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Consumption of underground storage organs is associated with improved energetic status in a graminivorous primate

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ABSTRACT

Early hominin species likely had access to open, grassy habitats where periodic reliance on underground storage organs (USOs) is hypothesized to have played a crucial dietary role. As the only living graminivorous primate today, geladas (*Theropithecus gelada*) provide a unique perspective for understanding the energetic consequences of seasonal consumption of USOs. Geladas rely heavily on above-ground grasses throughout the year, but when grass is seasonally less available, they feed more on USOs. To assess whether USOs fit the definition of fallback foods (i.e., foods that are difficult to access, less preferred, or both), we examined how foraging effort (measured via time spent feeding and moving) and energetic status (measured via urinary C-peptide) fluctuated during seasonal dietary changes in a population of wild geladas in the Simien Mountains National Park, Ethiopia. If, indeed, USOs are fallback foods, we predicted an increase in foraging effort and a decline in energetic status during the dry season, when geladas rely more heavily on USOs. We collected behavioral and physiological data from 13 adult gelada males across a 13-month period. As expected, we found that male geladas spent more time moving during drier months. However, counter to the hypothesis that USOs are fallback foods in geladas, urinary C-peptide concentrations were significantly higher during the dry season. We suggest that USOs may represent an energy-rich food item for geladas, but it remains unclear why USOs are not consumed year-round. Future work is needed to better understand seasonal variation in the availability, nutrient content, and digestibility of USOs. However, results indicate that exploiting USOs seasonally could have been a valuable dietary strategy for the evolutionary success of early hominins.

1. Introduction

When and how the diets of human ancestors diverged from other hominoids is central to our understanding of human evolution. Current reconstructions of early hominin ecology suggest a major dietary shift that included resources from more open, seasonal habitats (craniodental morphology: Hatley and Kappelman, 1980; Bobe and Behrensmeyer, 2004; Laden and Wrangham, 2005; dental microwear: Ungar and Sponheimer, 2011; Grine et al., 2012; stable carbon isotope analysis of tooth enamel: Sillen et al., 1995; Sponheimer and Lee-Thorp, 1999; Sponheimer et al., 2013). Diets likely needed to shift with annual changes in food availability, suggesting a periodic reliance on 'fallback foods' may have played a crucial dietary role (Marshall and Wrangham, 2007). Definitions vary (reviewed in Table 2: Lambert and Rothman, 2015), but fallback foods are typically categorized as foods that are eaten when preferred foods are unavailable and are relatively poor in nutritional quality (Byrne et al., 1993; Yamagiwa and Basabose, 2009) and/or have mechanical or chemical defenses that make processing difficult (Wrangham et al., 1998; Schoeninger et al., 2001; Constantino et al., 2009; Lucas et al., 2009).

Underground storage organs (USOs) are masses of underground plant tissue (e.g., bulbs, corms, tubers, and rhizomes) that are often found in drier habitats and have been implicated as a critical food item for early hominins (Wrangham et al., 1999; Conklin-Brittain et al., 2002; Dominy, 2012). Although the subterranean location

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of USOs makes them unavailable for most mammalian taxa, they represent a large food source for species that are able to exploit them, e.g., African mole rats (*Cryptomys* spp.; Yeakel et al., 2007), bushpigs (*Potamochoerus porcus*; Breytenbach and Skinner, 1982), and common warthogs (*Potamochoerus africanus*; Field, 1970). Several nonhuman primate species, including bearded capuchins (*Sapajus libidinosus*; Truppa et al., 2019), yellow baboons (*Papio cynocephalus*; Altmann, 1998), and chimpanzees (*Pan troglodytes*; Hernandez-Aguilar et al., 2007), are also known to rely on USOs during leaner seasons. In addition, there is some evidence of USOs in the diet of early *Homo sapiens* (Melamed et al., 2016), and modern human hunter-gatherers often rely on these underground food items on a seasonal basis (Campbell, 1986; Schoeninger et al., 2001).

Wild USOs (as opposed to domesticated tubers; Schoeninger et al., 2001) appear to fit the criteria for fallback foods: they tend to be used seasonally only when preferred foods are less available (Altmann, 1998; Marshall and Wrangham, 2007), are often lower in nutritional quality (Marlowe and Berbesque, 2009), and are more difficult to access due to challenges associated with food handling (Schoeninger et al., 2001), mechanical mastication (Dominy et al., 2008), and digestion (Wrangham et al., 1999), yet the nutritional and fitness implications for such a dietary shift for early hominins are unclear (Codron et al., 2008; e.g., Copeland, 2009). Few living primate models have quantified the energetic consequences of consuming these potential fallback foods; however, seasonal reliance on USOs is linked to decreased energy yield in chacma baboons (*Papio ursinus*; Byrne et al., 1993) and reduced energetic status in the Hadza hunter-gatherers in Tanzania (i.e., lower percent body fat, Marlowe and Berbesque, 2009).

As the only living graminivorous primate today, geladas (*Theropithecus gelada*) can provide an important perspective for understanding the energetic consequences of seasonal consumption of wild USOs. Furthermore, the gelada has long served as a useful model for understanding the behavioral ecology of early hominins (Jolly, 1970). Geladas live in the highlands of Ethiopia where pronounced seasonal variation in rainfall impacts the availability of above-ground food. In the wet season, the gelada diet can comprise more than 90% graminoid leaves (i.e., grasses and sedges; Jarvey et al., 2018), whereas during the dry season, above-ground plant productivity declines and geladas exhibit a dietary switch to incorporate USOs (Iwamoto, 1979; Hunter, 2001; Fashing et al., 2014; Jarvey et al., 2018). Although prior evidence from other taxa suggests USOs are a relatively low-quality dietary option (e.g., humans: Schoeninger et al., 2001), USOs may actually provide more, not less, caloric value than grass. A previous study in geladas suggested that bulk intake and total caloric intake is equivalent or even slightly higher during the dry season than during wet season (Hunter, 2001), contradicting the concept of USOs as a low-quality fallback food.

