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Carbon and strontium isotope ratios shed new light on the paleobiology and collapse of *Theropithecus*, a primate experiment in graminivory

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ABSTRACT

The rise and spread of tropical grasslands was a signal event in the Cenozoic, causing many ungulates to evolve adaptations to a diet of graminoid tissues, or graminivory. In parallel, a lineage of monkeys (*Theropithecus*) is distinguished among primates for its large size and commitment to graminivory, a trait expressed by species throughout the Plio-Pleistocene fossil record and *T. gelada*, the sole surviving species today. An open question concerns the mechanics of how fossil species of *Theropithecus* handled graminoid tissues. They might have exhibited preference, selecting tissues within a given tuft, or they might have practiced indiscriminate bulk-feeding in a manner similar to large grazing ungulates. To differentiate between these handling behaviors, we used time- and graminivore-calibrated carbon stable isotope values to show progressive reliance on high-throughput bulk-feeding graminivory. Variation in this behavior explains a significant amount of variation in body mass through time, and we describe these covarying traits, which peaked during the Pleistocene, as evolutionary traps. To support this characterization, we report evidence of temporal increases in strontium isotope variability among North African theropiths, a result that suggests greater lifetime travel and energetic costs in response to diminishing food resources, a probable factor in the extinction of *T. oswaldi*, the largest monkey that ever lived.

1. Introduction

Theropithecus is a genus of cercopithecid monkey that once flourished across Plio-Pleistocene Africa, southern Europe, and South Asia (Gupta and Sahani, 1981; Gibert et al., 1995) before veering abruptly toward extinction between ≈0.6 and 0.4 Ma (Leakey, 1993; Pickford, 1993). The sole surviving species is the gelada (*T. gelada*), which is today restricted to the Afroalpine grasslands of Ethiopia. Geladas subsist on graminoid tissues (57–97% of foraging time; review: Fashing et al., 2014), including leaf blades, flowers, seeds, and underground corms and bulbs—a curious diet for any primate and a potential factor in its isolated survival. Yet, a comparable level of graminivory is evident throughout the fossil record of the genus (Cerling et al., 2013), which complicates any explanation for why most species, but not all, were susceptible to extinction.

The importance of graminivory is evident in the postcranium and cranium of *Theropithecus*. For example, it has derived forelimbs to enable the fine visuomotor control necessary for selecting preferred tissues within a cluster of grasses or tuft of grass (Jolly, 1972; Jablonski et al., 2002). This food is then processed by thickly enameled, high-crowned molars with a cuspal pattern that increases in complexity during wear, thus maintaining an efficient grinding platform for reducing tough plant

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tissues (Jablonski, 1994; Venkataraman et al., 2014). Such dental anatomy bears a strong functional resemblance to the hypsodont teeth of grazing artiodactyls, but the convergence ends there. Geladas do not have the advantages of large body size or ruminant digestion (Dunbar and Bose, 1991).

The gastrointestinal tract of geladas has baboon- or human-like proportions, with some modest expansion of the caecum and large intestine (Hill, 1970; Mau et al., 2011). The absence of large fermentative chambers is a puzzle, and it has long motivated a question: *How do geladas digest so much fibrous plant matter?* Mau et al. (2009a, 2009b) explored the issue in a population of captive geladas and found ruminant-like salivary proteins, a trait that should accommodate the microbial activity (cellulolysis) necessary for accessing plant cell contents. Mau et al. (2011) affirmed this prediction when they used the gastrointestinal microbiota (GIM) of captive geladas to ferment hay; however, the performance was comparable to the GIMs of zebras and hamadryas baboons. In another study, the GIMs of captive geladas were used to ferment potato and grass, but the performance was similar to those of human vegetarians (Frost et al., 2014). Thus, the GIMs of captive geladas and zebras are either surprisingly poor at microbial cellulolysis or those of baboons and humans are surprisingly effective. At the same time, the microbiomes of wild geladas are enriched in *Fibrobacteres* (100× the abundance in modern humans), a phylum strongly associated with cellulolysis (Trosvik et al., 2018).

Against this backdrop, it is useful to examine how geladas handle graminoid tissues, and how descriptions vary in the literature. Some authors describe geladas as *selective graminivores* to emphasize the manual motor precision behind their discerning diet (Jablonski and Leakey, 2008; Souron, 2018). It is a mechanistic term that could be misunderstood as an expression of dietary narrowness; however, the manual facility of geladas enables a wide range of edible tissues. On the Guassa Plateau of Ethiopia the diet includes leaves (50.6%), underground storage organs (4.0%), and seeds (2.2%) of graminoid plants (= 56.8% of the diet), in addition to forbs (37.8%), invertebrates (2.8%), and other items (2.6%) (Fashing et al., 2014). It is analogous to the diets of medium-sized ungulate species (termed *intermediate feeders* by Hofmann, 1989), which complement graminoid tissues with those of browse and forbs (Jarman, 1974; Hofmann, 1989). Forbs are high-quality foods (Clauss et al., 2008b) that smaller geladas prefer when available (Fashing et al., 2014). Other populations of geladas devote 23–26% of their total feeding time to the storage organs and seeds of graminoid plants (Dunbar, 1977), crucial resources when preferred foods are scarce (Jarvey et al., 2018).

Some authors describe geladas as *bulk-feeders* (Dunbar, 1983; Iwamoto, 1993), with a preference for the greenest or youngest grass blades (Dunbar and Bose, 1991). Bulk-feeding in this context is analogous to grazing, where food selection is essentially indiscriminate and determined by local availability (Jarman, 1974; Hofmann, 1989). Clauss et al. (2008a) divided bulk-feeding into two approaches. First is the "efficiency approach," which relies on long digestive retention times. Rumination exemplifies this approach, but it is constrained by the need for small particle sizes and is therefore sensitive to high fiber content (Janis, 1976; Clauss et al., 2009). Second is the "intake approach," which prioritizes rapid intake and throughput, coupled with greater chewing efficiency. Equids and geladas, for instance, ingest food faster and chew more efficiently than ruminant artiodactyls do (Venkataraman et al., 2014). The intake approach is more tolerant to fiber content, allowing zebras to consume more grass stems than wildebeests inhabiting the same grassland (McNaughton, 1985).

A problem with describing geladas as either *selective graminivores* or *bulk-feeders* is that each term is overly prescriptive. Geladas alternate between these feeding strategies at hourly, daily, and seasonal temporal scales (Fashing et al., 2014), an ability that distinguishes them from most ungulates. For Jablonski and Leakey (2008), such dietary plasticity is crucial for mitigating the relatively high energetic costs of cortical processing and lactation. For our purposes, it is a trait that could explain why geladas evaded extinction. It is difficult, however, to differentiate grass-handling behaviors in the fossil record of *Theropithecus*, which is known for its "C_4 signature" (Lee-Thorp et al., 1989; Codron et al., 2005; Cerling et al., 2013; Levin et al., 2015; Robinson et al., 2017). A C_4 signature is an aphorism of stable isotope paleoecologists. It refers to high $\delta^{13}C$ values that are ultimately predicated on the C_4 photosynthetic pathway. The term is convenient but also inscrutable because it fails to distinguish between bulk-feeding grazing and selective graminivory. Accordingly, one of our goals here is to explore variation within C_4 signatures in order to differentiate the food-handling behaviors of fossil *Theropithecus*.

1.1. *Using stable carbon isotopes to discriminate food-handling behavior*

The leaves of C_4 grasses are low-quality food (Ehleringer et al., 2002), a view rooted in the high fiber content of C_4 species (Clauss et al., 2008b), itself a product of Kranz anatomy and dense bundle sheaths (Heckathorn et al., 1999). Thus, C_4 grasses tend to have low proportions of protein and carbohydrate by mass—in short, they are "nutritionally inferior" to C_3 grasses (Caswell and Reed, 1976; Barbehenn et al., 2004). The extent to which C_3 and C_4 grasses also differ in fracture toughness (resistance to crack propagation; Clauss et al., 2008b) and abrasivity (from siliceous particulate matter; Strömberg et al., 2016) is uncertain and a priority for future research. On balance, selective graminivores are expected to avoid C_4 grasses when possible (Yeakel et al., 2014).

