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Article in *American Journal of Physical Anthropology* · September 2014

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Gelada Feeding Ecology in an Intact Ecosystem at Guassa, Ethiopia: Variability Over Time and Implications for Theropithecine and Hominin Dietary Evolution

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KEY WORDS fallback foods; forbs; graminivory; habitat disturbance; *Paranthropus boisei*; *Theropithecus gelada*; *Theropithecus oswaldi*

ABSTRACT Recent evidence suggests that several extinct primates, including contemporaneous *Paranthropus boisei* and *Theropithecus oswaldi* in East Africa, fed largely on grasses and sedges (i.e., graminoids). As the only living primate graminivores, gelada monkeys (*Theropithecus gelada*) can yield insights into the dietary strategies pursued by extinct grass- and sedge-eating primates. Past studies of gelada diet were of short duration and occurred in heavily disturbed ecosystems. We conducted a long-term study of gelada feeding ecology in an intact Afroalpine ecosystem at Guassa, Ethiopia. Geladas at Guassa consumed ≥ 56 plant species, ≥ 20 invertebrate species, one reptile species, and the eggs of one bird species over a 7-year period. The annual diet consisted of 56.8% graminoid parts, 37.8% forb parts, 2.8% invertebrates, and 2.6% other items, although geladas exhibited wide variability in diet across months at

Guassa. Edible forbs were relatively scarce at Guassa but were strongly selected for by geladas. Tall graminoid leaf and tall graminoid seed head consumption correlated positively, and underground food item consumption correlated negatively, with rainfall over time. Geladas at Guassa consumed a species-rich diet dominated by graminoids, but unlike geladas in more disturbed habitats also ate a diversity of forbs and invertebrates along with occasional vertebrate prey. Although graminoids are staple foods for geladas, underground food items are important “fallback foods.” We discuss the implications of our study, the first intensive study of the feeding ecology of the only extant primate graminivore, for understanding the dietary evolution of the theropithecine and hominin putative graminivores, *Theropithecus oswaldi* and *Paranthropus boisei*. *Am J Phys Anthropol* 155:1–16, 2014. © 2014 Wiley Periodicals, Inc.

Diet has played an influential role in shaping the morphology, behavior, and ecology of humans and other animals. For example, many of the milestones in human evolution, including bipedalism and encephalization, are believed to have been associated with dietary changes (McHenry, 1982; Aiello and Wheeler, 1995). Understanding diet is therefore essential for reconstructing a species' evolutionary history and for predicting its future prospects (Grant, 1999; Lucas et al., 2008). While the diets of most living primate species can be characterized directly through long-term behavioral observation and nutritional analysis (e.g., Altmann, 1998), the diets of extinct primates can only be inferred indirectly from analysis of craniodental morphology, dental microwear, and stable isotopes, as well as from reconstructions of the paleoenvironment (Reed and Rector, 2007; Wood and Constantino, 2007; Ungar and Sponheimer, 2011; Scott et al., 2012; Sponheimer et al., 2013a). Although living primates are not perfect models for extinct ones, they can provide valuable insights for reconstructing the life-ways of seemingly ecologically similar, but extinct primates (Elton, 2006). In this article, we present data on the feeding ecology of an extant primate—gelada monkeys (*Theropithecus gelada*)—with a unique diet (dominated by grasses and sedges) living in an ecologically intact ecosystem and discuss how this research contributes to

recent efforts to reconstruct the diets of several extinct primates, including *T. oswaldi* and *Paranthropus boisei*, that likely incorporated large quantities of these food items into their diets as well.

The proliferation of early hominins in Africa accompanied the expansion of grasslands and retreat of forests during the Plio-Pleistocene. Mounting evidence suggests a major dietary shift to grassland-based resources

Grant sponsors: California State University Fullerton; Cleveland Metroparks Zoo; Gisela and Norman Fashing; Donna and Karl Krueger; Margot Marsh Biodiversity Foundation; Pittsburgh Zoo; Primate Conservation Inc.; Anita and Hans-Peter Profunser; Dean Gibson and San Diego Zoo; Christopher Schroen.

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Received 17 February 2014; revised 5 June 2014; accepted 6 June 2014

DOI: 10.1002/ajpa.22559
Published online 10 July 2014 in Wiley Online Library (wileyonlinelibrary.com).

occurred among some hominins and sympatric nonhuman primates beginning ~3.5 Ma (Codron et al., 2005; Lee-Thorp et al., 2010; Lee-Thorp et al., 2012; Cerling et al., 2013; Sponheimer et al., 2013a).

Tropical grasses and some sedges follow a different photosynthetic pathway (C_4) from those of trees, shrubs, and forbs (C_3) (Smith and Epstein, 1971). Recently, stable isotope analyses of tooth enamel have been used to identify the proportion of C_3 - and C_4 -derived foods in the diets of nearly a dozen early hominin species and several contemporaneous nonhuman primates (Codron et al., 2005; Cerling et al., 2013; Sponheimer et al., 2013a). Unlike the living African apes, whose diets consist entirely of C_3 foods (Sponheimer et al., 2006), most early hominins (from 3.5 Ma onwards) incorporated some C_4 foods in their diet (e.g., *Australopithecus afarensis*, *A. africanus*), and a few ate primarily C_4 foods (e.g., *A. bahrelghazali*, *Paranthropus boisei*) (Sponheimer and Lee-Thorp, 1999; Cerling et al., 2011; Lee-Thorp et al., 2012; Sponheimer et al., 2013a; Wynn et al., 2013). Intriguingly, the most extreme hominin C_4 food specialist (~80% of diet), *Paranthropus boisei*, was contemporaneous and probably sympatric across much of East Africa with the cercopithecoid primate, *Theropithecus oswaldi*, a species with a similar body size (50 kg) and carbon isotope signature (Cerling et al., 2011, 2013). *T. oswaldi*'s high C_4 signal is widely assumed to have been the product of a diet dominated by grass and sedge blades (i.e., leaves) (Codron et al., 2005; Cerling et al., 2013), while there is no consensus regarding the source of the strong C_4 signal in *P. boisei*. Potential foods accounting for *P. boisei*'s C_4 signal include the leaves, underground storage organs, or seeds of grasses or sedges or animals that themselves ate grasses or sedges, possibilities that isotopic analysis alone cannot distinguish between at present (Cerling et al., 2011; Lee-Thorp, 2011; Fontes-Villalba et al., 2013; Sponheimer et al., 2013b).

Although there are many grazing ungulates (with specialized dentition and morphology for consuming grasses and sedges), there is only one extant graminivorous (graminoid¹-eating) primate, the gelada monkey (*Theropithecus gelada*) (Dunbar, 1983; Dunbar and Bose, 1991). While living geladas are imperfect models for the diets of extinct primates (Elton, 2006; Codron et al., 2008; Swedell and Plummer, 2012), studies of gelada feeding ecology still have the potential to provide unique insights into the diets of extinct species like *T. oswaldi* (with whom geladas share many conserved dental and post-cranial traits) and *P. boisei* (Cerling et al., 2011, 2013). Indeed, several prior influential studies have used geladas to model hominin ecological or behavioral evolution (Jolly, 1970; Wrangham, 1980; Dunbar, 1983), though surprisingly no detailed study has ever been carried out to characterize the diet of living geladas.

T. gelada is the last remaining species of a once widespread and speciose genus whose extinct members inhabited grasslands and woodlands across large swathes of Africa (and one region of India) as recently as 60,000 years ago (Jolly, 1972; Eck, 1993; Foley, 1993; Pickford, 1993). Today, geladas are confined to the rapidly disappearing Ethiopian Highlands where they are threatened by climate change and the conversion of their alpine moorland habitat to farmland and livestock grazing areas (Dunbar, 1998; Beehner et al., 2007; Gippoliti and Hunter, 2008).

Available morphological evidence strongly suggests that geladas are highly specialized to exploit graminoids, which are renowned for their tough and abrasive properties (Jablonski, 1994; Venkataraman et al., in review). Geladas possess several major dental adaptations for efficiently comminuting graminoids and coping with the siliceous phytoliths and exogenous grit they contain, including reduced incisors, enlarged molars, deeply-crenellated cheek teeth with columnar cusps, and high-crowned (hypsodont) cheek teeth (Jolly, 1972; Szalay and Delson, 1979; Jablonski, 1994; Damuth and Janis, 2011; Hummel et al., 2011). Geladas are also able to pluck above-ground foods rapidly and dig for underground foods efficiently because of their elongated, robust thumb and reduced second finger, providing them with the highest opposability index of any nonhuman primate and the highest thumb robusticity index of any primate (Jolly, 1970, 1972; Iwamoto 1979; Dunbar and Bose, 1991). Lastly, the gelada locomotor apparatus enables them to shuffle forward in a sitting position while harvesting graminoids or other abundant terrestrial food items (Wrangham, 1980; Dunbar, 1983). Most of the specialized dental, manual, and locomotor traits possessed by geladas are considered to be primitive for the *Theropithecus* genus, suggesting a long heritage of graminivory (Jablonski 1994).

Previous studies of wild gelada feeding ecology have been of short duration (lasting a few weeks to several months each) and carried out in human- and livestock-dominated short-grass Afroalpine ecosystems (Dunbar and Dunbar, 1974; Dunbar, 1977; Iwamoto, 1979; Hunter, 2001). These studies (conducted in the Simien Mountains and at Bole, Ethiopia) suggest that geladas are "essentially primate horses" (Dunbar and Bose, 1991; p 2) consuming primarily graminoid leaves and, at times, graminoid seeds or graminoid and forb roots and storage organs (Dunbar and Dunbar, 1974; Dunbar, 1977; Iwamoto, 1979; Hunter, 2001). Their presumed dietary simplicity suggests that geladas engage in little complex food processing or extractive foraging behavior beyond digging for underground items in the dry season (Iwamoto, 1979). Little is known about gelada feeding ecology in more intact ecosystems, which geladas likely inhabited during most of their evolutionary history. Though there is no fossil record to help reconstruct the paleoenvironment in which *T. gelada* evolved (Jablonski, 1993), widespread anthropogenic disturbance of Afroalpine ecosystems is probably a recent phenomenon (Williams et al., 2005).