To test whether USOs are indeed a low-quality fallback food or can offer a potential energetic advantage, we provide the first comprehensive year-round data on foraging effort and energetic status of male geladas at the Simien Mountains National Park. We focus specifically on whether the dietary switch from graminoid leaves to USOs impacts foraging effort and whether this, in turn, alters energetic status. We use males as study subjects to avoid the effects of fluctuating energetic needs of females over the reproductive cycle (Emery Thompson, 2017). In addition, recent studies have demonstrated that male reproductive competition may also be influenced by energetic or seasonal constraints (reviewed in Emery Thompson and Georgiev, 2014).

Our study had two major goals. First, we examined if seasonal changes in foraging effort were predicted by variation in green graminoid leaf availability—as indexed by rainfall. Replicating previous studies in this and other gelada populations, we predicted that geladas would spend less time feeding on above-ground food items (mostly grass) and more time feeding on USOs as green grass—their preferred food—became less available (i.e., as rainfall declined). To compensate for reduced energy while relying on fallback foods, we also predicted that geladas would spend more time feeding and more time moving to access USOs, particularly because USOs are difficult to access (i.e., underground), spatially dispersed, and a contested resource (i.e., its consumption elicits intragroup aggression over access in geladas, Jarvey et al., 2024).

Second, we examined whether periods of low green graminoid leaf availability were associated with low energetic status, as measured by urinary C-peptide (uCP) concentrations. C-peptide is produced during insulin synthesis and can be analyzed relatively easily from urine samples as a noninvasive biomarker of energetic status, with higher concentrations related to higher caloric intake (e.g., orangutans, *Pongo pygmaeus*: Emery Thompson and Knott, 2008), increased food availability (e.g., chimpanzees, *Pan troglodytes schweinfurthii*: Emery Thompson et al., 2009; colobus monkeys, *Colobus guereza*: Harris et al., 2010), increased food intake (chacma baboons, *Papio ursinus*: Fürtbauer et al., 2020), and improved habitat quality (e.g., mountain gorillas, *Gorilla beringei beringei*: Grueter et al., 2014; chimpanzees, *Pan troglodytes schweinfurthii*: Emery Thompson et al., 2009). Based on the fallback food framework, we expected that gelada energetic condition—as reflected by uCP—would be lower during the dry season when rainfall and grass availability declined and USO consumption increased. Hypotheses, predictions, and results are summarized in Table 1.

2. Materials and methods

2.1. Study site and subjects

We collected data from a population of wild geladas living in the Simien Mountains National Park, Ethiopia (13°18′N, 38°06′E, 3200–4500 m above sea level). The Simien Mountains National Park encompasses an area of Afroalpine habitat (150 km^2), including open grassland plateaus and a few remnant forests. The Simien Mountains National Park gelada population has been under near-daily observation since January 2006 as part of the Simien Mountains Gelada Research Project. Data for the current study were collected during a one-year field season from 2017 to 2018. During this time, one author collected behavioral and physiological data from 13 adult ‘leader’ males belonging to 13 polygynous reproductive units. All research followed the Association for the Study of Animal Behavior/Animal Behavior Society/American Society of Primatologists Guidelines for the use of animals in research, was approved by the Institutional Animal Care and Use Committee at Stony Brook University (IACUC #2015–2202), and followed all laws and guidelines in Ethiopia. All data were collected observationally, and observers never interacted with animals.

2.2. Weather data

Rainfall (mm) and minimum and maximum temperature (°C) were recorded on a daily basis using a rain gauge and digital thermometer centrally located in the geladas' home range (Beehner and McCann, 2008). Seasonal variation in rainfall and temperature at the site during the study period were comparable to that observed in previous years (Supplementary Online Material [SOM] Fig. S1).

Table 1
Hypotheses, predictions, and results of the present study.

Hypothesis	Prediction	Result
Foraging effort increases as grass availability decreases (proxied by reduced rainfall)	Rainfall is • Negatively associated with time spent feeding • Negatively associated with time spent moving	• Rainfall did not vary with time spent feeding • Rainfall was negatively associated with time spent moving
Energetic condition improves with rainfall, decreasing as grass availability decreases (proxied by reduced rainfall)	Rainfall is • Positively associated with urinary C-peptide	• Rainfall was negatively associated with urinary C-peptide

2.3. Behavioral data collection

To assess foraging effort, we collected behavioral data from October 2017 through August 2018, using 30-min focal animal sampling (Altmann, 1974) on a subset of 11 male geladas ($n = 488$ hours of focal data, mean = 4.7 ± 2.2 hours per male per month). To accurately capture their daily activity budget, we observed males in a predetermined, random order across the day from 08:00 to 17:00 (n = four time-blocks per day), with the goal of observing all individuals in each of the four time blocks every month. Observations started after the geladas climbed up to the plateau from their sleeping cliffs and ended when they descended to the cliffs in the evening. During focal animal sampling, we recorded continuous data on behavioral activity, noting the start and end time of five mutually exclusive activity states: feeding on above-ground items, feeding on below-ground items, moving, resting, and socializing (including grooming and all agonistic interactions). We were unable to identify individual plant species that were fed upon because grazing by livestock prevents much of the graminoid cover from reaching its full height, which is necessary for species identification. However, we provide a table with an overview of underground plant parts consumed by geladas that have been identified at other study sites (Table 2).