Yet, C_4 grasses dominate East African grasslands today (exceeding 90% of the graminoid flora; Osborne et al., 2014), a fact that practically moots any aversion to them. Even so, a degree of C_4 aversion (hereafter, selectivity) is detectable using stable carbon isotopes. For example, gazelles (antilopines) are selective graminivores at the level of individual grasses (selecting the lowest-growing youngest grass leaves and seeds; Jarman, 1974) and within the grassland community, targeting those species, including dicotyledonous forbs (Bell, 1970), with low fiber contents (Hofmann, 1989). In consequence, the enamel of gazelles is depleted in ^{13}C relative to bulk-feeding grazers, such as zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) inhabiting the same C_4 grasslands (Fig. 1). If we view these C_4 signatures as a continuum—from selective graminivory on one end to bulk-feeding grazing on the other—it creates a practical frame of reference, or lens, for interpreting the paleobiology of *Theropithecus*.

The advantages of calibrating *Theropithecus* to these model graminivores are twofold: first, the teeth of gazelles (antilopines), horses (equids), and wildebeests (alcelaphines) are common and readily identified in the fossil record; and second, bulk-feeding grazers eat C_3 and C_4 grasses in proportion to their abundance in the habitat (sensu Paquette and Drapeau, 2021), functioning as mirrors of C_4 grass availability at a given time. Referencing *Theropithecus* to these coeval taxa allows us to control for the confounding effects of C_4 grass expansion through time (Patterson et al., 2019) and test classic theory on the positive relationship between bulk-feeding herbivory and larger body mass (Demment and Van Soest, 1985).

1.2. *Study design*

To detect shifts in the feeding behavior of *Theropithecus*—including *T. brumpti* and the *T. oswaldi* chronospecies (i.e., *T. oswaldi darti, T. oswaldi oswaldi,* and *T. oswaldi leakeyi* (for a detailed taxonomic review, see Jablonski and Frost, 2010))—we assembled published carbon stable isotope ($\delta^{13}C$) values spanning the Plio-Pleistocene (Table S1). A deficiency of this data set is the underrepresentation of C_3 ecosystems, including those of *T. gelada*, which, at the time of writing, was represented by a single published $\delta^{13}C$ value from the Simien Mountains, Ethiopia (Levin et al., 2008). To fill this empirical void, we focused our own sampling efforts on specimens of *Theropithecus* inhabiting C_3 ecosystems.

For example, we sampled fossil fauna from two North African

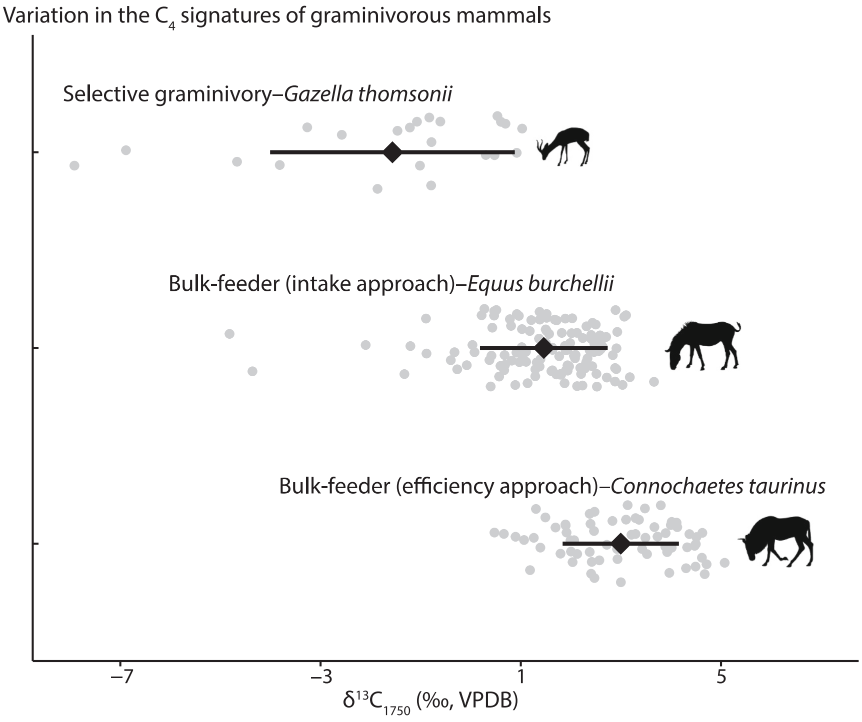

Fig. 1. Selective graminivores such as *Gazella thomsonii* are often depleted in ^{13}C relative to bulk-feeding graminivores such as *Connochaetes taurinus* and *Equus burchellii* inhabiting the same ecosystem. Data source: Cerling et al. (2015), but δ^{13}C values are adjusted to reflect pre-industrial levels of atmospheric CO_2.

sites—Ahl al Oughlam, Morocco dated to 2.5 Ma (33.57°, −7.51°; Alemseged and Geraads, 1998; Geraads, 2002) and Tighennif, Algeria dated to ca. 1.0 Ma (35.42°, 0.33°; Geraads, 2016), or slightly older (Pickford, 2020)—available in the Muséum National d'Histoire Naturelle, Paris, France. The taxonomy of *Theropithecus* at Ahl al Oughlam is debated. Some authors view these specimens as early exemplars of *T. o. oswaldi* (Pickford, 1993; Jablonski and Frost, 2010), whereas others classify them as a distinct species, *T. atlanticus* (Alemseged and Geraads, 1998). At Tighennif, our sample includes the largest member of the lineage: *T. oswaldi leakeyi* (Delson and Hoffstetter, 1993; Delson et al., 2000). Both sites existed in the Mediterranean floral region, a C_3 ecosystem (Bocherens et al., 1996).

This pair of assemblages invites some exploration of the factors that drove *T. oswaldi* toward extinction. Larger body sizes during the later Pleistocene predicts a greater commitment to bulk-feeding graminivory, a risky strategy if grasslands diminish in area and/or quality (Lee and Foley, 1993), factors that would increase daily travel costs or impel seasonal migrations among larger ungulates (McNaughton, 1985). Yet, the derived hindlimbs of *Theropithecus*—including a retroflexed femur and tibia (Guthrie, 2011)—increase travel costs over greater distances, being better equipped for seated 'shuffling' (Wrangham, 1980). Indeed, the mean daily travel distance of geladas ranges from 0.6 to 3.5 km depending on the study site, a fraction of that reported for similar-sized baboons (range: 3.6–13.2 km; Moua, 2015), suggesting that any evidence of longer-distance travel in the fossil record of *Theropithecus* is also evidence of ecological and energetic stress.

To explore whether *T. o. leakeyi* endured high travel costs relative to other species in the same assemblage, and relative to its congeneric predecessor at Ahl al Oughlam, we turned to strontium isotope ratios. Because the $^{87}Sr/^{86}Sr$ ratios of soils enter food webs through leaching by surface waters, variation exists at landscape-level spatial scales, which, in turn, is integrated into animal tissues (Bentley, 2006). Thus, when a population or species travels over greater distances it will express more variable $^{87}Sr/^{86}Sr$ ratios (Crowley and Godfrey, 2019; Hamilton et al., 2021). Fortunately, the landscapes surrounding Ahl al Oughlam and Tighennif are sufficiently variable in bioavailable strontium (by interpolation; Bataille et al., 2020), that high $^{87}Sr/^{86}Sr$ variability is expected among the wide-ranging equid species. If the $^{87}Sr/^{86}Sr$ variability of *T. o. leakeyi* approaches equid levels, it would suggest food limitation and high travel costs for a species then undergoing significant contraction in its overall geographic range (Pickford, 1993).

In addition, we sampled the tooth enamel of modern *T. gelada* from two sites, an ecologically-intact Afroalpine grassland in the Guassa Community Conservation Area, Ethiopia (10.25°–10.45°, 39.75°–39.82°; Fashing et al., 2014), and accessioned in the National Museum of Ethiopia, and from "highlands near Debre Birhan" (Ciochon, 1995), Ethiopia, and housed in the Laboratory for Human Evolutionary Studies, University of California, Berkeley (Fig. 2). Conditions at the latter site are unknown, but a population exists in the area today, where it subsists partly on C_4 grasses and sedges at elevations between 2735 and 2847 m a.s.l. (Yazezew et al., 2020). The geladas at Guassa forage at greater elevations (3200–3600 m a.s.l.), which predicts a C_3-dominated diet (Tieszen et al., 1979).

