewing efficiency.

That old individuals with worn teeth are poorly equipped to chew tough vegetation during the dry sea-

son highlights the adaptive value of a durable and functional occlusal surface. The dental morphology of geladas (and of members of the genus *Theropithecus* more generally) has long been associated with adaptations to prolong the functional life of the tooth crown in the face of abrasive wear (Jolly, 1970; Meikle, 1977; Jablonski, 1994). Such features include the increased height of the molar crowns and the deep clefts and basins of the molars (Jablonski, 1994). The tall buccal surfaces of the molar crowns, which extend apically into the root bifurcation, apparently permit the tooth to function until the crown is worn down to the root (Swindler and Beynon, 1993). Additionally, geladas have strikingly high values for molar enamel thickness (Shellis et al., 1998), which likely extends the lifetime of the tooth in the face of a highly silicated and/or gritty diet. The role of endogenous (phytolith silicates) versus exogenous (dust and grit, e.g., quartz silicates) agents in generating tooth wear is currently an issue of intense interest (Lucas et al., 2013). Experimental data have shown that a single contact with phytoliths does not result in enamel tissue loss while dust particle contact fractures and removes enamel tissue, although repeated insults of phytoliths could potentially remove enamel volume (Lucas et al., 2013). However, the finding that internal abrasives are related to enamel thickness (Rabenold and Pearson, 2011; Pampush et al., 2013) indicates that endogenous agents can also exert a selective pressure on dental design, a concept corroborated by experimentally induced wear using diets of varying abrasiveness in rabbits (Schulz et al., 2013; Müller et al., 2014). Resisting abrasive wear seems imperative for geladas to maintain the capacity to chew tough vegetation throughout their lives. At Guassa during the dry season, layers of dust coat the vegetation. Underground tissues, whether storage organs or the bottoms of graminoids, are often coated in exogenous grit. Many graminoids at Guassa, particularly *Festuca* grasses, are heavily silicated. Selective feeding may be critical for geladas in avoiding siliceous material. In contrast to ungulates, geladas are manual grazers and therefore capable of a high degree of selectivity (Jablonski, 1994).

For decades, researchers have acknowledged that shearing crests function in the fracture of tough foods (Kinzey, 1974; Kay, 1975; Kay and Hylander, 1978; Sheine and Kay, 1979). Shearing crests are maintained during the life of herbivorous mammals through the exposure of compensatory shearing blades with wear (Rensberger, 1973; Fortelius, 1985; Luke and Lucas, 1985; Lanyon and Sanson, 1986a; King et al., 2005). Because particle breakdown is little affected by digestive processing after swallowing, measuring fecal particle size represents an avenue for testing ideas about the performance of shearing crests. For example, King et al. (2005) measured the performance of compensatory shearing crests in a long-lived folivorous lemur, *Propithecus edwardsi*. Based on fecal particle size measurements, *P. edwardsi* molars appeared to maintain shearing function in the face of occlusal relief loss by the exposure of compensatory shearing blades, yet once occlusal surfaces were obliterated (i.e., compensatory shearing blades were lost and the occlusal surfaces were reduced to shallow dentine bowls surrounded by low-relief enamel bands), fecal particle size increased, indicating that shearing function was reduced. In this study of geladas, the most worn teeth (presumably from old individuals) showed a decrease in relative 3D shearing



crest lengths. Fecal particle size of old adults was higher than that of prime adults, and old adults experienced the greatest increases in fecal particle size between wet and dry seasons (Fig. 5). Our data, therefore, support the ideas that 1) shearing function decreases at the latest stages of life due to dental senescence, and that 2) relative 3D shearing crest lengths are a good proxy for the shearing functionality of molars.

Studies examining occlusal slope, angularity, and relief have typically been based on museum specimens for which diet and chewing efficiency are unknown (Ungar and Williamson, 2000; M'Kirera and Ungar, 2003; Ungar and M'Kirera, 2003; Bunn and Ungar, 2009; Klukkert et al., 2012). Therefore, the functional implications of wear-related changes in these variables remain ambiguous. Although the aim of this study was not to test whether these variables have functional significance, our data imply that they co-vary strongly with each other and that they could reflect some aspect of function, given that occlusal slope, angularity, and relief were lowest in the fifth wear stage. More research is needed, particularly on primate populations with known ages and diets, to test the functional significance of these variables.