We defined feeding behavior as foraging (i.e., plucking, excavating, and manipulating food items) and all ingestion and mastication of food items (Jarvey et al., 2018). Thus we could not determine whether feeding differences could be attributed to differences in ingestion/mastication or to processing time (which likely differs between plucking grass blades vs. excavating underground food items; see Iwamoto, 1979). We discuss the implications in the Discussion (section 4). Geladas occasionally ranged through harvested crop fields and fed on fallen grain, but this is a fairly rare occurrence (0.3% of mean annual time spent feeding: Jarvey et al., 2018; 2.1% of 186 time blocks: present study), and we did not expect this feeding behavior to have a substantial impact on gelada energetic condition. Data were recorded during the first two months of behavioral data collection (October–November) on Palm handheld computers using software designed for the Simien Mountains Gelada Research Project. Due to a project-wide switch in data collection equipment, all subsequent behavioral data were recorded in a comparable way on iPads with Animal Observer v 1.0 (Caillaud, 2017).

2.4. Urine collection and analysis

Energetic status was assessed via analyses of uCP (Sherry and Ellison, 2007; Emery Thompson et al., 2009). The connecting peptide (C-peptide) of insulin is cleaved from proinsulin during the formation of insulin and therefore represents circulating concentrations of insulin at an equimolar ratio (Kitabchi, 1977). Insulin functions as a major metabolic hormone regulating glucose homeostasis. Importantly, unlike insulin, C-peptide is excreted intact

Table 2
Plant taxa with underground parts that have been cited as food items for geladas. Species from the original sources; families assigned based on Plants of the World Online (2023).

Family	Species	Item	Site	Source
Apiaceae	*Agrocharis melanatha*	Root	Guassa Plateau	Fashing et al. (2014)
Asparagaceae	*Chlorophytum pterocarpum*	Root	Wonchit Valley	Kifle et al. (2013)
Asparagaceae	*Chlorophytum tetraphylum*	Root	Wonchit Valley	Kifle et al. (2013)
Asteraceae	*Cotula cryptocephala*	Root	Sankaber, Simien Mountains	Dunbar (1977)
Cyperaceae	*Cyperus rigidfolius*[a]	Root	Wonchit Valley	Kifle et al. (2013)
Poaceae	*Festuca* spp.	Root	Gich, Simien Mountains	Woldegeorgis and Bekele (2015a)
Geraniaceae	*Geranium arabicum*	Root	Gich, Simien Mountains	Iwamoto (1979)
Orchidaceae	*Habenaria vaginata*	Tuber	Guassa Plateau	Fashing et al. (2014)
Asteraceae	*Haplocarpha schimperi*	Root	Gich, Simien Mountains	Woldegeorgis and Bekele (2015a)
		Root	Guassa Plateau	Fashing et al. (2014)
Apiaceae	*Haplosciadium absyssinicum*	Root	Gich, Simien Mountains	Iwamoto (1979)
		Root	Guassa Plateau	Fashing et al. (2014)
Orchidaceae	*Holothrix unifolia*	Root	Wonchit Valley	Kifle et al. (2013)
Colchicaceae	*Merendera abyssinica*	Bulb	Gich, Simien Mountains	Iwamoto (1979)
		Bulb	Wonchit Valley	Kifle et al. (2013)
		Corm	Gich, Simien Mountains	Woldegeorgis and Bekele (2015a)
		Rhizome	Sankaber, Simien Mountains	Hunter (2001)
Iridaceae	*Romulea fischeri*	Bulb	Gich, Simien Mountains	Iwamoto (1979)
		Bulb	Wonchit Valley	Kifle et al. (2013)
Lamiaceae	*Thymus schimperi*	Root	Gich, Simien Mountains	Woldegeorgis and Bekele (2015a)
	Thymus spp	Root	Sankaber, Simien Mountains	Hunter (2001)
Urticaceae	*Urtica simensis*	Root	Guassa Plateau	Fashing et al. (2014)
Cyperaceae[b]	Unidentified spp	Corm	Guassa Plateau	Fashing et al. (2014)
Poaceae[b]	Unidentified spp	Corm	Guassa Plateau	Fashing et al. (2014)

[a] Possible C4 photosynthesis (Sage, 2016), but species not covered in recent phylogenies or phylogenomics (Besnard et al., 2009; Semmouri et al., 2018).

[b] C_4 photosynthesis common in this family (Sage, 2016).

in urine (Kruszynska et al., 1987) and can therefore be used as a biomarker of energetic condition. Higher C-peptide concentrations indicate that more insulin has been metabolized, which suggests higher energetic status.

We collected urine samples for C-peptide analyses after an identified male urinated and had moved away from the spot. Urine samples were pipetted off the ground or substrate (e.g., grass, rock, soil) and into 2.0-ml microcentrifuge tubes. Samples were then placed on ice in the field and subsequently frozen at −20 °C within 6 hours of collection. Samples remained frozen during transportation in a liquid nitrogen tank to the USA. To capture baseline energetic condition (and not the response of insulin after food intake), we collected early morning urine samples (between 07:30 and 11:30; Polonsky and Rubenstein, 1984). We only collected samples that were uncontaminated with feces or urine from other animals. We collected 290 urine samples (mean = 22.3 ± 15.4 samples per male) across a full year (September 2017—September 2018). Most males were sampled twice per month (mean = 2.6 ± 1.3 samples per male per month).