Last, we capitalized on the opportunity to compare the fracture toughness of C_3 grasses and forbs at Guassa (Venkataraman et al., 2014) with those of C_4 grasses and C_3 browse plants in Laikipia, Kenya, a C_4-dominated woodland savanna, using the same instrumentation and methods. Our intent with this modest data set is twofold. First, it enables us to approximate the mechanical properties of plant tissues chewed by *Theropithecus* during the Plio-Pleistocene and compare them to those eaten by *T. gelada* today. Second, it allows us to test the presumption that C_3-C_4 differences in fiber content correspond with differences in fracture toughness, two structural properties of plants that covary nonlinearly (Lucas et al., 2000).

To summarize, our paper reports data in the service of three formal predictions:

(P1) Greater bulk-feeding is correlated with increasing body size over evolutionary time

(P2) Later-Pleistocene *T. oswaldi leakeyi* ranged further than its congeneric predecessor

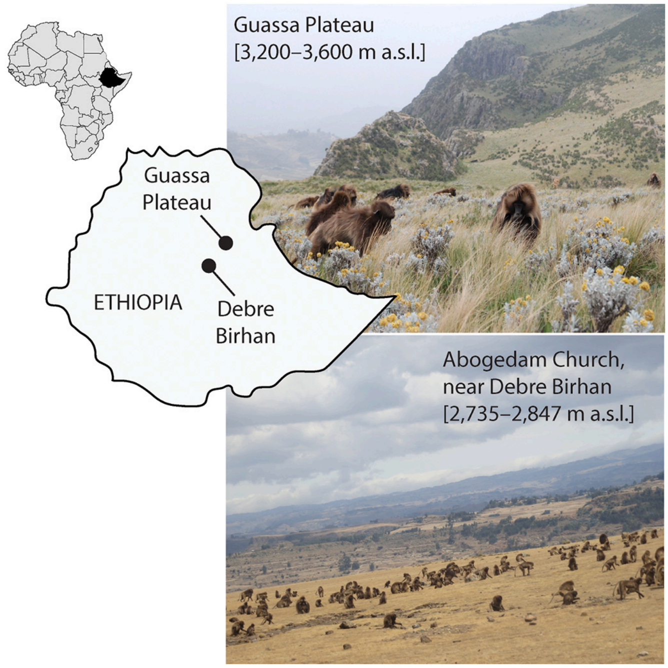

Fig. 2. Graminivorous foraging of geladas (*Theropithecus gelada*) in the Afroalpine grasslands of Ethiopia. The samples analyzed here were sourced from two isolated populations, those of the Guassa Plateau (photograph by author V.V.V.) and those living near Debre Birhan (photograph by Dereje Yazazew, reproduced with permission).

(P3) Assumed differences in the fiber content of C_3 and C_4 plant tissues correspond to differences in fracture toughness

The value of testing these predictions lies in their triangulating complementarity, the way each informs our attempts to understand the paleobiology and abrupt winnowing of fossil *Theropithecus*, as well as the adaptive history of *T. gelada*.

2. Materials and methods

2.1. Sample preparation and analysis

We sampled tooth enamel with a precision dental drill. The material (≈5 mg) was then washed in 2–3% NaOCl and soaked in 1 M acetic acid with calcium acetate buffer (pH = 5.2) to remove diagenetic carbonates. The samples were then washed, dried, and weighed (≈1.5 mg) for combustion in a Micromass Optima dual inlet mass spectrometer, Department of Earth and Planetary Sciences, University of California, Santa Cruz. Isotope ratios for C and O are presented as δ values, where

$$\delta^{13}C = 1000\left[\left(R_{sample}/R_{standard}\right) - 1\right] \tag{1}$$

$$\delta^{18}O = 1000\left[\left(R_{sample}/R_{standard}\right) - 1\right] \tag{2}$$

and R = either $^{13}C/^{12}C$ or $^{18}O/^{16}O$. Reference standards are Vienna PeeDee belemnite (VPDB) for carbon and standard mean oceanic water (SMOW) for oxygen ($\delta^{18}O$ reported in VPDB scale in Tables 1 and 2 based on the conversion in Wynn et al., 2016). Units were expressed as parts per thousand (‰). Analytical precision (±1 SD) based on the NBS 19 standard was $\delta^{13}C = 1.93 \pm 0.05‰$ ($n = 8$), very close to the known value of 1.95‰.

In some cases, excess enamel was prepared for strontium analysis. The samples were isolated to carbonate as before (0.25-mg:1-mL NaOCl and acetic acid + calcium acetate buffer; Fisher), dissolved in 2× Nitric Acid in teflon vials, boiled down at 65 °C, and reconstituted in HCl. Solutions were filtered through plastic columns containing a Sr-phillic resin (Strontium Spec Resin) with MilliQ water as the delivery agent. Strontium isotopic values were obtained using a Neptune Multiple Collector ICP-MS at the W. M. Keck Isotope Laboratory, UCSC. Isotope ratios for Sr are presented as atomic ratios ($^{87}Sr/^{86}Sr$) and are reproducible within 0.0004.

Table 1
Carbon and oxygen stable isotope values, and strontium isotope ratios, of fauna analyzed from Ahl al Oughlam, Morocco, dated to ca. 2.5 Ma. Specimens are stored provisionally in the Muséum National d'Histoire Naturelle, Paris, France; uncatalogued specimens are designated "UC". Taxonomy follows Alemseged and Geraads (1998).

Accession number	Taxon	$\delta^{13}C$	$\delta^{18}O$	^{87}Sr / ^{86}Sr
UC	Alcelaphini gen. sp.	−8.9	−3.3	
UC	Alcelaphini gen. sp.	−8.9	−4.3	
	Average (SD)	**−8.9** **(0.0)**	**−3.8** **(0.7)**	
UC	*Gazella* sp.	−11.5	−2.1	0.709044
UC	*Gazella* sp.	−12.2	−4.4	0.709082
UC	*Gazella* sp.	−11.9	−3.6	0.709089
	Average (SD)	**−11.9** **(0.4)**	**−3.4** **(1.2)**	**0.709072** **(2.4214e-5)**
UC	*Hiparion pomeli*	−12.0	−3.9	0.709333
UC	*Hiparion pomeli*	−11.5	−2.1	0.709154
AaO-3544	*Hiparion pomeli*	−11.5	−2.7	0.709956
	Average (SD)	**−11.7** **(0.3)**	**−2.9** **(0.9)**	**0.709481** **(0.000421)**
UC	*Kolpochoerus phacochoeroides*	−11.5	−2.4	
	Average	**11.5**	**2.4**	
UC	*Theropithecus atlanticus*	−11.0	−1.4	0.709010
AaO-45e	*Theropithecus atlanticus*	−13.1	−2.7	0.708902
AaO-51	*Theropithecus atlanticus*	−13.4	−2.2	0.708931
AaO-452	*Theropithecus atlanticus*	−13.4	−2.5	0.708962
AaO-662	*Theropithecus atlanticus*	−12.9	−0.3	0.709227
AaO-947	*Theropithecus atlanticus*	−11.3	−1.2	0.709126
AaO-3144	*Theropithecus atlanticus*	−12.1	−1.8	0.709068
AaO-4125	*Theropithecus atlanticus*	−11.8	−2.0	0.709116
AaO-4532	*Theropithecus atlanticus*	−12.7	−1.5	0.709137
AaO-4549	*Theropithecus atlanticus*	−12.6	−1.7	0.709087
	Average (SD)	**−12.4** **(0.8)**	**−1.7** **(0.7)**	**0.7090566** **(0.000103)**

Nota bene: pretreatment of fossil enamel with calcium acetate buffer is a standard practice (Crowley and Godfrey, 2019; Wallace et al., 2019), and given the large crystallite size of enamel there is little concern of lattice-bound transfer of calcium or strontium between buffer and sample. Others using this pretreatment step report strong agreement between enamel apatite and expected bioavailable values (Baumann and Crowley, 2015); however, we did not investigate pre- versus post-treatment effects on absolute $^{87}Sr/^{86}Sr$ ratios.