We carried out the first intensive study of gelada feeding ecology in an unusually intact tall-grass Afroalpine ecosystem on the Guassa Plateau, north-central Ethiopia. We collected detailed data on gelada diet in relation to food availability at Guassa over 15 months and documented foraging behaviors and compiled an exhaustive list of species and items eaten by the geladas over 7 years. We compare our results to those from shorter studies of gelada diets in more disturbed ecosystems and discuss the implications of our findings on gelada dietary diversity and exploitation of underground food items for understanding the diets of extinct putatively graminivorous primates, including *Theropithecus oswaldi* and *Paranthropus boisei*.

METHODS

Species, study site, and subjects

Geladas are terrestrial and sexually dimorphic cercopithecine monkeys similar in size and appearance to, though phylogenetically and ecologically distinct from,

¹Botanical term for grasses, sedges, and rushes, although extant geladas only consume grasses and sedges, so throughout this term refers only to these two plant groups.

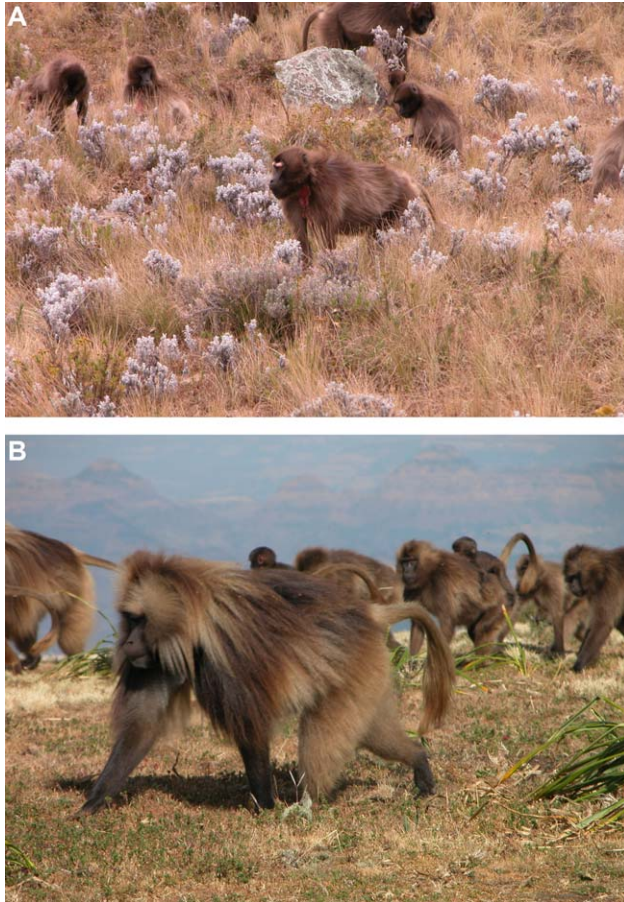


Fig. 1. Photos depicting differences in the habitats occupied by the (A) Guassa and (B) Simien Mountains gelada populations. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

baboons (*Papio* spp.) (Bergman and Beehner, 2013). Male geladas weigh, on average, 19.0 kg and females 11.7 kg (Bergman and Beehner, 2013), with immature animals weighing some fraction of the weight of adult females (e.g., large juveniles at Guassa appear to be $\sim 3/4$, medium juveniles $\sim 1/2$, and small juveniles $\sim 1/4$ of the size of adult females).

We conducted our study of geladas on the Guassa Plateau, a large (111 km²) 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 (Fig. 1A; see Ashenafi 2001 and Fashing et al., 2010 for further details). Protected by an indigenous conservation system dating to the 17th century (Ashenafi and Leader-Williams, 2005), Guassa is probably the largest tall-grass ecosystem remaining in the Ethiopian highlands and retains an intact large carnivore community, including Ethiopian wolves (*Canis simensis*), African wolves (*Canis aureus lupaster*), spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and servals (*Leptailurus serval*) (Ashenafi, 2001; Ashenafi and Leader-Williams, 2005; Rueness et al., 2011). Guassa's intactness (Fig. 1A) makes it an ideal site to compare to other Ethiopian Highland locales like Simien Mountains National Park where human and livestock disturbance have had a

greater impact on the ecology (Fig. 1B; Dunbar, 1977; Iwamoto, 1979; Hunter, 2001).

Our study focused on a ~ 220 -member gelada band (Steelers Band) at Guassa. We began habituating the members of this band to the presence of observers in December 2005. By January 2007, when we began systematic data collection on a near-daily basis, we could follow the geladas at distances of 5–10 m and recognize most individuals based on natural markings including scars, facial crease patterns, head shape, and external parasitic swellings. The swellings are caused by the parasite, *Taenia serialis*, and have occurred on 30% of known adults and 4% of immatures during our study at Guassa (Nguyen et al. in review).

Vegetation assessment

To provide a preliminary characterization of the vegetation available to our gelada study band, we established seven non-overlapping straight-line transects (mean transect length = 2.14 km; range = 1.00–3.00 km) placed randomly across their home range. At each 50 m interval along the transect line, we paused to create a temporary 0.7 m \times 0.7 m plot where we recorded a) GPS location, b) the major plant taxa present, and c) the approximate amount of ground cover accounted for by each plant taxon identified within the plot (Mueller-Dombois and Ellenberg, 1974). Identification of plants was carried out by Melaku Wondafresh of the National Herbarium in Addis Ababa based on voucher specimens collected during several preliminary transects. Through subsequent consultation with M.W., we compiled a list of 34 plant species we could visually identify with confidence while enumerating plots in the field. These plant species accounted for the vast majority of the vegetation cover in the plots and many of them collectively comprised the bulk of the geladas' diet (Fashing, pers. observ.). Most plants in the plots could be identified to species (e.g., the graminoids *Festuca macrophylla*, *Carex monostachya*), although some important plants (e.g., other graminoids including *Agrostis quinqueseta*, *Andropogon amethystinus*, etc.) had to be grouped into general categories (e.g., "other tall graminoid spp.," "mixed short graminoid spp.") due to the difficulty of identifying them during transects. Within each plot, we assigned scores for the percentage ground cover accounted for by each plant taxon present. These scores were "very low" (accounting for <1% of total coverage), "low" (1–9% coverage), "some" (10–50% coverage), and "high" (>50% coverage).

Climatic monitoring and food abundance measures

We collected data on rainfall and on maximum and minimum temperature every 24 h (at ~ 0700) using an All-Weather® metric rain gauge and two Taylor® Digital Waterproof Max/Min thermometers (Forestry Suppliers), respectively. Weather measurement equipment was attached to posts (covered posts for the thermometers so that they were shaded) in an open portion of our campsite situated near the center of Steelers Band's home range (Gelada Camp, 10°20'N, 39°49'E, Elev: 3438 m). We summed daily rainfall values (in mm) to produce monthly and yearly rainfall totals. In addition, we used daily maximum and minimum temperature (°C) to produce mean maximum and minimum monthly and yearly temperatures. We calculated average daily temperatures

by determining the mean of the daily maximum and minimum temperatures.

As part of our effort to longitudinally monitor changes in food availability for geladas at Guassa, we established three vegetation plots within the home range of Steelers Band. We selected relatively homogeneous patches of vegetation in which to locate the plots which were each 6 m × 1 m in size. Every 28–34 days, we randomly selected 1 of the 12, 0.5 m × 0.5 m squares within each plot for harvest of its above-ground biomass (Boutton et al., 1988; Hunter, 2001; Sala and Austin, 2000). As a result of our monthly harvesting regime (beginning in February 2007 and continuing through May 2013, with harvests occurring during 69 of the 76 months in that period), each plot had to be replaced with a nearby plot of similar size and composition on an annual basis. After monthly harvesting was complete, we sorted the vegetation from each plot into the following categories: 1) green graminoid leaves (emergent or mature), 2) brown graminoid leaves (senescent or dead), 3) forbs, 4) shrubs, and 5) other. We dried the sorted contents of each vegetation harvest in our tents until they achieved a constant dry weight (usually within 3–4 weeks).

We developed two initial measures for food availability based solely on graminoid leaf biomass because 1) geladas obtained more than half of their diet from green graminoid leaves (see Results), 2) geladas almost never consumed shrubs, and 3) forbs were small and scattered within plots, achieving very low dry weights. Our first initial measure of food availability involved calculating the mean green graminoid biomass per plot for each month of the study. This measure had the advantage of providing a simple, intuitive estimate for food availability based on the overall biomass of geladas' top food item at Guassa. Our second initial measure of food availability was based on the ratio of mean green graminoid biomass to mean brown graminoid biomass per plot for each month. Rather than approximating overall food abundance, this measure offers insight into the percentage of available graminoid leaves that are edible (i.e., green) for geladas during a given month. Both measures of monthly food availability were later correlated with measures of recent rainfall to obtain a simple index enabling us to track changes in food availability over time (see Data Analysis section; cf., Sinclair and Norton-Griffiths, 1979; Barton et al., 1992). Rainfall is usually the best predictor of actual food availability in grassland systems since it results not only in an increase in biomass, but triggers phenological activity (i.e., flowering, fruiting, or other periodic phenomena) as well (Pettorelli et al., 2011).