We analyzed uCP using a commercial C-peptide radioimmunoassay kit (Millipore-Sigma) in the Lu Endocrinology Lab at Stony Brook University. Assay sensitivity was 0.01 ng/ml. Prior to assay, urine samples were diluted 1:4 with deionized water to bring the samples into the working range of the assay. Serially diluted pooled gelada urine ran parallel to the C-peptide standard curve (analysis of covariance test of slopes: $p > 0.05$; SOM Fig. S2). Mean recovery was 110.1 ± 5.0%, indicating accuracy of our measurements (acceptance range for recovery: 80—120%, Andreasson et al., 2015). The intra-assay coefficient of variation calculated from the measurement of low- and high-value quality controls run in each assay were 5.9% and 3.7%, respectively, whereas the inter-assay coefficient of variation values were 8.1% and 4.9%, respectively ($n = 19$ assays). Values of uCP were adjusted for differences in urine concentration by specific gravity, measured using an ATAGO® PAL-10S digital handheld refractometer. Specific gravity is the ratio of the mass of a solution compared to the mass of an equal volume of water and was used to control for variable water content of urine samples (Miller et al., 2004).

2.5. Statistical analyses

Seasonal variation in activity patterns To assess seasonal variation in behavioral activities, we calculated total time spent feeding, feeding on below-ground items specifically, and time spent moving for each study subject on a monthly basis. To avoid analyzing proportion data (Warton and Hui, 2011), we constructed three negative binomial generalized linear mixed models with raw activity budget data (i.e., time spent engaged in each activity per male per month) as the dependent variable, rainfall as the primary fixed effect, and monthly sampling time (i.e., total monthly focal hours) as an offset term. We controlled for repeated measures by including male individual identity as a random effect. Because variation in temperature is likely an important factor affecting gelada energetics due to thermoregulatory stress during colder times of the year (Beehner and McCann, 2008; Tinsley Johnson et al., 2018), we included mean minimum temperature from the previous 30 days as an additional fixed effect. Green grass availability in the study area is known to be positively correlated with rainfall from the previous 30, 60, and 90 days (Jarvey et al., 2018: 115). We chose to use cumulative rainfall from the past 90 days in all activity pattern models because preliminary analyses indicated that out of the three possible metrics, the 90-day cumulative rainfall was the most highly correlated with time spent feeding above-ground (30-day cumulative rainfall: r = 0.467; 60-day cumulative rainfall: r = 0.499; 90-day cumulative rainfall: r = 0.520).

Seasonal variation in energetic status We used a generalized linear mixed model with a log-link function (for uCP data distribution, see SOM Fig. S3) to test for the effect of rainfall on uCP concentrations. We modeled uCP concentrations as the dependent variable, cumulative rainfall from the previous 30 days as the primary fixed effect, and male identity as a random effect. We used 30-day cumulative rainfall here because we were interested in the immediate effects of dietary change on baseline uCP levels. Mean minimum temperature from the previous 30 days was included as an additional fixed effect, as well as time of sample collection, which can impact uCP concentrations (Grueter et al., 2014). In addition, we included an interaction effect between the time of sample collection and rainfall. We did this because USOs likely have a higher glycemic index than graminoid leaves, which suggests seasonal consumption of these foods results in a higher and more immediate peak in insulin production (Jenkins et al., 2002), potentially confounding seasonal interpretations of gelada energetics (Roberts, 2000).

We also used a linear mixed model to examine the direct association between feeding behavior and uCP concentrations. Here, we modeled uCP concentrations of each sample as the dependent variable and the proportion of observational time spent feeding below-ground in the 30 days prior to sample collection as the fixed effect. We used feeding time over the last 30 days as our proxy for feeding because we were interested in the effects of dietary change on baseline uCP levels; this should be reflective of overall status and not the immediate response to food intake, which would warrant a much closer time window for behavioral analyses. As with previous models, we included minimum temperature from the previous 30 days and time of sample collection as additional fixed effects, and individual identity was modeled as a random factor.

Statistical analyses were performed in R v. 3.6.1 (R Core Team, 2020). All models were run in the R package 'lme4' v. 1.1 using either the 'glmer.nb' (behavioral data) or 'glmer' (uCP data) function (Bates et al., 2015), and 'lmerTest' (Kuznetsova et al., 2015).

3. Results

3.1. Seasonal variation in below-ground feeding

Feeding represented the majority of the gelada activity budget (monthly mean = 68.4%, range = 24.9—90.0%), with above-ground food resources accounting for the largest percent of the feeding budget (individual monthly mean = 74.6%, range = 11.7—100.0%). Below-ground feeding was negatively associated with cumulative rainfall (estimate = −0.644, SE = 0.082, $p < 0.001$; SOM Table S1), varying from a monthly mean of 43.1% of the feeding budget (range = 12.0—88.3%) during the four driest months of the year (Dec—Mar) to a monthly mean of 9.3% (range = 0.0—42.0%) during the four wettest months (May—Aug; Fig. 1). These data demonstrate that geladas spent more time feeding on below-ground foods during the dry season than during the wet season, but regardless of season (and grass availability), they spent the majority of feeding time on above-ground foods.

3.2. Seasonal variation in foraging effort and energetic status

Overall time spent feeding did not significantly vary with rainfall (estimate = 0.000, SE = 0.000, $p = 0.173$; Fig. 2A) or temperature (estimate = 0.020, SE = 0.000, $p = 0.201$; SOM Table S2). However, gelada males spent significantly more time moving as cumulative rainfall decreased (estimate = −0.0001, SE = 0.000, $p = 0.030$; Fig. 2B; SOM Table S3) and minimum temperature increased (estimate = 0.056, SE = 0.023, $p = 0.017$). Contrary to predictions, gelada energetic status was negatively associated with