2.2. Calculations and adjustments

To detect selective graminivory, we computed the mean $\delta^{13}C$ values of *Theropithecus* and coeval antilopines and calculated the differences (Δ) between them. When making this comparison, greater similarity (lower Δ values) is interpreted as a tendency toward selective graminivory. To detect bulk-feeding, we calculated Δ between *Theropithecus*

Table 2
Carbon and oxygen stable isotope values, and strontium isotope ratios, of fauna analyzed from Tighennif, Algeria, dated to ca. 1.0 Ma. Specimens are accessioned in the Muséum National d'Histoire Naturelle, Paris, France; uncatalogued specimens are designated "UC".

Accession number	Taxon	$\delta^{13}C$	$\delta^{18}O$	^{87}Sr / ^{86}Sr	Source
UC	*Ceratotherium mauritanicum*	−11.8	−7.3		This study
84600	*Ceratotherium mauritanicum*	−11.5	−1.5		Bocherens et al., 1996
MNHN 1931-8-39	*Ceratotherium mauritanicum*	−10.0	−6.5		This study
MNHN 1954-7-13	*Ceratotherium mauritanicum*	−11.6	−7.8		This study
MNHN 1955-13-117	*Ceratotherium mauritanicum*	−11.6	−8.8		This study
MNHN 1956-12-125	*Ceratotherium mauritanicum*	−11.3	−7.9		This study
	Average (SD)	**−11.3 (0.7)**	**−6.6 (2.6)**		
UC	*Connochaetes taurinus prognu*	−9.7	−5.9		This study
UC	*Connochaetes taurinus prognu*	−10.5	−4.3		This study
UC	*Connochaetes taurinus prognu*	−10.2	−4.1		This study
UC	*Connochaetes taurinus prognu*	−11.5	−8.0		This study
84700	*Connochaetes taurinus prognu*	−8.4	−2.5		Bocherens et al., 1996
84800	*Connochaetes taurinus prognu*	−12.5	−3.0		Bocherens et al., 1996
	Average (SD)	**−10.5 (1.4)**	**−4.6 (2.0)**		
63900	*Equus mauritanicus*	−11.3	−1.7		Bocherens et al., 1996
84500	*Equus mauritanicus*	−10.9	−1.4		Bocherens et al., 1996
TER 686	*Equus mauritanicus*	−10.7	−5.8		This study
TER 690	*Equus mauritanicus*	−10.9	−4.0	0.709281	This study
TER 693	*Equus mauritanicus*	−11.1	−5.6	0.709085	This study
TER 712	*Equus mauritanicus*	−11.2	−5.8	0.709509	This study
TER 717	*Equus mauritanicus*	−11.1	−6.1		This study
TER 794	*Equus mauritanicus*	−10.6	−6.3	0.709403	This study
TER 807	*Equus mauritanicus*	−11.2	−6.0	0.709102	This study
	Average (SD)	**−11.0 (0.24)**	**−4.7 (1.9)**	**0.709276 (0.000185)**	
UC	*Gazella* sp.	−12.2	−3.1	0.709248	This study
UC	*Gazella* sp.	−12.3	−3.1	0.709181	This study
UC	*Gazella* sp.	−10.3	−2.6	0.709240	This study
UC	*Gazella* sp.	−12.7	−5.5	0.709138	This study
UC	*Gazella* sp.	−11.8	−3.0	0.709139	This study
	Average (SD)	**−11.9 (0.9)**	**−3.5 (1.2)**	**0.709189 (5.3025e-5)**	
UC	*Hippopotamus sirensis*	−12.5	−10.7	0.708946	This study
63700	*Hippopotamus sirensis*	−12.0	−5.3		Bocherens et al., 1996
63800	*Hippopotamus sirensis*	−10.6	−4.0		Bocherens et al., 1996
64000	*Hippopotamus sirensis*	−10.0	−4.0		Bocherens et al., 1996
84400	*Hippopotamus sirensis*	−9.5	−4.9		Bocherens et al., 1996
MNHN 1955-13-1036	*Hippopotamus sirensis*	−11.4	−8.3	0.709381	This study
MNHN 1955-13-774	*Hippopotamus sirensis*	−11.3	−8.3	0.709137	This study
MNHN 1955-13-762	*Hippopotamus sirensis*	−11.1	−9.1		This study
MNHN 1955-13-237	*Hippopotamus sirensis*	−10.9	−9.0	0.709077	This study
	Average (SD)	**−11.0 (0.9)**	**−7.1 (2.5)**	**0.709135 (0.000182)**	
TER 1701	*Theropithecus oswaldi leakeyi*	−5.9	−4.4	0.708735	This study
TER 1789	*Theropithecus oswaldi leakeyi*	−12.0	−1.9		This study
TER 1791	*Theropithecus oswaldi leakeyi*	−11.7	−3.7		This study
TER 1792	*Theropithecus oswaldi leakeyi*	−12.4	−2.8	0.709339	This study
TER 1793	*Theropithecus oswaldi leakeyi*	−11.7	−1.1	0.708806	This study
TER 1795	*Theropithecus oswaldi leakeyi*	−13.4	−2.2		This study
TER 1798	*Theropithecus oswaldi leakeyi*	−11.0	−3.9	0.709120	This study
TER 1799	*Theropithecus oswaldi leakeyi*	−12.2	−4.2	0.709291	This study
TER 1801	*Theropithecus oswaldi leakeyi*	−11.0	−4.3	0.708816	This study
TER 1806	*Theropithecus oswaldi leakeyi*	−11.0	−2.2	0.708737	This study
TER 1808	*Theropithecus oswaldi leakeyi*	−12.1	−1.8	0.709373	This study
	Average (SD)	**−11.3 (1.9)**	**−3.0 (1.2)**	**0.709027 (0.000282)**	

and coeval equids and alcelaphines. In these cases, greater similarity (lower Δ values) is interpreted as a greater tendency toward bulk-feeding graminivory.

Atmospheric CO_2 has become increasingly depleted in ^{13}C since the industrial revolution—the "Suess effect" (Keeling et al., 2017). To account for this effect, and to calibrate the values of modern geladas to pre-industrial conditions ($\delta^{13}C_{1750}$), we adjusted the raw $\delta^{13}C$ values from near Debre Birhan by +1.00‰ (deaths in late 1974 or 1975; Russell Ciochon, pers. comm.) and those from Guassa by +2.00‰ (deaths between 2007 and 2014, or 2011 for present purposes). These adjustments are based on atmospheric $\delta^{13}C_{CO2}$ in 1975 (−7.3‰; Francey et al., 1999) and 2011 (−8.3‰; Keeling et al., 2010).

2.3. Measures of fracture toughness

To broaden the comparison of C_3 grasses and forbs published by Venkataraman et al. (2014), we measured the fracture toughness of leaves from C_4 grasses and C_3 browse at the Mpala Research Centre, Laikipia, Kenya, a semiarid savanna-woodland at ca. 1700 m a.s.l (0.28°, 37.88°; see Young et al., 1995 for detailed habitat descriptions). Fracture toughness was measured on fresh plant material with a portable universal FLS-1 tester (Lucas et al., 2001). A scissors test was used to cut tissue and measure the energy (in joules; J) required to initiate and control crack propagation. Fracture toughness (J/m^2) was calculated by dividing the area under the force–displacement curve by the length of the cut. We focused on C_3 dicotyledonous plants (browse species; Table S2) and common C_4 grass species (*Brachiaria lachnantha*, *Cynodon* *dactylon*, *Pennisetum mezzianum, P. stramineum*) in the diets of bulk-feeding grazers, cutting each leaf midway between the base and apex and perpendicular to the direction of venation (Dominy and Lucas, 2004).

2.4. Statistical analyses

Temporal trends are based on 'space-time units' (STUs; Du et al., 2019), defined as age-bracketed geological members or sub-members for a fossil locality (Table S1). We used correlation analysis to evaluate the relationship between median STU age (Ma) and Δ values, reporting the strength of correlations as r^2 values together with bootstrapped 95% confidence intervals (re-sampled with replacement at original sample sizes over 10,000 reiterations; Banjanovic and Osborne, 2016). In the case of antilopines, we performed our analysis at the tribe (Antilopini) and genus (*Gazella*) taxonomic levels. *Gazella* is preferable as a proxy for selective graminivory (Bell, 1970), but it suffers from a paucity of unequivocal δ^{13}C values (Cerling et al., 2015). We also examined variation in the estimated body masses of *Theropithecus*—gathered from the literature or estimated per Delson et al. (2000)—as a function of Δ values. If both male and female body masses were available for a given species and STU, we used the mean value in our analysis.