Among primates, geladas focus on a high intake of relatively poor-quality vegetation (Dunbar and Bose, 1991; Swedell, 2011; Fashing et al., in press). For such a species, efficient chewing is essential. Yet geladas experiencing dental senescence may have few options at behavioral modification to counteract the effects of tooth wear. Geladas experience notable deterioration in body condition during the dry season at Guassa (VV Venkataraman, pers. obs.), suggesting potential fitness consequences resulting, at least in part, from reduced chewing efficiency. This phenomenon is expected to be magnified in older individuals. It is possible that the old geladas in our study were compensating for tooth wear through behavioral mechanisms, but given the observed increases in fecal particle size, such measures appear to have been insufficient. As grazers, geladas spend much of the day feeding [up to 80% (Iwamoto, 1979, 1993)] and are heavily constrained by time (Dunbar, 1992). Increasing daily feeding time at the expense of other important activities (e.g., resting and socializing) imposes severe costs, and more selective feeding upon more nutritious and/or brittle foods is likely impossible in the dry season due to lack of availability (Fashing et al., in press). For geladas experiencing dental senescence, maintaining a high intake rate of tough foods, despite compromised chewing efficiency, may be the most viable survival strategy. The observation that geladas in the Simien mountains increase their feeding rates and total daily food intake during the dry season, perhaps due to the reduced digestibility of graminoids, supports this idea (Iwamoto, 1979; Hunter, 2001). The purported strategy of geladas of coping with resource scarcity differs from the one adopted by ungulates, which tend to reduce food intake but increase gut mean retention times to more thoroughly digest food, and which additionally relies on the accretion of substantial fat stores during the productive season (Meyer et al., 2010). Given their smaller body mass, this strategy is an unlikely option for geladas (Lindstedt and Boyce, 1985).

### Captive vs. wild and interspecific comparisons

Fecal particle size data from zoo geladas provide further insight into the design and function of gelada

molars. The diet of captive geladas generally differs from that of their free-ranging conspecifics (Mau et al., 2011). Differences in fecal particle size between wild and captive specimens of the same species have been interpreted as indicators of whether the species' dentition is suited for the efficient comminution of the diet in captivity (Hummel et al., 2008). Given the diverse wear states and mechanical food properties represented in this sample, it is likely that our study captured a substantial portion of the possible variation in gelada chewing efficiencies. We found that zoo geladas had fecal particle size values most similar to old Guassa geladas. The low chewing efficiencies of zoo geladas compared with wild geladas support the concept that the species is adapted to a natural diet of graminoid and herbaceous vegetation and cannot reduce particle size in the feeds offered in captivity (even if the feeds include fresh graminoids) with a similar efficiency (cf. Hummel et al., 2008 for similar results comparing captive and wild browser ungulates).

The chewing efficiency of geladas is particularly striking when compared with that of other mammals. For example, Dunbar and Bose (1991) found that geladas' mean fecal particle size was similar to that of zebra (*Equus burchelli*), despite an enormous body size difference between these species. Since fecal particle size increases with body mass across mammals (Fritz et al., 2009), including primates (Matsuda et al., 2014), these findings highlight fundamental differences in dental performance between primates and ungulates. Matsuda et al. (2014) found that proboscis monkeys (*Nasalis larvatus*) had, when compared to 13 other primate species, particularly small fecal particle sizes, indicating a high chewing efficiency. The authors interpreted this result as indicating either particle size reduction through dental adaptation, or as supporting the assumption, based on behavioral observations (Matsuda et al., 2011), that this species employs a "rumination" strategy. We found that during the wet season at Guassa, geladas had higher chewing efficiencies than any primate previously measured, including other simple-stomached primates in addition to colobines with adaptations for foregut fermentation and rumination (Fig. 6). During the dry season, however, gelada chewing efficiency decreased to what would be expected for a primate of their body size (Fig. 6). These results for geladas, in which a "rumination" strategy has not been observed, suggest that particularly fine fecal particles can be achieved by a special dental design only, similar to observations made for equids (Fritz et al., 2009). Contrasting the molar morphologies of geladas and proboscis monkeys with those of other primates could elucidate the morphological features that determine the chewing efficiency of primates.

### Fallback foods of geladas

A consideration of potential gelada fallback foods may elucidate the evolutionary ecology of geladas and their dental functional morphology in relation to diet. A fallback food is one whose consumption is negatively correlated with the availability of preferred foods, while a preferred food is one favored disproportionately relative to its abundance in the environment (Marshall and Wrangham, 2007). Fallback foods are expected to exert ecological and evolutionary pressures upon dental form due to their pronounced mechanical resistance relative

to preferred foods (Marshall and Wrangham, 2007; Marshall et al., 2009). Several studies have shown associations between aspects of masticatory morphology and the mechanical properties of consumed fallback foods (Yamashita, 1998; Lambert et al., 2004; Taylor, 2006; Vogel et al., 2008).

The fallback food framework would predict that the gelada dentition is adapted to chew vegetation that is available year-round but not preferred. By the criteria outlined above, the preferred food of geladas should be edible forbs, which are disproportionately selected by the animals in relation to their abundance (Fashing et al., in press). Because edible forb abundance is very low relative to graminoids, however, geladas cannot live off them (Fashing et al., in press). The obvious candidate for a fallback food is underground storage organs (USOs, including roots, corms, and tubers), the consumption of which is strongly correlated with low three-month cumulative rainfall (Fig. 4 in Fashing et al., in press), presumably because digging is not energetically advantageous during the wet season when lush grasses are widely available. If USOs are hard (resistant to deformation) (Dominy et al., 2008), it may be argued that geladas should show morphological [specifically, processing (Marshall and Wrangham, 2007)] adaptations to reflect hard-object consumption.