Diet

We collected systematic feeding data on an average of 15.9 ± 3.5 (SD) days each month for members of Steelers Band from February 2007 to April 2008. On most mornings, we first encountered the geladas at their sleeping cliffs before 0800 and followed them throughout the day until 1730 or 1800 when they neared their cliffs for the night. We conducted instantaneous scan samples (Altmann, 1974) at 30-min intervals on the activities of up to five individuals nearby. Activities included feeding, resting, walking, grooming, or other social activity. To avoid overestimating eye-catching or ephemeral activities, we scanned individuals in order of occurrence from left to right, recording the first activity they engaged in

that lasted ≥ 3 s. The open grassland conditions and large size of gelada aggregations at Guassa meant it was easy (except during very foggy weather) to obtain instantaneous data on five individuals during most scans. We collected a total of 9,994 feeding records across geladas of all age groups over the 15-month study period.

Feeding was defined as any occasion during which a monkey plucked food items, pulled food items towards its mouth, masticated, or swallowed. If a monkey was feeding at the time of a scan, we recorded the food item and, if possible, the species upon which it was feeding. We designated food items as tall graminoid spp. leaves, short graminoid spp. leaves, graminoid seed heads, graminoid corms, graminoid crowns/rhizomes, forb leaves, forb roots, forb tubers, forb pith, forb flowers, unidentified underground items, unidentified above-ground items, or invertebrates.

Items identified as “graminoids” consisted of grasses or sedges, which proved difficult to consistently distinguish from one another rapidly during behavioral data collection. “Tall graminoid” included those taxa reaching ≥ 10 cm in height when fully grown, while “short graminoid” consisted of taxa < 10 cm tall when fully grown. “Graminoid crowns” were the base from which the leaves grow and were sometimes eaten in association with the rhizomes. “Rhizomes” were the creeping root-stalks and “corms” were the swollen storage organs of graminoids. “Forbs” consisted of a wide variety of non-graminoid herbs. “Unidentified underground items” were items the geladas obtained through digging that were too small for observers to see well enough to identify.

It was sometimes impossible to identify food items to species in the grassland environment at Guassa because many different species are tightly clustered and distinctions between species are often subtle. However, whenever a new species was clearly eaten by the geladas, we collected voucher specimens and later deposited them at the National Herbarium for identification. We began this collection in January 2007 and have continued it to the present time. Because the percentage of different species-specific food items in the diet could not be quantified, we provide a categorical assessment of how often each species-specific food item was consumed during the study. The categories we used for this assessment were “often” (regular part of diet year round), “sometimes” (regular part of diet seasonally or consumed at low to moderate levels throughout the year), “rare” (> 5 feeding incidents per year though not a common food item), and “very rare” (< 5 feeding incidents per year).

Data analysis

Using the temporary plots from the vegetation assessment, we calculated vegetation abundance in two ways (Mueller-Dombois and Ellenberg, 1974). First, we determined the percentage of total plots in which each taxon was present. Second, we tabulated the percentage contribution of each taxon to the total ground cover within each of the plots. For this measure, we first assigned a single ground cover score for each plant taxon derived from the percentage ground cover score assigned to the taxon (if present) during the vegetation assessments (e.g., very low = 0.5% coverage, low = 4.5% coverage, some = 25% coverage, and high = 70% coverage). We then took the mean across all plots of the single ground

TABLE 1. Percentages of (a) the ground cover accounted for by the different plant species surveyed and (b) the plots (0.7 m×0.7 m; n=300) in which each species appeared.

Species	Family	Category ^a	% Coverage ^b	% Plots
<i>Festuca macrophylla</i>	Poaceae	graminoid, tall	15.30	72.67
<i>Thymus schimperi</i>	Lamiaceae	forb (not eaten)	14.35	73.33
<i>Alchemilla abyssinica</i>	Rosaceae	forb (not eaten)	12.72	82.67
Bare ground (soil)	---	soil	9.36	73.67
"Other tall graminoid" spp.	Poaceae/Cyperaceae	graminoid, tall	6.20	73.33
"Mixed short graminoid" spp.	Poaceae/Cyperaceae	graminoid, short	5.46	57.67
<i>Euryops pinifolius</i>	Asteraceae	shrub	5.46	43.33
<i>Helichrysum splendendum</i>	Asteraceae	shrub	4.59	49.00
Rock	---	rock	3.63	25.67
<i>Carex monostachya</i>	Cyperaceae	graminoid, tall	2.88	10.00
<i>Trifolium</i> spp.	Fabaceae	forb	2.02	66.33
<i>Agrocharis melanantha</i>	Apiaceae	forb	1.85	66.66
<i>Erica arborea</i>	Ericaceae	shrub	1.51	10.67
<i>Commelina africana</i>	Commelinaceae	forb	0.83	58.67
<i>Agrolobium ramosissimum</i>	Fabaceae	forb	0.78	44.33
<i>Kniphofia foliosa</i>	Asphodelaceae	forb	0.48	1.33
Unidentified lichen	Unidentified	lichen	0.43	7.67
<i>Ranunculus</i> sp.	Ranunculaceae	forb	0.35	18.00
<i>Haplosciadium abyssinicum</i>	Apiaceae	forb	0.30	14.33
<i>Kniphofia insignis</i>	Asphodelaceae	forb	0.30	14.00
<i>Hypericum revolutum</i>	Hypericaceae	shrub	0.21	3.00
<i>Aeonium leucoblepharum</i>	Crassulaceae	forb	0.17	0.67
<i>Rubus apetalus</i>	Rosaceae	shrub	0.10	1.33
<i>Lobelia rhynchopetalum</i>	Lobeliaceae	forb	0.10	1.00
Unidentified fern	Unidentified	fern (not eaten)	0.10	1.00
<i>Anthriscus sylvestris</i>	Apiaceae	forb	0.07	2.33
<i>Galium simense</i>	Rubiaceae	forb	0.05	1.67
<i>Carex simensis</i>	Cyperaceae	graminoid, short	0.05	1.67
<i>Carduus nyassanus</i>	Asteraceae	forb	0.05	1.33
"Mixed herb" spp.	Unidentified	forb	0.04	1.67
<i>Hebenstretia angolensis</i>	Scrophulariaceae	forb (not eaten)	0.03	0.67
<i>Salvia merjamie</i>	Lamiaceae	forb (not eaten)	0.03	2.33
<i>Helichrysum formosissimum</i>	Asteraceae	shrub	0.02	0.67
<i>Silene burchellii</i>	Caryophyllaceae	forb	0.02	3.00
<i>Anthemis tigreensis</i>	Asteraceae	forb	0.01	2.33
<i>Delosperma schimperi</i>	Aizoaceae	forb	0.01	1.33

^a Entries categorized as '(not eaten)' were taxa that geladas were never observed consuming.

^b Approximately 10% of the ground cover within the plots consisted of plant species we were unable to identify.

cover scores for each taxon which we call the taxon's "overall ground cover" score.

In grassland ecosystems (like Guassa), net primary productivity (i.e., quantity of vegetative matter produced per unit time) tends to be influenced by seasonal variation in precipitation (e.g., Burke et al., 1990). Following periods of rainfall, grassland plants exhibit phenological activity (Burke et al., 1990), thus increasing green biomass (Pandey and Singh, 1992), which, in turn, can affect the kind and extent of herbivory (Coe et al., 1976). Therefore, we expected that rainfall would influence the availability (Pandey and Singh, 1992) and quality of gelada food items at Guassa (van Soest, 1994). In particular, we predicted that rainfall would be correlated with our initial measures of monthly food abundance—1) the total amount of edible food in the plots (i.e., the mean weight of green graminoids per m²) and 2) the relationship between the ratio of edible to inedible food in the plots (i.e., the mean green to brown graminoid ratio in the plots). To determine the measure of rainfall that best predicted food availability, we tested rainfall 15, 30, 45, 60, 75, and 90 days before the date of each vegetation plot harvest against both of our initial measures of monthly food availability over the entire study period using Pearson's correlation coefficients.

To avoid sampling bias, we ensured that the relative representation of the different age/sex classes in the dietary records did not differ significantly across months. We did not attempt to determine if diet differed between individuals with visible parasitic swellings and those without them, but have no reason to suspect there were substantive dietary differences between these classes of individuals. To determine the "annual diet," we obtained the means of the 15 mean monthly diets and then calculated the mean of the four possible annual diets (Feb 07–Jan 08, Mar 07–Feb 08, Apr 07–Mar 08, May 07–Apr 08). We calculated rough "selection ratios" for above-ground a) tall graminoid, b) short graminoid, and c) forb parts by dividing percentage contribution to the annual diet by percentage contribution to vegetation cover for each of these three groupings.

For all statistical tests, "significance" was defined as $P \leq 0.05$ and a "trend" was noted when P was > 0.05 but ≤ 0.10 .