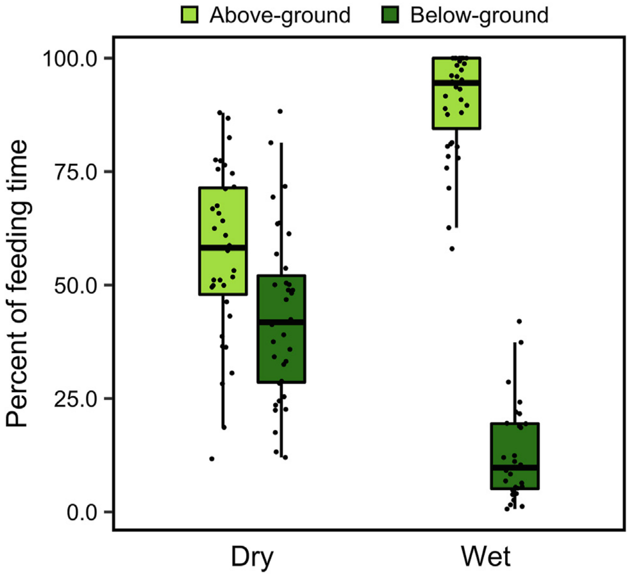

Figure 1. Rainfall and feeding behavior. Median percent of total feeding time (black lines) and time spent feeding on above-ground (light green bars) and below-ground (dark green bars) foods during the four driest months (December–March: 'Dry') and four rainiest months (May–August: 'Wet'); boxes indicate distance between the 1st and 3rd quartiles (interquartile range); whiskers are 1.5× interquartile range. Dots are individual values per male per month (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

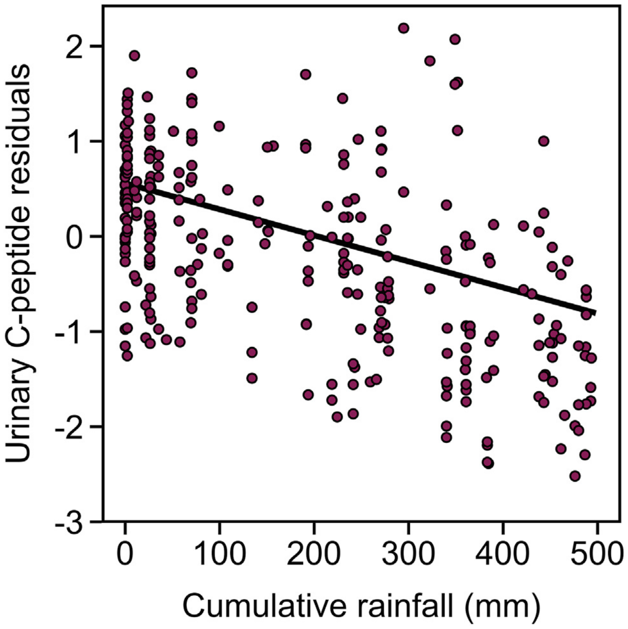

Figure 3. Urinary C-peptide concentrations (uCP). Partial residual plot of uCP concentrations indexed by specific gravity according to cumulative rainfall, controlling for minimum temperature and individual identity.

cumulative rainfall (estimate $= -0.540$, SE $= 0.053$, $p < 0.001$; Fig. 3; SOM Table S4), with uCP concentrations being highest during the driest months when grass availability was lowest. Energetic status was also negatively associated with minimum temperature (estimate $= -0.150$, SE $= 0.058$, $p = 0.010$; SOM Fig. S4), with uCP concentrations being highest during the coldest months. In addition, uCP concentrations were higher later in the morning (estimate $= 0.151$, SE $= 0.052$, $p = 0.004$), suggesting that some of the variation in insulin captures its response to food intake (rather than being purely reflective of baseline energetic condition). There was also a significant interaction effect between time and cumulative rainfall on uCP, expected due to the higher glycemic index of USOs translating into higher early morning values in the dry season (estimate $= 0.157$, SE $= 0.054$, $p = 0.003$, SOM Fig. S5). Lastly, time spent feeding on below-ground foods was positively associated with uCP concentrations (estimate $= 13.262$, SE $= 2.771$, $p < 0.001$; SOM Table S5). Thus, geladas had the highest uCP concentrations during the dry season, when they focused on below-ground rather than above-ground food items (Fig. 4).

4. Discussion and conclusions

Our results corroborate previous studies demonstrating that graminoid leaves and other above-ground plant parts make up the majority of the gelada diet and that incorporation of below-ground USOs occurs during drier months when grass availability declines (Iwamoto, 1979; Hunter, 2001; Fashing et al., 2014; Woldegeorgis and Bekele, 2015a; Jarvey et al., 2018; Yazezew et al., 2020; but see Abu et al., 2018). We also found increased time spent moving during the dry season, which supports the hypothesis that USOs are more dispersed than grass and therefore require greater search

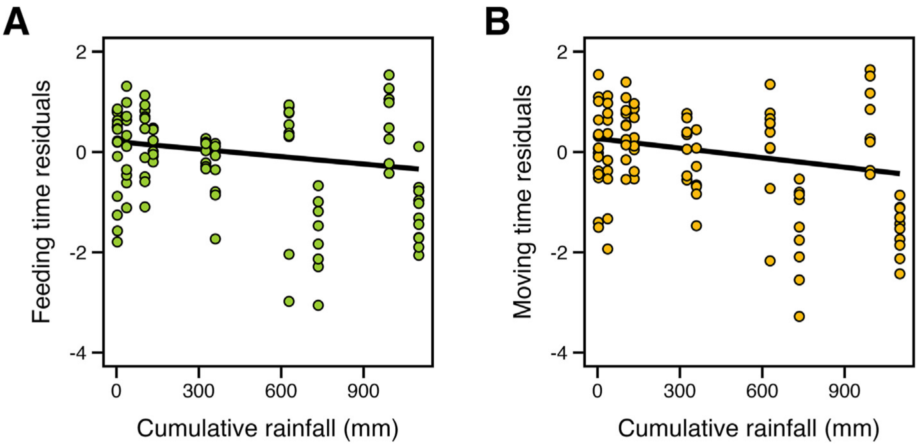

Figure 2. Rainfall and activity budgets. Partial residual plot of monthly time spent (A) feeding and (B) moving according to cumulative rainfall. Dots represent the partial residuals from the generalized linear mixed models controlling for minimum temperature, individual identity, and total monthly observation time. For visual representation only; the lines come from simple linear regressions.