To compare patterns of landscape use, we calculated standard deviations of ^{87}Sr/^{86}Sr ratios for each species at Ahl al Oughlam and Tighennif, and we used Levene's Test to compare the magnitude of seawater-normalized variance in specimens of *T. atlanticus* and *T. o. leakeyi.* To assess the strength of this latter test, we calculated the effect size per Nakagawa et al. (2015). In the case of *T. atlanticus*, we combined ^{87}Sr/^{86}Sr ratios from P4 and M2 despite developmental differences in crown formation time—in geladas, the M2 mineralizes ca. 18 months later than P4 at 3 years of age (Swindler and Beynon, 1993), and before initial male dispersal around 4.5 years of age (Beehner et al., 2009). Thus, ^{87}Sr/^{86}Sr ratios from P4 and M2 are expected to reflect natal landscapes for both sexes.

We used Welch's *t*-test to compare variation in Suess-corrected carbon isotope values of modern geladas, and ANOVA for comparisons between Ln-transformed data on the fracture toughness of leaves across four functional categories of plants edible to African ungulates. All statistical tests were performed in JMP 15 Pro and α was set at 0.05.

3. Results

Our results from Ahl al Oughlam and Tighennif are reported in Tables 1 and 2, respectively. In both assemblages, the magnitude of ^{13}C-depletion across graminivores, including *Theropithecus*, speaks to the dominance of C_3 grasses in each ecosystem, affirming expectations. In our data set representing *T. gelada*, we found a comparable range of δ^{13}C values after correcting for the Suess effect (Table 3), affirming the dominance of C_3 grasses in high-elevation grasslands. However, the δ^{13}C values of geladas from Guassa (mean $\delta^{13}C_{1750} \pm 1$ SD: -11.5 ± 0.4‰) differ from those near Debre Birhan (mean $\delta^{13}C_{1750} \pm 1$ SD: -5.9 ± 0.5‰; $t_{7.3} = -19.2$, $p < 0.0001$), indicating the regular exploitation of C_4 resources by the latter population (Yazezew et al., 2020).

3.1. Discriminating between selective graminivory and bulk-feeding graminivory

To explore temporal trends in selective graminivory, we combined our findings with published values (Table S1) and calculated the mean δ^{13}C values of *Theropithecus* and coeval antilopines before calculating the difference (Δ) between them. We found that Δ values varied erratically through time regardless of whether our analysis included all antilopines (Fig. S1) or *Gazella* ($r^2 = 0.09$, $p = 0.50$, $n = 7$ assemblages). Further, Δ values explained little variation in the estimated body mass of *Theropithecus* (Fig. S2), which suggests that antilopine- or gazelle-like δ^{13}C values are a poor measure of selective graminivory.

Table 3

Carbon and oxygen stable isotope values of *Theropithecus gelada*. Specimens from Guassa are accessioned in the National Museum of Ethiopia, whereas those from near Debre Birhan are housed in the Laboratory for Human Evolutionary Studies, University of California, Berkeley. To account for the Suess effect, raw δ^{13}C values were calibrated to pre-industrial conditions ($\delta^{13}C_{1750}$), see text for details.

Sample ID	Source	Year of death	δ^{13}C	$\delta^{13}C_{1750}$	δ^{18}O	Source
MCA 442	Guassa Plateau	~2011 2	−13.3	−11.3	−0.3	This study
MCA 444	Guassa Plateau	~2011	−13.8	−11.8	−0.4	This study
MCA 601	Guassa Plateau	~2011	−13.6	−11.6	−0.9	This study
MCA 604	Guassa Plateau	~2011	−13.9	−11.9	−1.0	This study
MCA 631	Guassa Plateau	~2011	−13.7	−11.7	0.8	This study
MCA 632	Guassa Plateau	~2011	−12.8	−10.8	0.0	This study
	Guassa Plateau Average (SD)			**−11.5 (0.4)**	**−0.3 (0.7)**	
*T. gelada*1	"near Debre Birhan"	1974–1975	−6.4	−5.4	0.5	This study
*T. gelada*2	"near Debre Birhan"	1974–1975	−6.6	−5.6	2.0	This study
*T. gelada*3	"near Debre Birhan"	1974–1975	−6.7	−5.7	1.9	This study
*T. gelada*4	"near Debre Birhan"	1974–1975	−7.8	−6.8	1.1	This study
*T. gelada*5	"near Debre Birhan"	1974–1975	−6.8	−5.8	1.6	This study
	Debre Birhan Average (SD)			**−5.9 (0.5)**	**1.4 (0.6)**	
ET05-SMN-06	Simien Mountains	2000	−10.2	−8.5		Levin et al., 2008

To explore temporal trends in bulk-feeding graminivory, we calculated the mean δ^{13}C values of *Theropithecus* and coeval alcelaphines and equids and calculated the differences (Δ) between each pair. In both cases, we found that Δ values diminished steadily through time, indicating increasing behavioral convergence between *Theropithecus* and alcelaphines (Fig. 3a) and equids (Fig. 3b). This same pattern exists within the *T. oswaldi* chronospecies (i.e., *T. o. darti–T. o. oswaldi–T. o. leakeyi*) and to some extent *T. brumpti* (Fig. S3; see supplementary discussion). In accord with our prediction (P1), variation in these Δ values explains a significant amount of variation in the estimated body mass of *Theropithecus* (Fig. 4a,b) and, most strikingly, the *T. oswaldi* chronospecies (Fig. S4). Such results demonstrate robust temporal coupling between bulk-feeding graminivory and selection for larger body size.

3.2. Strontium isotope variation

To compare landscape use, we measured ^{87}Sr/^{86}Sr ratios in the assemblages from Ahl al Oughlam (Table 1) and Tighennif (Table 2). At Ahl al Oughlam, the greatest variance was evident in a bulk-feeding grazing equid (*Hipparion*), whereas that of *T. atlanticus* was lower and similar in magnitude to a selective graminivore, *Gazella* (Fig. 5a). Tellingly, the variance within *Gazella* is similar at Tighennif, whereas that of *T. o. leakeyi* differs decidedly—indeed, it matches or exceeds that of a