RESULTS

Vegetation composition

At least 34 species from >21 families were recorded in the 300 vegetation assessment plots (Table 1). These

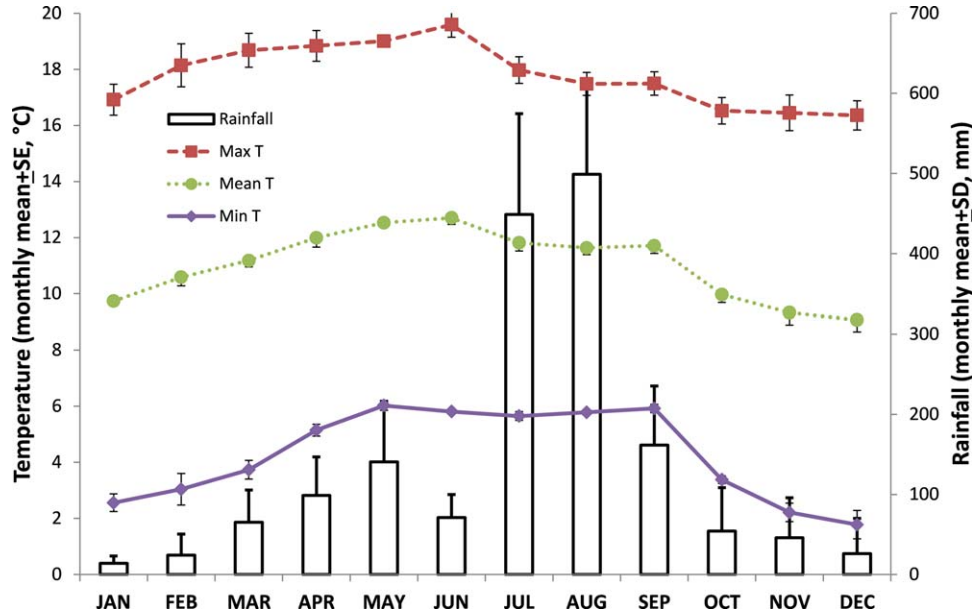


Fig. 2. The weather at Gelada Camp, Guassa, Ethiopia (2007–2012). Mean daily maximum, minimum, and average temperatures ($^{\circ}\text{C}$) and mean total rainfall (mm) for each month of the year over a recent 6-year period (Jan 2007 to Dec 2012) at Guassa, Ethiopia ($n = 6$ monthly means for each month). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

values represent substantial underestimates because $\sim 10\%$ of the ground cover within the plots consisted of many plant species (nearly all of them uncommon) we were unable to identify in the field during surveys. The three species found in the highest percentage of plots (*Alchemilla abyssinica*: 82.7%, *Thymus schimperi*: 73.3%, *Festuca macrophylla*: 72.7%) were identical to those accounting for the highest percentage of overall ground cover, albeit in different order (*Festuca macrophylla*: 15.3%, *Thymus schimperi*: 14.4%, *Alchemilla abyssinica*: 12.7%). However, there were some species that were found in a high percentage ($\geq 40\%$) of plots, but that occurred at such low densities that they accounted for a very small percentage ($\leq 2\%$) of overall ground cover, including several forb taxa that proved to be common food items for geladas (e.g., *Agrocharis melanatha*, *Agrolobium ramosissimum*, *Trifolium* spp.).

Tall graminoids accounted for 24.4% of the ground cover in the vegetation assessment plots, nearly five times the 5.5% of the ground cover accounted for by short graminoids (Table 1). Forbs eaten by geladas represented 7.4% of the ground cover, though two abundant forbs not eaten by geladas (*Thymus schimperi*, *Alchemilla abyssinica*) accounted for an additional 27.1% of the ground cover. The remaining ground cover consisted of shrubs (11.9%), bare soil (9.4%), rocks (3.6%), lichens (0.4%), ferns (0.1%), or unidentified species (10.2%).

Climatic monitoring and food abundance measures

From 2007 to 2012, the average monthly temperature at Guassa was 11.0 ± 1.2 (SD) $^{\circ}\text{C}$ (Fig. 2). Mean monthly low and high temperatures were 4.3 ± 0.5 (SE) and 17.8 ± 0.3 (SE) $^{\circ}\text{C}$, respectively. Rainfall averaged 1650 ± 243 (SD) mm per year (Fig. 2). Rainfall was strongly seasonal exhibiting a unimodal peak during

July and August when more than half of the annual rainfall occurred (Fig. 2).

Rainfall appears to be driving the temporal variation in graminoid availability at Guassa. The green graminoid biomass (g m^{-2}) and the ratio of green to brown graminoids in the longitudinal vegetation monitoring plots were both significantly correlated with the cumulative amount of rainfall that fell 60, 75, and 90 days prior to the date of vegetation plot harvesting, with the strongest correlations occurring when using the 90 days (i.e., 3 months) prior measure of rainfall (green graminoid biomass: $r = 0.370$, $n = 69$ months, $P = 0.002$; green graminoid to brown graminoid ratio: $r = 0.574$, $n = 69$ months, $P < 0.001$). We therefore regard cumulative rainfall 3 months prior to the end of each study month to be the best indicator of monthly food availability to the geladas at Guassa in the dietary results presented below.

Feeding ecology

Species consumed. Geladas at Guassa consumed ≥ 56 plant species from ≥ 22 families between 2007 and 2013 (Table 2). They were generally selective about the parts eaten from different species. Leaves were the most common item consumed from most species, while fruits were eaten from only a few species (and never during feeding scans).

Geladas at Guassa also consumed ≥ 20 varieties of invertebrates belonging to ≥ 12 different families or orders (Table 2). Among the invertebrates, snails, ants, and caterpillars were eaten most frequently. Geladas ate crane flies briefly, but in large quantities, each June when they appeared *en masse* shortly before the onset of the rainy season. Geladas consumed desert locusts (*Schistocerca gregaria*) in extraordinary quantities, mostly to the exclusion of graminoids and forbs, during

TABLE 2. Foods eaten by geladas and their relative frequencies of consumption at Guassa, Ethiopia (2007–2013)

Family	Species	Category	Items	Frequency
Plants				
Aizoaceae	<i>Delosperma schimperi</i>	(Succulent) Forb	F, L	V, V
Apiaceae	<i>Agrocharis melanatha</i>	Forb	L, F, R, S	O, R, S, R
	<i>Anthriscus sylvestris</i>	Forb	P	S ^a
	<i>Haplosciadium abyssinicum</i>	Forb	F, L, R	R, O, S
Asphodelaceae	<i>Kniphofia foliosa</i>	Forb	F, N, P, Z	R, V, R, V
	<i>Kniphofia insignis</i>	Forb	F, P, Q, Z	R, S ^a , R ^a , R
Asteraceae	<i>Anthemis tigrensis</i>	Forb	F	R ^a
	<i>Bidens</i> sp.	Forb	L	R
	<i>Carduus nyassanus</i>	Forb	F, L	R, V
	<i>Carduus schimperi</i>	Forb	F, S	R, R
	<i>Cotula cryptocephala</i>	Forb	F, L	V, O
	<i>Crepis rueppellii</i>	Forb	F, L	R, R
	<i>Dianthoseris schimperi</i>	Forb	X ^b	R
	<i>Euryops pinifolius</i>	Shrub	E, U	V, V
	<i>Haplocarpha schimperi</i>	Forb	L, R	S, V
	<i>Helichrysum formosissimum</i>	Shrub	X ^b , L	V, V
	<i>Helichrysum splendidum</i>	Shrub	F, U	V, V
	<i>Sonchus bipontini</i>	Forb	F, L	V, R
Caryophyllaceae	<i>Cerastium octandrum</i>	Forb	F	R
	<i>Silene burchellii</i>	Forb	S	R
Colchicaceae	<i>Merendera schimperiana</i>	Forb	L	R
Commelinaceae	<i>Commelina africana</i>	Forb	L	R
Crassulaceae	<i>Aeonium leucoblepharum</i>	(Succulent) Forb	L, Q	V, V
	<i>Crassula granvikii</i>	(Succulent) Forb	L	V
	<i>Crassula schimperi</i>	(Succulent) Forb	L	V
Cyperaceae	<i>Carex monostachya</i>	(Tall) Sedge	F, L, S	V, R, R
	<i>Carex petitiana</i>	(Tall) Sedge	S	V
	<i>Cyperus rigidifolius</i>	(Short) Sedge	L, S	S ^a , V
	<i>Eleocharis marginulata</i>	(Tall) Sedge	L ^c	S
Ericaceae	<i>Erica arborea</i>	Shrub	P, K	S, V
Fabaceae	<i>Argyrolobium ramosissimum</i>	Forb	S	S ^a
	<i>Trifolium acaule</i>	Forb	F, L	R, S
	<i>Trifolium</i> unk. sp.	Forb	F, L	R, O
Hypericaceae	<i>Hypericum revolutum</i>	Shrub	U	V
Lamiaceae	<i>Salvia nilotica</i>	Forb	F, L	V, V
Lobeliaceae	<i>Lobelia rhynchopetalum</i>	(Giant) Forb	E, L, Q	V, V, V
Malvaceae	<i>Malva verticillata</i>	Forb	L	V
Orchidaceae	<i>Habenaria vaginata</i>	Forb	T	S ^a
	<i>Holothrix squamata</i>	Forb	F, Z	R, R
Poaceae	<i>Agrostis quinqueseta</i>	(Tall) Grass	L	O
	<i>Andropogon amethystinus</i>	(Tall) Grass	S	R
	<i>Festuca macrophylla</i>	(Tall) Grass	L, S	S, S
	<i>Hordeum</i> sp.	(Domesticated) Grass	S	R
	<i>Microchloa kunthii</i>	(Short) Grass	L	S
	<i>Pennisetum humile</i>	(Short) Grass	L, S	O ^a , R
	Aquatic grass unk. sp.	(Tall) Grass	L	S
Poaceae or Cyperaceae	Corm unk. sp. #1	Grass or Sedge	C	S
	Corm unk. sp. #2	Grass or Sedge	C	S
Ranunculaceae	<i>Ranunculus</i> sp.	Forb	L	O
Rosaceae	<i>Rubus apetalus</i>	Shrub	D	S ^a
Rubiaceae	<i>Galium simense</i>	Forb	D, L	R, O
	<i>Galium spurium</i>	Forb	L	V
	<i>Oldenlandia monanthos</i>	Forb	L	R
Unknown	Aquatic algae unk. sp.	Algae	A	R
	Lichen sp.	Lichen	Y	V
Urticaceae	<i>Urtica simensis</i>	Forb	F, L, Q, R	V, R, S ^a , V
Animals				
Acrididae	Grasshopper	Invertebrate	I	R
	<i>Schistocerca gregaria</i>	Invertebrate	I	R ^d
	Locust #2	Invertebrate	I	V
Aphididae	Aphid	Invertebrate	I	V
Carabidae	Carabid beetle (green)	Invertebrate	I	V
Cicadellidae	Leafhopper	Invertebrate	I	V
Formicidae	Ant #1 (small)	Invertebrate	I	R
	Ant #2 (medium)	Invertebrate	I	R
	Ant larvae	Invertebrate	I	V
Gryllidae	Cricket	Invertebrate	I	V
Tipulidae	Crane fly	Invertebrate	I	R
Araneae ^e	Spider	Invertebrate	ES	V