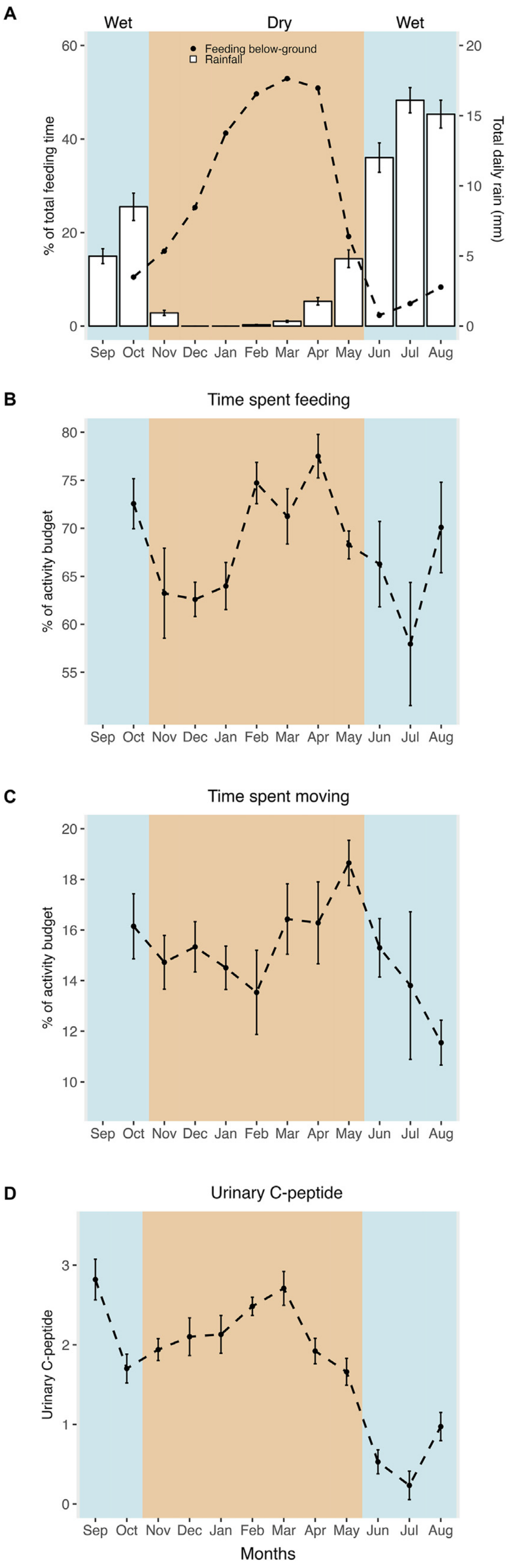

Figure 4. Seasonality of rainfall, temperature, foraging effort, and urinary C-peptide concentrations during the study period. A) Mean percentage of total feeding time spent feeding below-ground by month ± standard error (points) and total daily rainfall by month (bars); B) mean time spent feeding by month (±standard error bars); C) mean time spent moving by month (±standard error bars); D) mean logarithm of urinary C-peptide concentrations indexed by specific gravity by month (±standard error bars). Background colors indicate season: orange = dry season; blue = wet season. Abbreviations: Sep = September; Oct = October; Nov = November; Dec = December; Jan = January; Feb = February; Mar = March; Apr = April; May = May; Jun = June; Jul = July, Aug = August (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

effort. Surprisingly, however, the observed increase in foraging effort during drier months was accompanied by higher uCP concentrations, suggesting that feeding on USOs may provide a nutritional advantage compared to grass-eating, despite their relative inaccessibility. The better energetic status may have, in turn, allowed the geladas to move more during the dry season.

4.1. Seasonal variation in activity patterns

Previous studies on geladas and other nonhuman primates have suggested that USOs are spatially dispersed and difficult to access (Iwamoto, 1993; Wrangham et al., 1999; Schoeninger et al., 2001; Fashing et al., 2014). Additionally, USOs are a contested resource for this population of geladas (Jarvey et al., 2024). Based on these observations, we predicted that geladas would expend more foraging effort, as measured by time spent feeding and moving, during drier months when diets focused more on USOs. Consistent with our predictions and with previous findings, we found that gelada males spent more time moving during the dry season (Hunter, 2001; Woldegeorgis and Bekele, 2015b).

Accessing USOs requires digging through soil, excavating the item, and removing grit particles prior to consumption, yet there was no significant seasonal variation in gelada feeding time. We defined feeding behavior as time spent foraging, manipulating, and ingesting and were therefore unable to disentangle the impact of the geladas' dietary switch on these separate behavioral components. One possibility is that feeding on USOs requires additional manipulation time compared to feeding on grass, but ingesting USOs is comparably fast. Alternatively, while search time during the dry season increases, there may simply not be an accompanying increase in manipulation or ingestion time. Geladas have a suite of morphological adaptations that support their dietary specialization across seasons; complex molars and a high opposability index enables precise manual grasping of grass blades, high thumb robusticity supports excavation of underground foods, and complex, hypsodont molars aid in processing tough foods such as grass and USOs (reviewed in Fashing et al., 2014). Despite our inability to parse out the seasonal variation in processing time vs. consumption time, our results clearly suggest that additional search time (as measured by moving) is needed for geladas to fulfill their nutritional requirements during the dry season ('energy-maximizing' strategy; reviewed in Hemingway and Bynum, 2005).