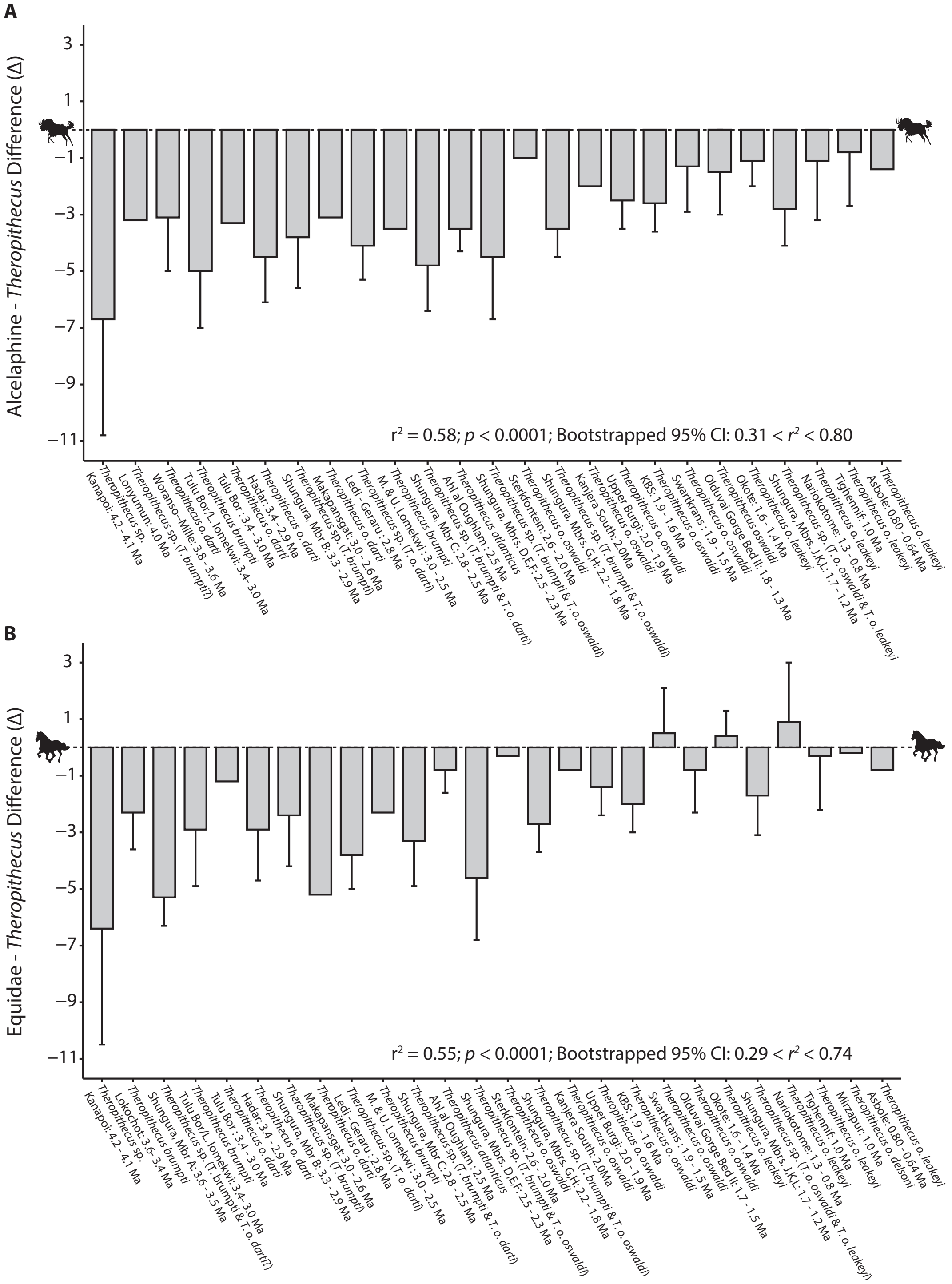

Fig. 3. Progressive increase in the bulk-feeding behavior of *Theropithecus* through the Plio-Pleistocene. Bars represent the mean difference (Δ) and 1 SD (whiskers) between the δ^{13}C values of *Theropithecus* in a given STU and coeval (A) alcelaphines and (B) equids, ordered by time interval. Data used are available in Table S1 and raw values are available supplemental dataset.

bulk-feeding grazing equid (*Equus*), indicating that both taxa ranged widely at the time of tooth mineralization (Fig. 5b). The seawater-normalized difference in the variances of *T. atlanticus* and *T. o. leakeyi* is highly significant despite a small sample size ($F_{1,16} = 29.11$, $p < 0.0001$), a result with a moderately large effect size (LnCVR = −0.47; Cohen's d equivalent = 0.61).

3.3. *Graminoid fracture toughness*

Finally, we compared variation in the fracture toughness of leaves from different forms of C_3 and C_4 plants edible to African ungulates (Table S2). Contrary to our prediction (P3), the fracture toughness of leaves from C_3 and C_4 graminoid plants did not differ, although, collectively, we found that graminoid leaves are tougher than those of forbs or woody browse (Fig. 6).

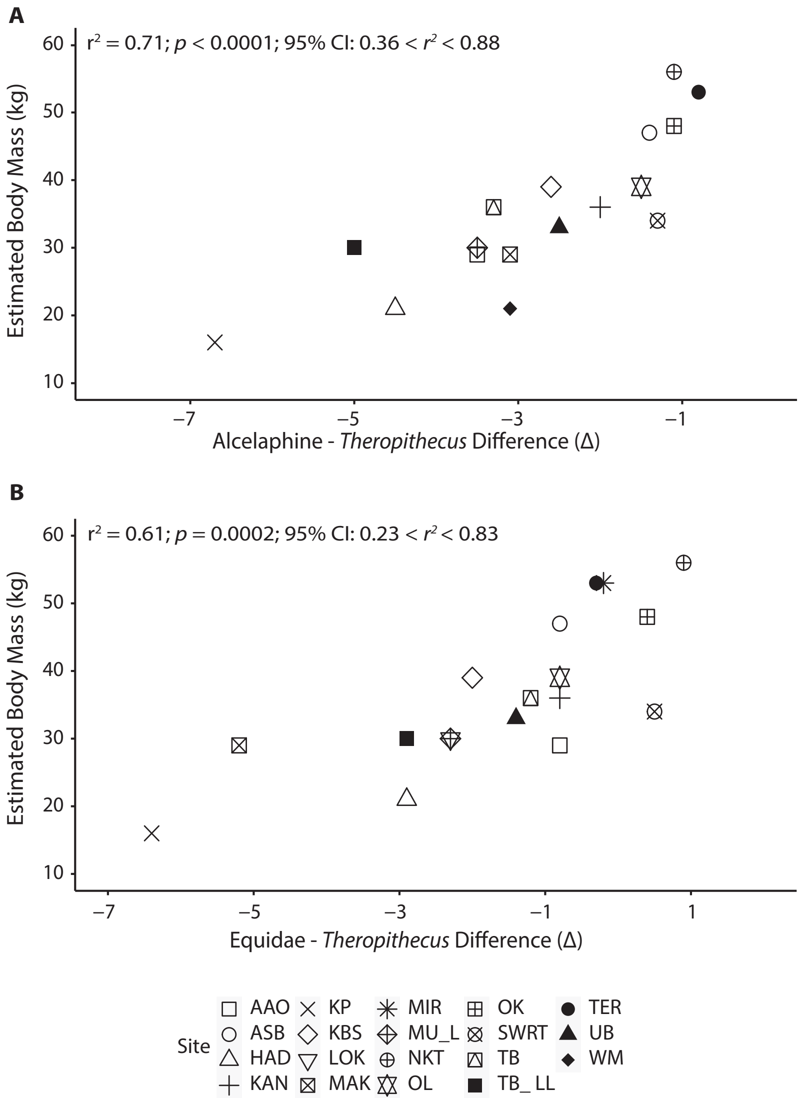

Fig. 4. Larger species of *Theropithecus* engaged in greater bulk-feeding behavior. Median body mass of *Theropithecus* in a given assemblage plotted as a function of mean difference (Δ) in δ^{13}C values between it and coeval (A) alcelaphines and (B) equids. Key to STU names: AAO: Ahl al Oughlam; ASB: Asbole; HAD: Hadar (SHM, DDM, KHM); KAN: Kanjera South; KP: Kanapoi; KBS: KBS, Koobi Fora; LOK: Lokochot, Koobi Fora; MAK: Makapansgat; MIR: Mirzapur, Indian Siwaliks; MU_L: Middle and Upper Lomekwi, Nachukui; NKT: Nariokotome, Nachukui; OL: Olduvai Gorge; OK: Okote, Koobi Fora; SWRT: Swartkrans; TB: Tulu Bor, Koobi Fora (*T. darti*); TB_LL: Tulu Bor, Koobi Fora / Lower Lomekwi, Nachukui (*T. brumpti*); TER: Tighennif; UB: Upper Burgi, Koobi Fora; WM: Woranso-Mille.

4. Discussion

Our paper reports data in the service of three predictions. First, we found that differences (Δ) in the mean δ^{13}C values of *Theropithecus* and coeval equids and alcelaphines narrowed steadily over the course of 3.5 million years. This convergence in carbon isotope values explains a significant amount of temporal variation in the body mass of *Theropithecus*, affirming our prediction (P1) of form-functional synergies between grass-handling behavior and morphology. This finding is especially pronounced for the *T. oswaldi* chronospecies. Second, we found that variation in the ^{87}Sr/^{86}Sr ratios of North African *Theropithecus* differed between 2.5 and 1.0 Ma, supporting our prediction (P2) that *T. o. leakeyi* ranged greater distances during the juvenile period of strontium bioaccumulation. Third, we found little difference in the fracture toughness of C_3 and C_4 grass blades, contrary to P3. This result suggests that *T. gelada* faces the same mechanical challenges to feeding as its Plio-Pleistocene predecessors, even if the overall quality of its diet is higher. By themselves, these disparate data do little more than fill a few empirical voids, but together they shine new light on the paleobiology of *Theropithecus*.