TABLE 2. Continued

Family	Species	Category	Items	Frequency
Coleoptera ^e	Grub	Invertebrate	I	R
Lepidoptera ^e	Caterpillar #1 (medium)	Invertebrate	I	R
	Caterpillar #2 (small)	Invertebrate	I	R
	Butterfly	Invertebrate	I	V
	Moth	Invertebrate	I	R
Haplotaxida ^e	Earthworm	Invertebrate	I	R
Stylommatophora ^e	Snail #1(medium)	Invertebrate	I	S
	Snail #2 (large)	Invertebrate	I	R
Aves ^f	Bird	Bird	BE	R ^a
Scincidae	<i>Trachylepis megalura</i>	Reptile	M	V
Cercopithecidae	<i>Theropithecus gelada</i>	Gelada	AS, PL, PU, SE	V, V, R, R
OTHER				
None	Rock face	None	O	R
None	Soil	None	H	R

Item Key: A = Algae, C = Corm, D = Fruit, E = Buds, F = Flower, G = Grass blade, H = Soil, I = Invertebrate, K = Bark, L = Leaf, M = Meat, N = Nectar, O = Rock, P = Pith, Q = Dead leaf, R = Root, S = Seed, T = Tuber, U = Unidentified, X = Stem, Y = Lichen, Z = Stalk, AS = Amniotic sac, BE = Egg, ES = Egg sac, PL = Placenta, PU = Pus, SE = Semen

Consumption Frequency: O = often (regular part of diet year round), S = sometimes (regular part of diet seasonally or consumed at low to moderate levels throughout the year), R = rare (>5 feeding incidents per yr though not a common food item), V = very rare (<5 feeding incidents per yr)

^a Item whose contribution to the diet increased over the study (e.g., *Rubus apetalus* fruits were not eaten in 2007-08, but were substantial contributors to the diet on a seasonal basis in subsequent years; *Habenaria vaginata* tubers were categorized as 'V' in 2007-08 but their consumption increased to 'S' over the years of study; *Hordeum* sp. was first consumed in 2012).

^b Stem only eaten near base of plant.

^c Though technically a stem in *Eleocharis*, the part eaten is analogous to leaves in other graminoid taxa.

^d Only available during a 3-day period in 2009 when millions of desert locusts invaded Guassa, but eaten in huge quantities.

^e Identified only to Order.

^f Identified only to Class.

a unique 3-day invasion of Guassa and the lowlands to the east in June 2009 (detailed in Fashing et al., 2010).

We never observed geladas eating bird eggs during the first 5.5 years of study. Then, in July 2012, an adult female gelada, Rerun, appeared to "discover" bird eggs were edible and the behavior began to spread. Over the next 4 months, at least a dozen geladas (all adults) were observed peering into bird's nests and consuming eggs when they were encountered. Geladas also consumed soil and licked vertical rock faces at specific locations which they visited several times during most years.

Lastly, in November 2013, an adult male gelada, Enguerrand, was observed capturing and consuming a grasstop skink (*Trachylepis megalura*). Though skinks are frequently observed running atop tussock grasses at Guassa, Enguerrand's skink consumption was unprecedented and no further skink hunting has been observed among the geladas.

Food processing behavior. Geladas at Guassa displayed a varied repertoire of food processing behaviors. Several forbs (e.g., *Anthriscus sylvestris*, *Kniphofia foliosa*, *K. insignis*) had to be forcibly pulled from the ground, requiring considerable strength and dexterity. Geladas then peeled the outer layers of skin from the lower portion of these forbs, consuming only the pith and discarding the leaves. In the case of *K. insignis*, once the discarded leaves were reencountered weeks later and had turned brown, the geladas consumed them as well.

Several forb species consumed by geladas had physical protection from stinging hairs or spines. To avoid the stinging properties of the green leaves and stalks of *Urtica simensis*, for example, geladas nearly always waited for the leaves to turn brown before consuming them.

Because of the cold climate and rocky soil, the ground was difficult to penetrate at Guassa, yet geladas there used their powerful hands (Jolly, 1972) to dig successfully for a variety of foods, including forb roots and tubers, graminoid corms and rhizomes, and earthworms. Forb roots and graminoid rhizomes were usually cleaned with the hands before consumption and the brown peel or tunic surrounding corms was typically spit out once processed in the mouth.

Flying insects like locusts, crane flies, and butterflies, had to be chased and pounced upon. Once they had captured locusts, most geladas removed the wings and legs before consuming them. The flesh of snails was consumed, but the shells were usually spit out. Similarly, bird eggs were placed in the mouth whole, then the shells were typically spit out.

Annual diet. Graminoid parts cumulatively accounted for 56.8% of the annual diet of geladas at Guassa (Fig. 3). Tall graminoid leaves (41.9%) were the biggest components of the annual diet, though the leaves of short graminoids (8.7%), graminoid crowns/rhizomes (2.4%), tall graminoid seed heads (2.2%), and graminoid corms (1.6%) also contributed to the diet.

Forb parts cumulatively accounted for 37.8% of the annual diet (leaves: 28.6%, roots: 7.5%, pith 1.3%, flowers 0.4%, tubers <0.1%). Invertebrates comprised 2.8%, other unidentified underground items 1.9%, and unidentified above-ground items 0.7% of the annual diet.

Monthly diet. Geladas exhibited wide temporal variability in diet, with monthly percentage consumption of graminoids, forbs, and invertebrates ranging from 35 to

74% (mean = 56%), 19–61% (mean = 38%), and 0–8% (mean = 3%), respectively (Table 3). Graminoids were the leading contributors to the diet during 11 months, while forbs were the leading dietary items during the other 4 months.

During months when they fed heavily on graminoid leaves, geladas reduced their consumption of forb leaves and underground food items. Notably, monthly ($n = 15$) forb leaf consumption was significantly negatively correlated with monthly tall graminoid leaf ($r = -0.763$, $P = 0.001$) and short graminoid leaf ($r = -0.615$, $P = 0.015$) consumption. In addition, monthly ($n = 15$) underground food item consumption was significantly negatively correlated with monthly tall graminoid ($r = -0.553$, $P = 0.032$),

short graminoid ($r = -0.507$, $P = 0.054$), and invertebrate ($r = -0.792$, $P < 0.001$) consumption.

Food type selection relative to ground cover. Though graminoids were difficult to identify to species in the field, geladas appeared to consume all the abundant Poaceae (grass) and Cyperaceae (sedge) taxa at Guassa. The leaves and seed heads of tall graminoids combined comprised 44.1% of the annual diet (Fig. 3) and tall graminoids accounted for 24.4% of the ground cover at Guassa (Table 1), resulting in a selection ratio for above-ground tall graminoid parts of 1.8. Short graminoid leaves provided 8.7% of the diet and accounted for 5.5% of the ground cover, for a selection ratio of 1.6. Forb leaves, pith, and flowers together accounted for 30.3% of the diet and edible forbs (a category that excludes abundant forb taxa like *Alchemilla abyssinica* and *Thymus schimperi* that the geladas did not consume) accounted for 7.4% of the ground cover, resulting in a selection ratio for above-ground edible forb parts of 4.1.

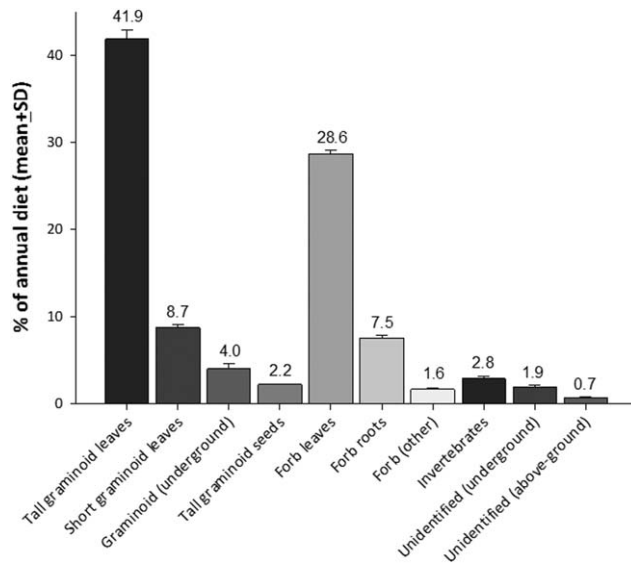


Fig. 3. Percentage accounted for by different items in the annual diet of geladas at Guassa, Ethiopia. Values represent the mean ± SD of the four possible annual diets (Feb 07 to Jan 08, Mar 07 to Feb 08, Apr 07 to Mar 08, May 07 to Apr 08) over the 15-month study period. “Graminoid (underground)” includes crowns/rhizomes (2.4%) and corms (1.6%). “Forb (other)” includes pith (1.3%), flowers (0.4%), and tubers (<0.1%).