4.2. Seasonal variation in energetic status

Contrary to what we expected, we found that uCP concentrations were higher during the dry season, when grass is patchily distributed and the geladas shift to USOs. One explanation may be that USOs are an energy-rich food source, albeit one that requires a lot more time to exploit. Indeed, high-ranking female geladas displace low-ranking females for access to these underground resources (Jarvey et al., 2024). This is further supported by a previous study on the Simien Mountains population that found total caloric intake for geladas to be equivalent or even slightly higher during the dry than during the wet season (Hunter, 2001). However, for a number of reasons, these latter interpretations are of limited value. Hunter's (2001) study did not identify individual monkeys, and the limited study period did not capture the full extent of seasonal variation. In addition, the study relied on Iwamoto's (1979) energy data for USOs to assess caloric intake. This method may overestimate the energy content of USOs because Iwamoto's calculations did not distinguish edible from inedible USO parts (Schoeninger et al., 2001).

Furthermore, higher uCP during the dry season may possibly result from the immediate effects of eating starchy USOs with a presumably high glycemic index vs. grass, rather than differences in energy balance that result from calories consumed. The nutritional literature clearly shows that starchy foods commonly consumed in contemporary environments (e.g., potatoes) result in a more immediate increase in insulin (Foster-Powell et al., 2002), although this effect is likely much smaller when foods are uncooked (Allen et al., 2012). While we attempted to control for this complication in our analysis, it remains possible that some differences in uCP concentrations during the dry vs. wet seasons are attributed to these effects. Clarifying the energy content of USOs eaten by geladas should therefore be of primary importance for future studies.

One surprising finding of our study was that uCP concentrations were high during periods with colder minimum daily temperatures. Daily minimum temperatures in the Simien Mountains can drop below 5 °C in the dry season, when geladas exhibit increases in glucocorticoids—a potential biomarker for physiological stress, including cold stress (Beehner and McCann, 2008). In humans, exposure to cold temperatures stimulates insulin secretion and energy expenditure, resulting in an increase in core body temperature (Sanchez-Alavez et al., 2010; Wijers et al., 2010). Therefore, higher uCP concentrations during the dry season (when it is also colder) may be driven by thermoregulatory demands (i.e., exposure to cold) as well as diet (i.e., consumption of USOs).

Despite these caveats, gelada reproductive patterns also suggest that energetic status is improved during the dry season. Both the resumption of cycling for female geladas and the peak in male—male competition for male geladas occur during the dry season (Pappano and Beehner, 2014; Tinsley-Johnson et al., 2018). Since reproduction is hypothesized to be energetically constrained (Ellison, 2001), these patterns lend further support to the idea that USOs have a higher energetic return relative to grass, albeit with a larger foraging investment. Such reliance on high-quality fallback foods has been observed in other primates, such as chimpanzees (*Pan troglodytes*, Wrangham et al., 1991) and gorillas (*Gorilla beringei*, Rothman et al., 2006), in which herbaceous piths are suggested as a decent alternate energy source when preferred fruits are scarce (see also: 'handoff strategy' in yellow baboons, *Papio cynocephalus*: Alberts et al., 2005).

4.3. Underground storage organs—a preferred food item?

The idea that USOs may be a relatively high-quality resource during periods of low grass availability is not new (Orthen, 2001; Singels et al., 2016). Geophytes (perennial herbaceous plants) use USOs as energy storage organs to evade unfavorable environmental conditions such as low rainfall. During periods of seasonal dormancy, the above-ground parts die back, while the plants remain as USOs below-ground until the next growing season (Dafni et al., 1981). Such a system is based on a large reserve of carbohydrates that are stored in the USO for future growth. For example, in one analysis of nonstructural carbohydrates in the USOs of 30 species of geophytes, 50—80% of the USO dry weight was composed of starch, fructan, and other reserve carbohydrates (Ranwala and Miller, 2008). This suggests that USOs may be an alternative and relatively decent source of energy for geladas when the region's green grass availability seasonally declines. If this is the case, however, why do geladas only eat them during the dry season?

Several explanations are possible. The most obvious one is that USOs may not be readily available during the wet season. Contrary to this hypothesis, a recent study at our study site found that the dry mass of underground foods did not differ between the wet and dry seasons (Jarvey et al., 2018). However, this study was limited in two ways. First, the study was only represented by one month in the dry season and one month in the wet season, potentially failing to capture representative averages of each season. Second, it relied on the total dry mass of USOs as a measure of quality, thus treating USOs as a homogenous group. Previous studies have demonstrated that the energy content of USOs can differ across plant species (Ranwala and Miller, 2008) and within a species across the year (Ruiters and McKenzie, 1994; Paine et al., 2019), suggesting that more fine-grained identification of underground plant species, along with determining their availability and carbohydrate content across the year, are needed to address USO preference during the dry season.

Preferences for USOs may also be influenced by seasonal variation in soil condition. Although geladas are equipped with morphological features that support efficient digging, dry-season soil becomes hard and extraction of underground foods is likely challenging. Particulate matter such as sand or soil on the surface of USOs may also play a role (e.g., Fannin et al., 2021). Like other primates (e.g., Altmann, 2009), geladas try to remove grit from the surface of USOs. If grit varies seasonally (e.g., is harder to remove during the wet season) and is a major factor in the selection of food, the observed 'preference' during the dry season would be a secondary consequence of grit removal ability. Thus, future studies should consider seasonal differences in grit removal and extraction efficiency to better understand gelada food preferences.

