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Research Article

Seasonal niche shifts and foraging plasticity of the Southern Gelada (*Theropithecus gelada obscurus* Heuglin, 1863) (Cercopithecidae, Papionini) within the extreme Afro-alpine ecosystem of the Abune Yosef Zigit Community Conservation Area, Ethiopia

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Abstract

Understanding how primates adapt their foraging strategies to fluctuating environmental conditions is a central theme in behavioral ecology. The extreme Afro-alpine ecosystem presents a unique setting to test predictions of Optimal Foraging Theory and the Fallback Food Hypothesis due to its severe seasonal shifts in resource availability. This study investigated the dietary composition, seasonal variation, food preferences (dietary selectivity), and foraging plasticity of the Southern Gelada (*Theropithecus gelada obscurus*) in the Abune Yosef Zigit Community Conservation Area, Ethiopia. Using instantaneous scan sampling and vegetation surveys across dry and wet seasons, we recorded 761 feeding records encompassing 25 food items. Forbs dominated the diet (55.7%), followed by grasses (42.7%), and insects (1.6%). Geladas exhibited a consistent bimodal feeding pattern but demonstrated pronounced seasonal niche shifts. In the dry season, they highly expanded their dietary breadth (Shannon H' = 2.31) and relied heavily on underground roots, aligning with fallback food strategies. In the wet season, the dietary niche narrowed (H' = 1.92), with greater reliance on grass blades and young shoots. Electivity indices revealed highly dynamic, context dependent selectivity rather than fixed preferences, with preference rankings shifting between seasons. These findings highlight the remarkable behavioral plasticity of geladas and underscore their ability to dynamically adjust foraging strategies to survive in extreme, highly seasonal environments.

Key words: Afro-alpine ecosystem, dietary selectivity, foraging plasticity, niche ecology

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Introduction

Primate foraging behavior is characterized by remarkable behavioral plasticity, serving as a critical adaptive strategy to cope with spatial and temporal environmental changes. To survive fluctuating conditions, primates employ a suite of adaptive strategies, ranging from altering activity budgets and shifting ranging patterns to modifying dietary composition (Lee et al. 2021). As anthropogenic climate change accelerates the frequency and severity of climatic extremes, understanding the limits of this behavioral plasticity has become a critical priority in primatology (Kalbitzer and Chapman 2018; Bernard and Marshall 2020).

The expression of these adaptive strategies is governed by a complex interplay of influencing factors. Specifically, macro-level climatic fluctuations dictate local plant phenology and resource availability, which are further filtered by habitat heterogeneity and intensified by interspecific competition (Korstjens et al. 2010; Lee et al. 2021). To understand these behaviors, ecological frameworks, particularly Optimal Foraging Theory (OFT) and the Fallback Food Hypothesis (FFH), are frequently applied. Optimal Foraging Theory posits that foragers maximize their net energy intake per unit of time by selectively targeting high-quality resources while minimizing the costs of search and handling (Pyke et al. 1977; Felton et al. 2009). However, in highly seasonal environments where preferred foods become scarce, primates rely on the FFH, shifting their diet to include fallback foods, which are resources that are typically lower in quality, more widely distributed, but require higher processing effort (Marshall and Wrangham 2007). While OFT and FFH remain foundational, modern nutritional ecology increasingly integrates these theories with the Geometric Framework, which posits that foragers balance the intake of multiple macronutrients rather than simply maximizing energy (Felton et al. 2009). The use of fallback foods allows populations to survive periods of nutritional stress but often requires a broader dietary niche. In extreme environments, such as high-altitude Afro-alpine zones, these factors are amplified by acute thermal stress and seasonal vegetation desiccation, forcing distinct behavioral adaptations (Hill 2006).

Geladas (*Theropithecus gelada* (Rüppell, 1835)) provide an exceptional empirical system to evaluate how OFT, FFH, and modern nutritional frameworks operate under extreme environmental constraints. Unlike the predominantly frugivorous primates that traditionally dominate this theoretical literature (Felton et al. 2009), geladas offer a rare opportunity to examine these strategies in a specialized graminivore. Geladas are among the most terrestrial nonhuman primates and show morphological adaptations for a predominantly graminivorous diet. They inhabit Afro-alpine grasslands and cliffs between 1,800 and 4,400 m a.s.l. (Bergman and Beehner 2013; Fashing et al. 2014; Snyder-Mackler et al. 2022), and their foraging behavior illustrates the theoretical tension between optimal foraging and fallback reliance. Recent research highlights that high-altitude environments impose compounded energetic costs, forcing primates to negotiate trade-offs between thermoregulation and foraging efficiency (Kalbitzer and Chapman 2018). While grasses constitute their dietary staple, geladas show notable seasonal flexibility. In accordance with OFT, they select high-quality grasses when available; as vegetation desiccates in the dry season and nutritional stress intensifies, they shift to energetically expensive fallback foods such as underground roots and rhizomes, as predicted by the FFH (Kifle et al. 2013; Fashing et al. 2014). Most studies on this dietary plasticity have been conducted in mixed ecosystems containing both Afro-alpine and sub-Afro-alpine zones across Ethiopia (Fashing et al. 2014; Woldegeorgis and Bekele 2015; Abie et al. 2017; Moges 2019). However, the feeding ecology of the Southern Gelada (*Theropithecus gelada obscurus* Heuglin, 1863) in the Afro-alpine Abune Yosef Zigit Community Conservation Area (AYZCCA) of Ethiopia remains unknown.