Correlations between rainfall and diet. Rainfall patterns strongly impacted the diet of geladas at Guassa (Fig. 4). Cumulative rainfall during the three most recent months was significantly correlated with the monthly percentage consumption of tall graminoid leaves (Fig. 4A) and tall graminoid seed heads (Fig. 4C). Conversely, cumulative rainfall during the three most recent months was significantly negatively correlated with the monthly percentage consumption of underground food items (Fig. 4H). This pattern was driven mostly by forb roots (Fig. 4F) though underground graminoid part consumption also increased (albeit not significantly) during dry periods (Fig. 4D). Gelada consumption of graminoid short leaves (Fig. 4B), forb leaves (Fig. 4E), and invertebrates (Fig. 4G) were not associated with cumulative rainfall during the three most recent months.

DISCUSSION

At Guassa, a largely intact Afroalpine grassland in north-central Ethiopia, we found that geladas ate a

TABLE 3. Percent monthly plant part consumption by geladas at Guassa from February 2007–April 2008

Month	N ^a	Graminoid				Forb			Unidentified		Invertebrates
		Tall leaves	Short leaves	Tall seeds	Underground	Leaves	Roots	Other	Underground	Above-ground	
FEB 07	599	54.2	7.5	1.2	0.7	19.8	15.2	0.3	1.0	0.2	0.0
MAR 07	586	45.6	10.3	0.7	2.7	23.2	14.1	0.2	2.0	0.2	1.0
APR 07	631	45.6	22.4	0.2	0.3	19.7	3.1	0.5	0.6	0.0	7.6
MAY 07	634	36.8	7.5	1.1	1.1	42.2	2.3	2.0	0.3	0.2	6.6
JUN 07	627	32.7	5.5	0.5	1.8	45.5	4.8	1.4	0.8	0.5	6.5
JUL 07	714	56.6	16.5	0.6	0.1	17.6	1.3	2.7	0.4	0.7	3.6
AUG 07	812	56.0	14.0	3.3	0.7	18.2	0.5	2.3	0.4	1.5	3.1
SEP 07	209	54.3	3.3	2.4	2.9	25.1	2.4	1.9	2.9	1.0	3.8
OCT 07	800	41.4	10.4	13.0	5.4	19.5	1.4	1.0	5.3	0.8	1.9
NOV 07	614	30.9	4.6	4.4	10.6	31.2	11.7	0.8	5.0	0.7	0.0
DEC 07	830	27.7	2.9	0.1	5.8	45.9	13.5	1.0	1.6	1.3	0.2
JAN 08	749	36.3	1.6	0.1	7.5	29.1	19.4	3.5	1.2	0.7	0.7
FEB 08	928	38.4	5.9	0.0	6.3	29.9	15.1	1.7	1.5	0.6	0.4
MAR 08	426	43.5	13.7	0.0	8.0	17.6	11.3	1.6	2.8	0.2	1.2
APR 08	835	34.0	12.2	0.1	6.1	27.5	12.1	2.3	3.1	0.5	2.2

^a = total number of feeding records.

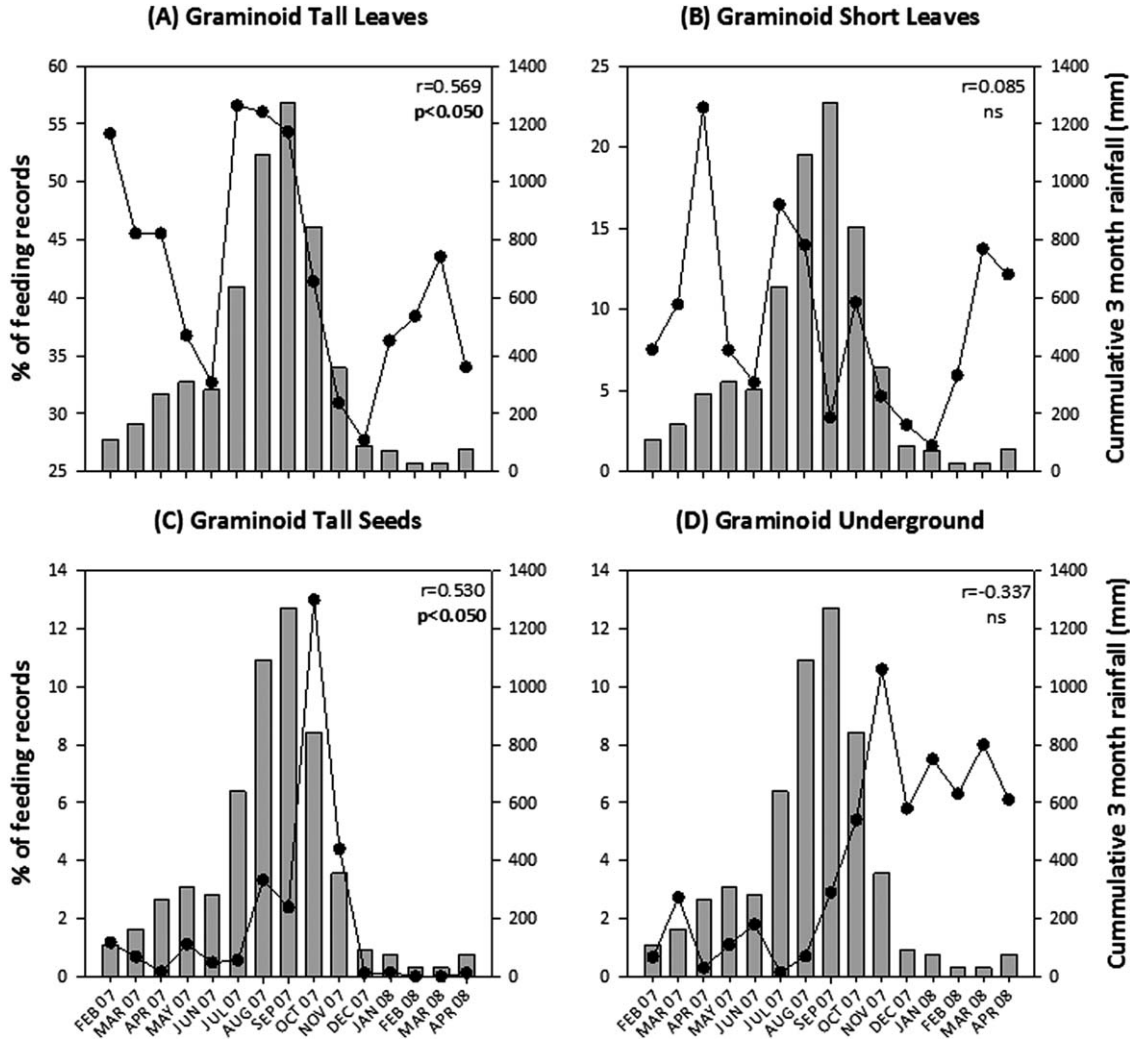


Fig. 4. Relationship between cumulative 3-month rainfall (mm) and percent of monthly diet consisting of different gelada food items—(A) graminoid tall leaves, (B) graminoid short leaves, (C) graminoid tall seeds, (D) graminoid underground, (E) forb leaves, (F) forb roots, (G) invertebrates, (H) all underground items—over a 15-month period (February 2007 to April 2008) at Guassa. “All underground items” consists of a combination of “graminoid underground,” “forb roots,” and “unidentified underground.” In each plot (A–H), cumulative rainfall is represented by the solid bars and the percent of feeding records (for different food items) is represented by the solid line.

diverse and species-rich diet of plant and animal foods. Geladas at Guassa consumed ≥ 56 plant species from ≥ 22 families and ≥ 20 varieties of invertebrates belonging to 12 different families or orders, the eggs of an unidentified bird species, and one reptile species. The annual diet of geladas consisted of 56.8% graminoid parts, 37.8% forb parts, 2.8% invertebrate prey, and 2.6% other items. In addition, geladas at Guassa exhibited wide variability in diet across months. Tall graminoid leaf and tall graminoid seed head consumption correlated positively, and underground food item consumption correlated negatively, with rainfall over time.

Comparison of gelada diets in intact and disturbed ecosystems

The impacts of anthropogenic habitat disturbance on the diets of forest primates are well-documented (Schwitzer et al., 2011). In disturbed forests, primate

diets are often less diverse or of lower quality than in intact habitats (Riley, 2007; Tesfaye et al., 2013). The impact of disturbance on the diets of primates inhabiting grassland ecosystems remains largely unstudied, however, including for geladas which are unique among primates in that they permanently inhabit the Afroalpine grassland habitats of the Ethiopian Highlands. Based solely on short-term studies at sites with histories of intensive disturbance by humans and their livestock, geladas have long been regarded as obligate graminivores (Dunbar and Dunbar, 1974; Dunbar, 1977; Iwamoto and Dunbar, 1983; Iwamoto, 1993a; Hunter, 2001).