Another possibility is that a year-round grass diet may impose major challenges on the digestive system, potentially making USOs a comparably more nutritious and easier-to-digest food resource during the dry season. Much of the nutrients in graminoid leaves are protected by the plants' relatively indigestible cell walls (Oftedal, 1991). Unlike some folivorous primates (e.g., colobines: Kay and Davies, 1994) and ruminants (Hofmann, 1989), geladas do not have a specialized digestive system for this high-fiber diet (Mau et al., 2011). A recent study suggested that seasonal shifts in gut microbiome composition in geladas may help compensate for some of these digestive demands (Baniel et al., 2021), but the high fiber content of grasses during the dry season (Iwamoto, 1979) likely inhibits gelada digestion and reduces chewing efficiency (Venkataraman et al., 2014). Therefore, the costs of grass digestion may be greater during the dry season, contributing to the apparent preference for USOs at this time. On the other hand, studies on USO cooking (e.g., sweet potatoes) have demonstrated that starches in the raw form in USOs tend to be hard to digest (reviewed in Allen et al., 2012). Further disentangling whether USOs are the preferred food will depend on detailed comparisons of nutrient content and digestibility of both grasses and USOs across the year.

An additional explanation for USO preference during the dry season may involve macronutrient balancing. Primates select food items based on a combination of nutritional, chemical, and mechanical attributes of the food item (i.e., the 'packaging problem' sensu Altmann, 1998). Nutritionally, this involves the need to balance intake of a variety of macronutrients (i.e., carbohydrates, lipids, and protein) as well as micronutrients (Whiten et al., 1991). If geladas are seasonally prioritizing carbohydrate intake, another nutrient may be consumed in excess or in deficit (geometric framework for nutrition: Raubenheimer et al., 2009). For example, nonprotein (rather than protein) energy prioritization plays an important role in diet selection in mountain gorillas (*Gorilla beringei*, Rothman et al., 2011). Alternatively, the gelada preference for USOs during the dry season may be explained by protein needs (blue monkeys, *Cercopithecus mitis*, Takahashi et al., 2021). In orangutans, for example, a constant amount of protein is maintained in the diet despite changes in the availability of fruits (Vogel et al., 2017). In one of few studies that examines nutrient content of USOs across seasons, USOs had a higher protein-to-fiber ratio in the dry season than in the wet season (Paine et al., 2019), suggesting protein content could play a role in dietary selection. Only detailed studies of dietary quality will be able to establish what nutrients geladas may be prioritizing across the year and whether geladas experience a seasonal shortfall of available energy.

Lastly, we cannot rule out that grasses could actually serve as a fallback food for geladas. For example, Marshall and Wrangham (2007: 1219) define staple fallback foods as those that are ‘available year-round, tend to be eaten throughout the year, and seasonally can constitute up to 100% of the diet.’ In the present study, we show that grasses a) are available year-round, b) are eaten throughout the year, and c) can represent 100% of the gelada diet. Indeed, even during the dry season when green graminoid availability significantly declines, grass still represents at least half of the diet of gelada males.

4.4. Implications for early hominin evolution

The results of the present study indicate USOs may be a relatively high-quality fallback food for wild geladas during the dry season, suggesting that it may be an advantageous strategy for other primates, including early hominins. The original proposition that USO-gathering was a viable fallback strategy for hominin evolutionary success (Hatley and Kappelman, 1980; Wrangham et al., 1999; Laden and Wrangham, 2005) assumes that hominins could meet their dietary needs despite spending more energy to access difficult to process foods. The potential success of this strategy ultimately depends on the energetic value of the USOs that hominins were dependent upon, relative to their primary foods during lusher seasons.

Current reconstructions of early hominin dietary ecology support an increasingly drier, more seasonal landscape where the bulk of hominin dietary calories came from plants (Ungar and Sponheimer, 2011), likely with some meat in the diet of australopiths (McPherron et al., 2010; Balter et al., 2012). Isotopic data suggest that over time, the use of open areas increased and C_4 grasses and/or sedges were becoming essential components of the early hominin diet (Sponheimer et al., 2013). Before 4 Ma, hominins had a primarily C_3 diet (*Ardipithecus ramidus*, *Australopithecus anamensis*; Sponheimer et al., 2013), but by ca. 3.5 Ma, an early shift to the inclusion of more C_4 resources was observed (*Australopithecus bahrelghazali*; Lee-Thorp et al., 2012). This was followed by mixed C3/C4 diets in many hominins with stronger inclusion of C4 resources (Sponheimer et al., 2013) and additional shifts to more C_4 resources in *Paranthropus boisei* and the genus *Homo* in East Turkana later in time (Patterson et al., 2019; Wynn et al., 2020; Sponheimer et al., 2023).

Overall, at least six *Australopithecus* specimens have carbon isotope values that place them within the range of extinct, grass-eating geladas (reviewed in Sponheimer and Dufour, 2009; Sponheimer et al., 2013). Some values approach or even overlap those of obligate grazers, suggesting some hominins (e.g., *P. boisei*) relied mostly on sedges and grasses (Cerling et al., 2011; Sponheimer et al., 2023). In some cases, as in *Paranthropus robustus* and *Australopithecus africanus*, isotopic values changed seasonally or between years, indicating the variable use of open areas and C_4 resources (Lee-Thorp et al., 2010; Sponheimer et al., 2023). These data suggest an increasing use of resources from open areas and, hence, a dietary scenario in which USOs may have constituted one of the more calorically dense resources available. However, the nutritional properties of USOs are complex and require further study (Henry et al., 2019; Paine et al., 2019; Schoeninger et al., 2001). Furthermore, any reconstruction of the importance of USOs in hominin diets requires information from additional comparative studies, confirming that the high energy yield of USOs consumed by geladas is representative of other USO taxa.

CRediT authorship contribution statement

Rachel F. Perlman: Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jacinta C. Beehner:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Andreas Koenig:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Amy Lu:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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