4.1. Distinguishing between bulk-feeding and selective graminivory

Our findings are significant for cutting through the fog of raw δ^{13}C values, a blunt instrument that cannot explain variation in body mass (Fig. S5) because the photosynthetic pathways of graminoid plants vary in space and time. Our results also refine the typology of ‘graminivore,’ as we show that grass-handling behavior changed steadily, and further, that a greater reliance on bulk-feeding graminivory explains selection for the increasingly large size of *T. oswaldi*, which topped out at 128 kg in *T. o. leakeyi* (Delson et al., 2000). Energetic explanations for this co-varying relationship are multifaceted, including the benefits of lower relative metabolic needs (Jarman, 1974), longer gut passage times (Demment and Van Soest, 1985), and greater fasting endurance (an extension of Cope’s Rule; Bhat et al., 2020), all of which are familiar arguments for ungulates. In the case of *Theropithecus*, however, the absence of gastrointestinal fermentative chambers sets a higher floor and lower (grass) ceiling for occupying a graminivorous niche—in other words, Pleistocene members of *Theropithecus* faced far narrower digestive constraints than grazing ungulates did.

Seasonal migration is unknown for any primate, and it is especially improbable for *Theropithecus* (Jablonski and Leakey, 2008), so bulk-feeding graminivory is tenable only when high-quality grass is hyper-abundant. If this resource dwindles, the benefits of large body size can become an evolutionary trap (sensu Schlaepfer et al., 2002). Our strontium isotope results hint at such a trap, with the elevated ^{87}Sr/^{86}Sr variability of *T. o. leakeyi* pointing to greater, equid-like travel costs relative to baseline—i.e., their predecessors at Ahl al Oughlam, which

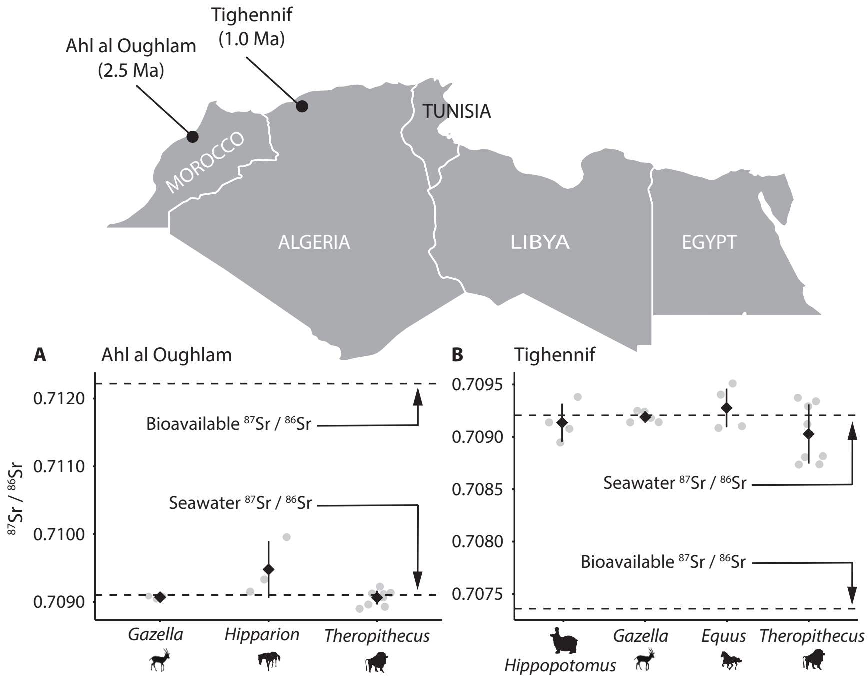

Fig. 5. Strontium isotope variability in two North African fossil assemblages (A) Ahl al Oughlam, Morocco dated to 2.5 Ma and (B) Tighennif, Algeria dated to 1.0 Ma. See Tables 1 and 2 for species taxonomy. Dashed lines represent the measured $^{87}Sr/^{86}Sr$ ratio of seawater at each time interval (Hess et al., 1986) and the interpolated bioavailable $^{87}Sr/^{86}Sr$ ratio for each location (Bataille et al., 2020). The “sea spray effect” is evident for both assemblages, which refers to the influence of sea spray and/or marine-derived precipitation on terrestrial bioavailable strontium pools up to 160 km inland (Wallace et al., 2019). Diamonds are means, whiskers are 1 SD.

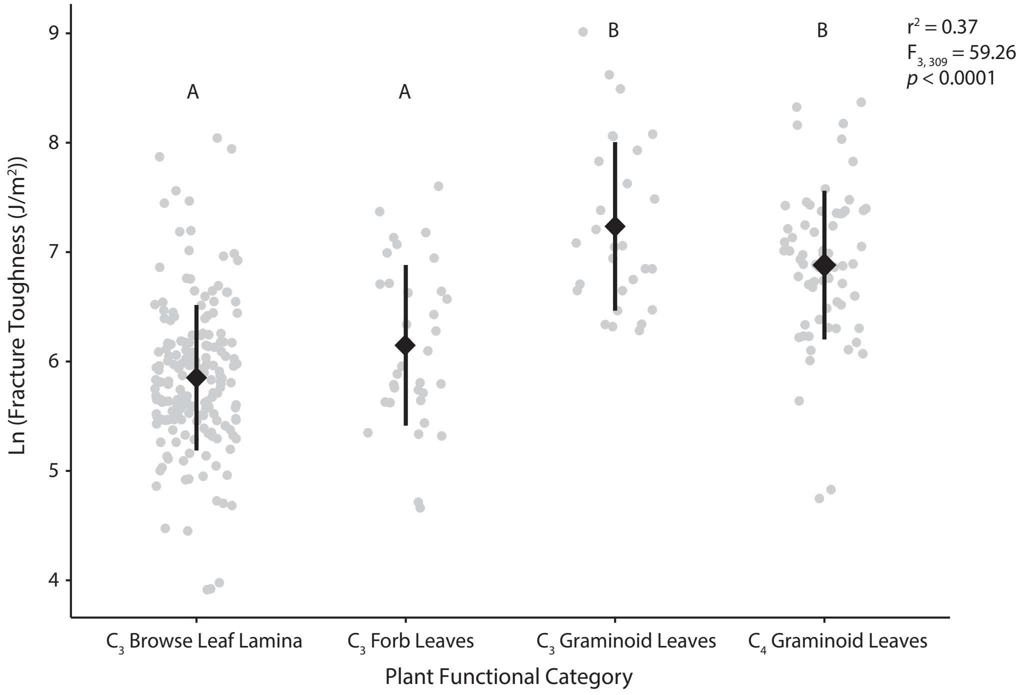

Fig. 6. Leaf fracture toughness of individual plants varied as a function of plant growth form but did not significantly differ between C_3 and C_4 grasses. Diamonds are means; whiskers are 1 SD. Differential lettering represents a statistical difference based on Tukey HSD post-hoc tests. Raw individual values are available as a supplemental data set, whereas plant species means are available in Table S1.

some authors view as the same species (for a parallel interpretation from Pleistocene Australia, see Price et al., 2017). Of course, our preferred interpretation assumes that the $^{87}Sr/^{86}Sr$ ratios of *T. o. leakeyi* are exceptionally variable instead of the alternative (that those of Ahl al Oughlam are exceptionally invariant), which is a weakness of comparing only two fossil assemblages.

Another explanation for our findings concerns sex differences in dispersal behavior. It is plausible that four outlier values of *T. o. leakeyi* are those of males that emigrated from natal groups farther from the coast. But this argument is weakened by the corollary premise of sex-biased sampling—an overrepresentation of females, the philopatric sex of cercopithecid monkeys—in our sample from Ahl al Oughlam. Such bias is unlikely given that the probability of sampling 10 females in an assemblage with a 1:2 female to male sex ratio (Alemseged and Geraads, 1998) is vanishingly small (0.0017%). Assuming a comparable proportion of males in both collections of tooth fragments is parsimonious, and it argues for both sexes of *T. o. leakeyi* enduring greater travel costs.