Our research in the relatively intact ecosystem at Guassa revealed that geladas there consumed a much more varied diet than geladas at more human-dominated sites (Table 4). During the rainy season and early dry season, graminoids accounted for $>90\%$ of the diet at the disturbed gelada study sites (Bole, Sankaber, Gich) (Dunbar, 1977; Iwamoto, 1993a; Hunter, 2001),

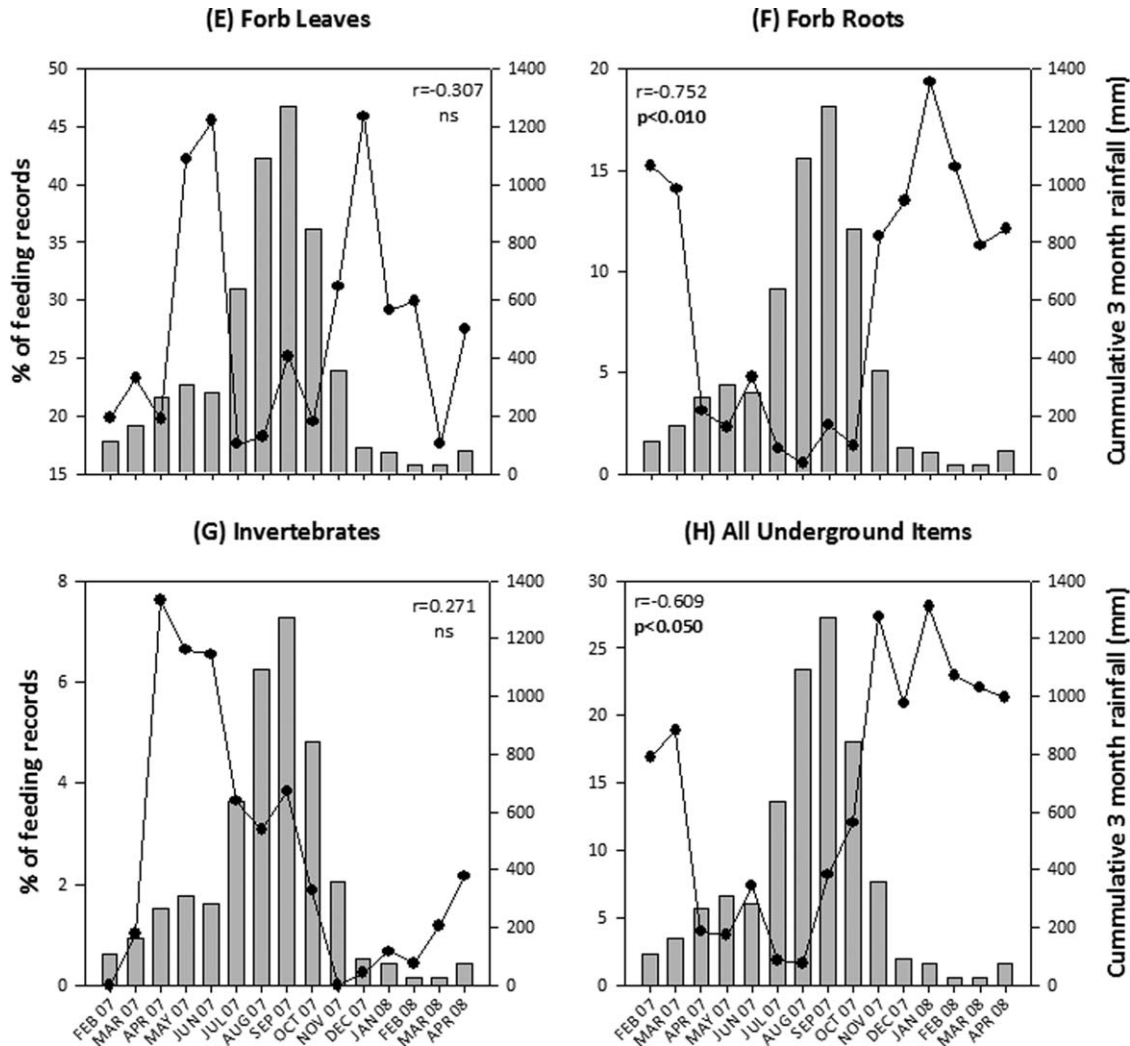


Fig. 4. Continued

whereas even in the rainiest months at Guassa graminoids never reached 75% of the diet. At Guassa, forbs comprised $>20\%$ of the diet in all 15 months of study as well as 38% of the annual diet.

Considering the relatively small (7%) contribution of edible forbs to ground cover and their even lower contribution to vegetative biomass, the geladas' level of consumption of forbs at Guassa is notable. Geladas may be seeking out forbs opportunistically because their leaves are typically more nutritious and less tough than the leaves of graminoids (Seip and Bunnell, 1985; Fashing et al., in prep.; Venkataraman et al., in review). The bulk feeding strategy imposed by the geladas' large body size and occupancy of a graminoid-dominated habitat (Dunbar, 1983; Dunbar and Bose, 1991), however, probably prevents forbs from being the primary component of gelada diets for more than short periods. Intriguingly, the diets of immature geladas, which according to the Jarman-Bell Principle require less food overall affording them the opportunity to subsist on higher-quality foods than adults (Gaulin, 1979; Pérez-Barbería et al., 2008; Müller et al., 2013), consist of a higher percentage of forbs and a lower percentage of graminoids than the diets of adult geladas at Guassa (Fashing et al., in prep.).

The relatively high consumption of forbs among geladas at Guassa is also intriguing because some forbs, including some *Trifolium* (clover) species, contain phytoestrogens which have been found to disrupt animal physiological processes and inhibit conception (Adams, 1995). Indeed, Iwamoto (1993b) has suggested that geladas at Gich may limit their consumption of forbs to avoid excess intake of phytoestrogens. While the strong selection for forbs (including *Trifolium* spp.) at Guassa seems inconsistent with this suggestion, the possibility that geladas may limit their intake of phytoestrogen-rich plant foods warrants more detailed investigation, particularly in light of recent interest in phytoestrogen impacts on wild primates (Wasserman et al., 2012, 2013).

Another notable difference in gelada diets across sites is that the graminoids consumed at the disturbed sites were short in stature (Dunbar, 1977; Iwamoto, 1993a; Hunter, 2001) while most of the graminoids eaten by geladas at Guassa fell in the tall (≥ 10 cm) graminoid category. This difference can be explained at least partly by the loss of much of the tall grass habitat at the more human-dominated sites due to chronic livestock grazing (Iwamoto, 1979; Hunter, 2001).

TABLE 4. Comparison of gelada diets across study sites in Ethiopia

Site	Elevation (M)	Months	Percent of diet											Reference
			Tall graminoid leaves	Short graminoid leaves	Graminoid underground	Graminoid seeds	Forb leaves	Forb roots	Flowers	Fruit	Invertebrates	Other	# Species	
Guassa	3450	15 ^a	41.9 ^f	8.7	4.0	2.2	28.7	7.5	0.4	0.0 ^h	2.8	3.8	≥78 ⁱ	This study Hunter (2001)
Sankaber, Simien Mts.	3300	6 ^b	0.0 ^g	55.2	11.9	1.8	5.6	20.5	0.6	3.3	0.1	1.1	---	
Sankaber, Simien Mts.	3300	5 ^c	(45.0)		24.5	23.2	1.4	1.4	1.1	1.0	0.1	2.3	---	Dunbar (1977)
Gich, Simien Mts.	3900	3 ^d	(68.8)		8.0	5.1	15.7	2.5	0.0	0.0	0.0	0.0	≥35 ^j	Iwamoto (1979, 1993a)
Bole	2300	6 ^e	(91.4)		0.5	5.0	0.3	0.0	0.3	2.0	0.0	0.5	≥14	Dunbar and Dunbar (1974)

^a study conducted over 15 contiguous months (Feb07-Apr08), though values here represent the mean of the 4 possible annual diets (Feb 07 - Jan 08, Mar 07 - Feb 08, Apr 07 - Mar 08, May 07 - Apr 08).
^b Mean diet from 3 wet season and 3 dry season months.
^c Mean diet from 3 several day to two-week periods during 5 months.
^d Mean diet from 3 non-contiguous months (1 wet season and 2 dry season months).
^e Mean diet from 82 hours of observation during 3 non-contiguous periods of 1-3 months.
^f Tall graminoids' defined as graminoid species that reach ≥10 cm at maturity.
^g Tall graminoids' defined as graminoid species that reach ≥15 cm at maturity.
^h Fruits were eaten at Guassa (see Table II) but never during feeding scans.
ⁱ Dietary species richness data collected over a 7-year period; consists at least 56 plant species, 20 invertebrate species, 1 bird species (eggs), and 1 reptile species.
^j Dietary species richness data collected over an 8-month period.

At the more disturbed sites, reliance on underground food items was also more intensive, particularly during the dry season when they accounted for more than 1/2 of the geladas' diet at Sankaber (Hunter, 2001). While consumption of underground items also exhibited significant negative correlations with rainfall at Guassa, they never exceeded 28% of the diet in any month. Because they are consumed most during dry periods when above-ground food availability is at its lowest (Hunter, 2001; this study), underground items appear to serve as "fallback foods" (Marshall and Wrangham, 2007)—and perhaps as sources of water as well (Schoeninger et al., 2001; Dominy et al., 2008)—for geladas at both Sankaber and Guassa. However, the need to exploit underground items, which require substantial physical effort for geladas to obtain, appears to be higher in the more degraded ecosystem at Sankaber.

Invertebrates were almost never eaten (≤0.1% of the diet) at the disturbed sites (Dunbar, 1977; Iwamoto, 1993a; Hunter, 2001), but accounted for 2.8% of the annual diet (and as much as 7.6% of the monthly diet) at Guassa. We suspect that the intact ecosystem at Guassa supports more invertebrates, both in terms of species richness and overall numbers (c.f. Knops et al., 1999), enabling the geladas there to feed more heavily on invertebrates (a potentially important source of protein, fats, and carbohydrates: Raubenheimer and Rothman, 2013) than at the disturbed sites. Lastly, probably also due to the challenges posed by the intact ecosystem they inhabit, the geladas at Guassa engaged in a wider variety of complex foraging behaviors (including peeling and discarding the outer layers of several plant foods, excavating and cleaning underground plant foods, and stalking, capturing, and sometimes removing the wings/appendages of flying invertebrates) than described from the more disturbed sites (Iwamoto, 1979, 1993a; Hunter, 2001). Clearly, while capable of near total graminivory when required in degraded habitats, gelada diets in intact ecosystems are far more diverse than has generally been assumed in the primatological and paleoanthropological literature (Dunbar and Bose, 1991; Jablonski, 1994; Dunbar, 1998; Cerling et al., 2013).