Although we did not measure the hardness of gelada foods in this study, hard foods deserve some brief discussion as potential fallback foods. For example, it is perhaps telling that geladas place graminoid corms and forb roots posteriorly in the dental row to be fractured by the molars (VV Venkataraman, pers. obs.), a behavior that presumably reflects the higher bite forces produced at more posterior bite points (Spencer, 1995; Lucas, 2012). Our anecdotal impression, however, is that geladas do not experience difficulty processing any of these putatively “hard” items, nor do they reject items after “test bites,” as do such hard-object feeders as sooty mangabeys (e.g., Daegling et al., 2011), suggesting these items may not be particularly hard. Graminoid seeds have featured prominently in the literature on geladas and were once believed to be a major component of the gelada diet (Jolly, 1970). Yet at Guassa seed consumption is heavily seasonal, comprising no more than 13% of scan samples in any month at the population level (Fashing et al., in press), and this peak (in October) coincides with high three-month cumulative rainfall and high availability of lush graminoids. Thus, seeds may be consumed opportunistically but are certainly not a food resource vital to survival during the dry season. That feeding on hard objects during fallback episodes is an important aspect of the gelada diet is further rejected by microwear texture analysis. Despite a comparatively diverse diet involving USOs at Guassa, only one Guassa specimen exhibited  $M_2$  microwear texture that qualifies as “complex” (Shapiro AE, Venkataraman VV, Nguyen N, Fashing PJ. Inferring dietary niche breadth in fossil *Theropithecus* from dental microwear in geladas, in prep), a characteristic equated with the consumption of hard objects (but see Schulz et al., 2013).

As other investigators have surmised (Daegling et al., 2011), fracture toughness may be more relevant to geladas than hardness. At Guassa, gelada diets for all age-sex classes are tough (if not extraordinarily tough) throughout the entire annual cycle, with moderate seasonal increases that reflect altered food selection when the availability of preferred foods is reduced. We found

that such increases were associated with reduced chewing efficiency, particularly in older individuals, due to the consumption of tough grasses. This inference is supported by the fecal particle analysis, which demonstrates that uncomminuted grass tissue is responsible for increases in particle size in the dry season, not unprocessed seeds or USOs. In addition to underground items, *Festuca macrophylla* (grass) blades (leaves) represent another candidate for a fallback food because they a) account for more ground cover than any other plant species at Guassa (Fashing et al., in press), b) are one of the toughest species in the gelada diet (*Festuca* blades and pseudo-stems consumed “sometimes”: mean  $\pm$  SD =  $4729.8 \pm 1751.6 \text{ J m}^{-2}$ ), and (c) we have anecdotally observed that they are consumed more often in the dry season. Because we could not easily classify tall graminoids consumed during scan samples to the species level, the frequency of *Festuca* consumption is unknown. However, it is notable that, similar to the feeding behavior reported for giant pandas (*Ailuropoda melanoleuca*) on bamboo leaves (Sanson, 2006), geladas fold these long grasses before placing them on the molar row for comminution. This manipulation may facilitate particle breakdown by introducing notches into the grass, which is notoriously notch-resistant (Lucas, 2004). Generally, when *Festuca* grasses are consumed, a preference for younger stems is clearly apparent (VV Venkataraman, pers. obs.). The consumption of extraordinarily tough *Festuca* and other tall graminoids during the dry season may be an important selective pressure acting on gelada dental morphology. However, because the gelada diet is tough throughout the annual cycle, invoking a role for fallback foods does not seem necessary to explain dental adaptation in geladas (see McGraw et al., 2014 for a similar argument regarding sooty mangabeys). It is also possible that the gelada dentition is equipped to comminute both tough and hard foods. For example, the relatively thick molar enamel of geladas (Shellis et al., 1998) could arrest cracks at the enamel-dentine junction from hard-object consumption while simultaneously increasing the life of the tooth crown against wear (Rabenold and Pearson, 2011; Pampush et al., 2013). Additional research on this topic is clearly warranted.

A final point is that our study shows fecal particle size to be a practical indicator of chewing efficiency in primates and holds promise for testing hypotheses regarding dental adaptation to characteristic diet types. Using food selection alone to characterize primate responses to fallback episodes may be incomplete, not only because food selection relies on several sensory modalities, but also because food selection is not necessarily related to chewing efficiency. Chewing efficiency has been linked with fitness in primates (King et al., 2005), and it is probable that reduced chewing efficiency from consumption of nonpreferred foods during fallback episodes contributes to negative physiological consequences, such as weight loss and disease. Measuring chewing efficiency performance in tandem with food selection may provide a more complete picture of primate physiological responses to fallback episodes and contribute to refining hypotheses and tests of dental adaptation.

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