Our findings invite discussion on the survival and isolation of *T. gelada* in the highlands of Ethiopia. Behavioral observations of geladas describe selective graminivory as a prevailing foraging strategy (Fashing et al., 2014; Jarvey et al., 2018; Souron, 2018), a sharp reversal to the long-term trend reported here but corroborating those who argue that the size and dietary behavior of *T. gelada* are reflective of stem character traits (Jablonski, 1993). Indeed, we found that the $\delta^{13}C_{1750}$ values of some geladas (those near Debre Birhan) resemble those of the earliest members of the genus at Kanapoi, Kenya, ca. 4.2 Ma (Frost et al., 2020; Manthi et al., 2020). Still, it is uncertain whether the primitive traits of geladas were retained in a 'refuge' habitat (Tappen, 1960) or secondarily evolved after colonizing a resource-limited 'ecological island' (Dunbar, 1998). In the latter case, our results would suggest that colonizing individuals experienced little change to the toughness of their diet even if the overall quality improved due to the (presumed) lower fiber content of C_3 graminoid species (Fig. 6). Such questions are priorities for future research.

4.2. *Scenario for the rise and collapse of Theropithecus*

In the footsteps of Lee and Foley (1993) and in the spirit of Greene (2017), it is useful to fold our farrago of findings into a scenario that accounts for the rise and collapse of the genus. It begins by calling attention to 'grazing lawns', a distinct type of short-statured grassland in Africa that is associated with intense grazing (McNaughton, 1984). Grazing ungulates are attracted to these lawns because each tuft of grass has a low proportion of stem tissue, which encourages repeat grazing and suppresses tall-grass growth forms that would otherwise outcompete lawn species for light (Hempson et al., 2015). As water concentrates ungulates, grazing lawns tend to form around lake and river margins, where they provide an exceptionally nutritious and stable food resource for papionin primates, including geladas (Dunbar, 1993; Eriksen, 2017).

In light of our carbon isotope results, we envision the origins of *Theropithecus* in a waterside habitat and premised on a diet of forbs and graminoid tissues, a form of selective graminivory similar to that of geladas today (Souron, 2018). By two million years ago, the *T. oswaldi* lineage shifted to obligate bulk-feeding graminivory, a behavior that only increased in magnitude through time. It is probably associated with grazing lawns for two reasons: first, allometric increases in foraging time, coupled with daylight constraints, would have imposed limits on larger-bodied species, forcing them to forage almost exclusively on the highest-quality, highest-density graminoid tissues available (Fig. 7); and second, the fossil record points to strong associations between *T. oswaldi* and paleolake margins and river courses (Geraads et al., 1986; Leakey, 1993; Reed, 2008; Quinn, 2015; Curran and Haile-Selassie, 2016; Bobe et al., 2020). We agree with Dunbar (1993) that lake- or river-mediated grazing lawns are essentially the only habitat that could support a monkey engaged in high-throughput, bulk-feeding graminivory.

The problems of being fettered to this niche are fourfold. First, the bulk-feeding graminivory of the largest species *T. o. leakeyi* would represent an excessive proportion of its daily activity budget—exceeding 95% in the most extreme cases (Fig. 7). Second, perpetual mastication would come at the expense of essential social behaviors, such as allogrooming (Iwamoto and Dunbar, 1983; Dunbar, 1992). Third, reduced grooming is expected to destabilize group cohesion (Dunbar, 1993) and increase predation risk (Lin et al., 2020), including at the hands of early *Homo* (Shipman et al., 1981). Last, classic life history theory predicts a tension between development and reproduction, with bulk-feeding favoring slower growth rates, larger bodies, and delayed reproduction (Lu et al., 2016), whereas a greater risk of predation is expected to favor earlier reproductive maturity and smaller adult body sizes. These conflicting pressures are predicted to result in demographic fragility and greater susceptibility to extinction (Lee and Foley, 1993).

Collapse was perhaps inevitable as lake basin hydrology became increasingly variable (Potts, 1998) in response to greater climatic variability between 1.2 and 0.8 Ma (deMenocal, 2004). Rapid fluctuations in lake hydrology would have affected the total area and productivity of grazing lawns (Hempson et al., 2015), forcing *T. oswaldi* to travel greater distances over the landscape—but not seasonal migration (Jablonski and Leakey, 2008)—in search of food, further exacerbating constraints on an activity budget with little margin for non-feeding behaviors (Fig. 7). Such a dire scenario of increasing food and travel stress predicts greater strontium isotope variability among the largest, end-Pleistocene members of the genus, which is precisely what we report here.

5. Conclusions

We conclude that the evolution of *Theropithecus* during the Plio-Pleistocene (4.2–0.7 Ma) is defined by a progressive reliance on high-throughput bulk-feeding graminivory. We found that variation in bulk-feeding behavior explains a significant amount of variation in body

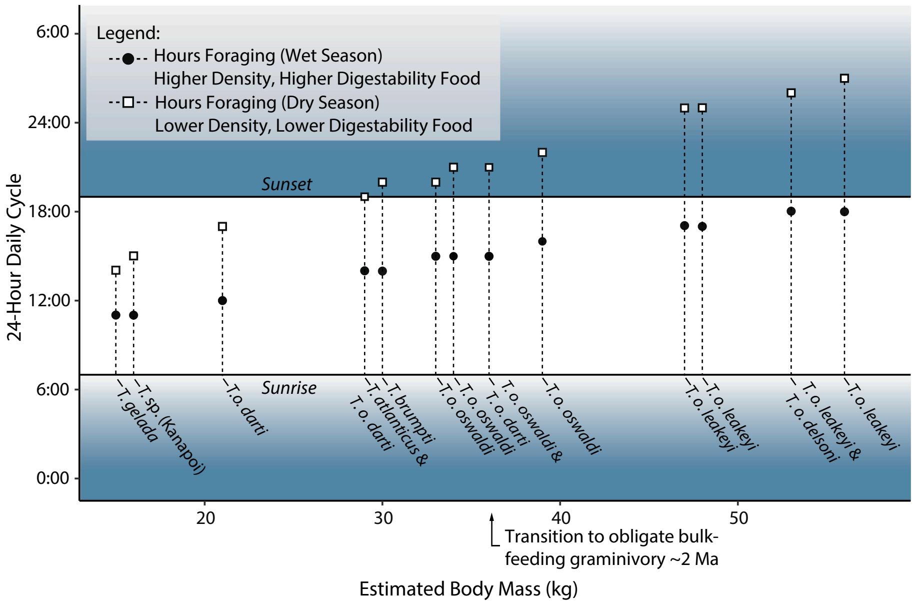

Fig. 7. Cercopithecid primates are uniformly diurnal and geladas begin feeding soon after sunrise. This figure illustrates equatorial daylight hours and the feeding duration of *T. gelada* during the wet season (when food is denser, more digestible, and intake rates are lower) and the dry season (when food is patchier, less digestible, and intake rates are higher; Iwamoto, 1993; Hunter, 2001; Venkataraman et al., 2014). If we assume that tradeoffs in food intake rate and digestibility extend to the fossil past, and if we extrapolate this pattern to larger body sizes (source: Table S1) and their attendant basal metabolic rates (assumptions and calculations in Lee and Foley, 1993), it is evident that species with a median mass exceeding 30 kg cannot turn to lower-quality foods, as geladas do, and preserve a strictly diurnal activity pattern. We view body masses >30 kg as an evolutionary trap because survival depends on the continuous availability of the highest-quality food patches ('grazing lawns'). Our model suggests that *T. oswaldi leakeyi* reached the viable limit of bulk-feeding graminivory for any primate, devoting nearly all of its daylight hours to feeding, leaving scant time for allogrooming (~2 h per day for *T. gelada*) or other essential behaviors.

mass, and we describe this behavior and corresponding large size, both of which peaked in the Pleistocene, as evolutionary traps. To support this characterization, we report evidence of temporal increases in strontium isotope variability among North African theropiths, a result that indicates greater ranging costs in response to diminishing food resources, a probable factor in the extinction of *T. oswaldi*, the largest monkey that ever lived.

Data availability

All raw data to support the findings of this study are available in the main text tables and within the online Supplemental material.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110393.

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