Implications for understanding theropith and hominin dietary evolution

Living cercopithecids, or Old World monkeys, have long been recognized as imperfect but important models for the behavior and ecology of some extinct primates, including hominins (e.g., Jolly, 1970; Elton, 2006; Swedell and Plummer, 2012; Macho, 2014). Reconstructions of the paleoenvironment suggest that during the Plio-Pleistocene, a drying climate led to the retreat of forests and the expansion of woodlands and grasslands in Africa (Sponheimer and Lee-Thorp, 2003; Reed and Rector, 2007). Hominins diversified, adopting a variety of strategies to meet their dietary needs (Sponheimer et al., 2013a). Carbon isotope analyses suggest hominins began incorporating C₄ foods (tropical grasses and sedges) in their diets ~3.5 Ma, and at least two species, *Australopithecus bahrelghazali* in Chad and *Paranthropus boisei* in East Africa, appeared to specialize on these foods (Cerling et al., 2011; Lee-Thorp, 2011; Lee-Thorp et al., 2012), with *P. boisei* exhibiting the strongest C₄ signal of any extinct hominin (Cerling et al., 2011; Sponheimer et al., 2013a). Intriguingly, *P. boisei* was contemporaneous in East Africa with a theropith that had a similarly

strong C_4 signal and similar body size (50 kg), the now extinct giant gelada (*Theropithecus oswaldi*) (Cerling et al., 2013). We therefore suggest that modern geladas—as the only extant primates whose diets consist mostly of graminoids—have the potential to offer unique insights into the dietary evolution of these extinct Plio-Pleistocene primates. We acknowledge that the gelada model has limitations, including that most geladas occupy alpine grassland habitats with different plant and animal communities than the lowland woodlands and grasslands inhabited by *P. boisei* and *T. oswaldi* during the Plio-Pleistocene. Based on phylogeny (and several shared morphological adaptations consistent with a graminivorous lifestyle), modern geladas are expected to yield the most insights into the diets of extinct theropithecids, though the apparent dietary similarities between *T. oswaldi* and *P. boisei* suggest that geladas might offer some useful insights into *P. boisei* dietary evolution as well. Indeed, as noted recently by Cerling et al. (2011, 2013), *T. oswaldi* and *P. boisei* may have competed for similar resources.

What might we be able to infer from modern geladas about the putative graminoid-eating lifestyles of extinct primates? Our results from Guassa, combined with recent isotopic analyses of the remains of several extinct primates (e.g., *T. oswaldi*, *P. boisei*), offer insights into recent debates about the diets of these primates, including their dietary diversity and consumption of succulent plants, animal matter, and underground foods.

First, our results are consistent with the notion that the extinct primate graminivores *T. oswaldi* and *P. boisei* probably did not consume many (if any) succulent plants. Although isotopic signals from succulents (plants using the crassulacean acid metabolism or CAM pathway) and C_4 plants are virtually indistinguishable (Sponheimer et al., 2013a), there are several reasons why scientists suspect isotopic signals for the extinct primates *T. oswaldi* and *P. boisei* were due to C_4 (and not CAM plant) consumption. Succulents are today relatively uncommon outside of desert or semi-desert regions (Dortch, 2011) and many CAM plants are toxic if uncooked (Peters and Vogel, 2005; Grine et al., 2012). At Guassa, CAM plants occurred in only 2% of the plots along our vegetation transects, though one species, *Aeonium leucoblepharum*, grew in large groves along the rock faces of gelada sleeping cliffs. Moreover, geladas at Guassa consumed four CAM species (including *A. leucoblepharum*), but they cumulatively accounted for only 0.03% of the species' annual diet. Because geladas do not supplement their diet with large quantities of succulents (nor do other extant primates: Sponheimer et al., 2007; Grine et al. 2012), we concur with the prevailing notion that it is unlikely that extinct theropithecids or hominins were reliant on CAM plants either.

Second, our results support the notion that animal matter likely did not make up a substantial portion of the diets of *T. oswaldi* and *P. boisei*. Although substantial meat-eating may apply to some hominins, especially in the *Homo* lineage (Bunn, 2007), at present, stable isotope techniques cannot be used to distinguish between C_4 signatures resulting from the consumption of C_4 plants and those resulting from the consumption of animals that themselves ate C_4 plants (Ungar and Sponheimer, 2011). The C_4 signals of species like *P. boisei* are, however, too high (~80%) to be the product of primarily animal consumption (Lee-Thorp, 2011). Given the consensus among stable isotope researchers that

T. oswaldi and *P. boisei* ate mostly graminoids (Cerling et al., 2011, 2013; Lee-Thorp, 2011; Sponheimer, 2013), what evidence is there that extant primate graminivores incorporate animals into their diet? At Guassa, animals are not a major component of the gelada diet, contributing only 2.8% to the diet, though their percentage contribution likely underestimates their nutritional significance as sources of protein and fats. Neither *T. oswaldi* nor *P. boisei* have dental anatomy suggesting a heavy reliance on meat either (Sponheimer et al., 2013b), though, like geladas, they may have opportunistically consumed an array of invertebrates, bird eggs or small reptiles (Sponheimer et al., 2007).

Third, our data on gelada diets at Guassa are consistent with the idea that even graminoid-eaters can consume a wide variety of food items. Wood and Schroer (2012) recently argued that because most extant primates eat varied diets, extinct primates, including *P. boisei*, should have been no different. However, neither the specific plant parts nor the species identities of dietary items can be inferred at present from stable isotope analysis, making it impossible to determine the dietary breadth of the putatively graminoid-eating extinct primates, *T. oswaldi* and *P. boisei* (Sponheimer et al., 2007; Cerling et al., 2011, 2013). The diet of geladas at Guassa reflects the complexity of the grassland they inhabit; they consumed 56 plant species (including 13 species of graminoids—7 grass, 4 sedge, 2 unknown—and 35 species of forbs) as well as 20 invertebrate species, bird eggs, and a skink. These results suggest that even graminivorous primates, often regarded as having among the most specialized of dietary strategies (Dunbar, 1976; Swedell, 2011), rely on a wide variety of food items and species.

Finally, our results from geladas at Guassa suggest that extinct graminoid-eating primates may have relied on underground foods during periods of scarcity. During the lengthy dry season when both green graminoid biomass and green graminoid to brown graminoid ratio values fell, geladas significantly increased their consumption of underground food items at Guassa. Most of these underground “fallback foods” consisted of forb roots though tubers and graminoid corms and rhizomes were also eaten. Plio-Pleistocene habitats in East Africa also experienced seasonal variation in rainfall (Reed and Rector, 2007). Although our ability to use stable isotope analysis to examine the extent to which extinct primate diets varied across the seasons—if at all—in response to changes in resource abundance is limited (Lee-Thorp et al., 2010), it seems reasonable to conjecture that *T. oswaldi*, with its similarly shaped fingers to modern geladas (Krentz, 1993; Berger and Hilton-Barber, 2006), increased exploitation of underground food items in the lean season as well.

Because of the phylogenetic and morphological differences between modern geladas and *P. boisei*, however, it is harder to speculate about how *P. boisei* diets might have changed across the seasons. Some have suggested that *P. boisei* relied mostly on sedge corms year-round (Dominy, 2012; Macho, 2014), while others envision a more varied (gelada-like) diet of above- and below-ground grass and sedge items, possibly coupled with opportunistic consumption of invertebrates, bird eggs, and small reptiles and mammals (Cerling et al., 2011; Grine et al., 2012; Wood and Schroer, 2012). Unlike *T. gelada* and *T. oswaldi* which both possessed specialized hands for digging (Jolly, 1970; Dunbar, 1983),

P. boisei may have required tools to access underground food items to have consumed them in large quantities (Sponheimer et al., 2013b).

Despite a lack of consensus on *P. boisei*'s level of reliance on underground foods, most researchers agree that, like *T. gelada* and *T. oswaldi*, *P. boisei* almost certainly ate some underground foods. The behaviors of modern geladas following the excavation of underground foods may be informative here as well—geladas at Guassa consistently cleaned the dirt from roots and spit out the dirty outer peel or tunic from corms, behaviors which may function to avoid grit and limit tooth wear. If *T. oswaldi* and *P. boisei* engaged in similar cleaning behavior of underground food items, it could help to explain why dental microwear patterns of these species are broadly similar with one another as well as with *T. gelada* (Teaford, 1993; Grine et al., 2012; Venkataraman et al. in review).

More than 40 years after Jolly's (1970) influential gelada-based model for hominin dietary evolution, geladas have in recent years become increasingly important to paleoanthropologists again. Some of the techniques used by paleoanthropologists to study the diets of extinct primates can be fruitfully used on modern geladas as well. Because of their intact ecosystem and seasonal variability in diet, the geladas at Guassa are an ideal population in which to examine how diet and dietary variability over time is reflected in the stable isotope signatures and dental microwear patterns of an extant graminivorous primate which would provide useful indices for reconstructing the diets and dietary strategies of extinct primates. Our ongoing research on gelada stable isotope signatures and dental microwear patterns has the potential to yield greater insights into the diets of the extinct primates *T. oswaldi* and *P. boisei*.

ACKNOWLEDGMENTS

The authors thank the Ethiopian Wildlife Conservation Authority, Amhara Regional government, and Mehal Meda Woreda for permission to conduct this research. Zelealem Ashenafi provided valuable advice about working at Guassa and Badiloo Muluyee, Ngadaso Subsebey, Bantilka Tessema, Shoafera Tessema, Talegeta Wolde-Hanna, and Tasso Wudimagegn provided important logistical support. We thank Tyler Barry, Ryan Burke, Barret Goodale, Sorrel Jones, Bryce Kellogg, Laura Lee, Carrie Miller, Niina Nurmi, Malcolm Ramsay, Jason Reynolds, Kathrine Stewart, and Taylor Turner for their vital assistance with the research. Our research was entirely noninvasive and satisfied the legal requirements of Ethiopia.

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