Reaching 4,284 m, the AYZCCA lacks the sub-Afro-alpine buffer zones found at other study sites (Gebrehiwot et al. 2018). This geographic constraint is expected to result in lower floristic diversity and severe seasonal vegetation dieback, drastically reducing habitat heterogeneity and amplifying the effects of climatic fluctuations.

Consequently, it is an ideal natural laboratory to evaluate the limits of gelada foraging plasticity when influencing factors are at their most severe. Grounded in OFT and FFH, this study investigates the dietary composition, seasonal variations, food preferences (dietary selectivity), and foraging plasticity of Southern Geladas in the AYZCCA to elucidate their adaptive strategies under extreme environmental conditions. We tested two predictions: (1) geladas will exhibit pronounced seasonal niche shifts, broadening their dietary niche during the dry season to incorporate fallback foods (e.g., underground roots) as predicted by the FFH, while narrowing their niche to selectively forage on high quality grasses during the wet season as predicted by OFT; and (2) geladas will exhibit nonrandom, context-dependent feeding behavior, targeting specific plant species based on seasonal phenological quality rather than consuming vegetation solely in proportion to its abundance.

Materials and methods

Study area

Abune Yosef Zigit Community Conservation Area (AYZCCA) is located in the North Wollo Zone of Amhara National Regional State, northeast of the historic town of Lalibela (Saavedra and Dantart 2009) in Ethiopia. It lies between 12°03'36"N and 12°01'42"N, 039°09'00"E and 039°17'06"E, with elevations ranging from 3,505 to 4,284 m a.s.l. (Fig. 1). The area is situated 730 km north of Addis Ababa and approximately 48 km north of Lalibela, covering a total area of 80.59 km^2, though the potential habitat for geladas is about 13.09 km^2 (ACTPO 2014; AZACCA 2018). Mount Abune Yosef, with its highest point at Rim Gedel, is the seventh tallest mountain in Ethiopia, reaching an elevation of 4,284 m a.s.l. (Saavedra and Dantart 2009; Friis et al. 2011). The region also features two other notable peaks: Big Zigit at 4,080 m and Small Zigit at 4,035 m a.s.l. (Saavedra and Dantart 2009).

The conservation area's boundaries are shared with the North Wollo (Lasta and Gidan districts) and Wag-Himra (Gazgibla district) zones of the Amhara National Regional State (Saavedra and Dantart 2009). The area receives uni-modal rainfall, averaging about 790 mm per year, with the highest rainfall occurring from June to August (Friis et al. 2011; ACTPO 2014; Gebrehiwot et al. 2018). Temperatures range from 10 to 24 °C in the wet season and from 5 to 21 °C in the dry season (Saavedra and Dantart 2009; Weather Atlas 2021).

It has a high diversity of mammals, with 43 species of mammals recorded; the endemic and endangered Ethiopian Wolf (*Canis simensis* Ruppell, 1840), which coexists with Southern Geladas in the highlands (Sillero-Zubiri et al. 2004; Saavedra and Dantart 2009; Marino and Sillero-Zubiri 2011). Of 221 bird species identified in the area (Lepage 2006), six of them are endemic, including the Yellow-fronted Parrot (*Poicephalus flavifrons*) (Saavedra and Dantart 2009).

The main ecosystem type of the AYZCCA is Afro-alpine (Friis et al. 2011). The Afro-alpine ecosystem (> 3,500 m) is covered with herbaceous plant genera such as *Alchemilla*, *Potentilla*, *Helichrysum*, *Senecio*, *Carex*, *Poa*, *Festuca* and *Agrostis*, and the endemic Giant Lobelia (*Lobelia rhynchopetalum* Hemsl., 1877) (Saavedra and Dantart 2009; Friis et al. 2011).

In the north direction, it is dominated by grasslands (with *Poa*, *Agrostis*, *Carex*, *Festuca* spp.), most of them with short grasses due to heavy overgrazing. Very steep slopes and a high degree of humidity with long grasses exist only in some

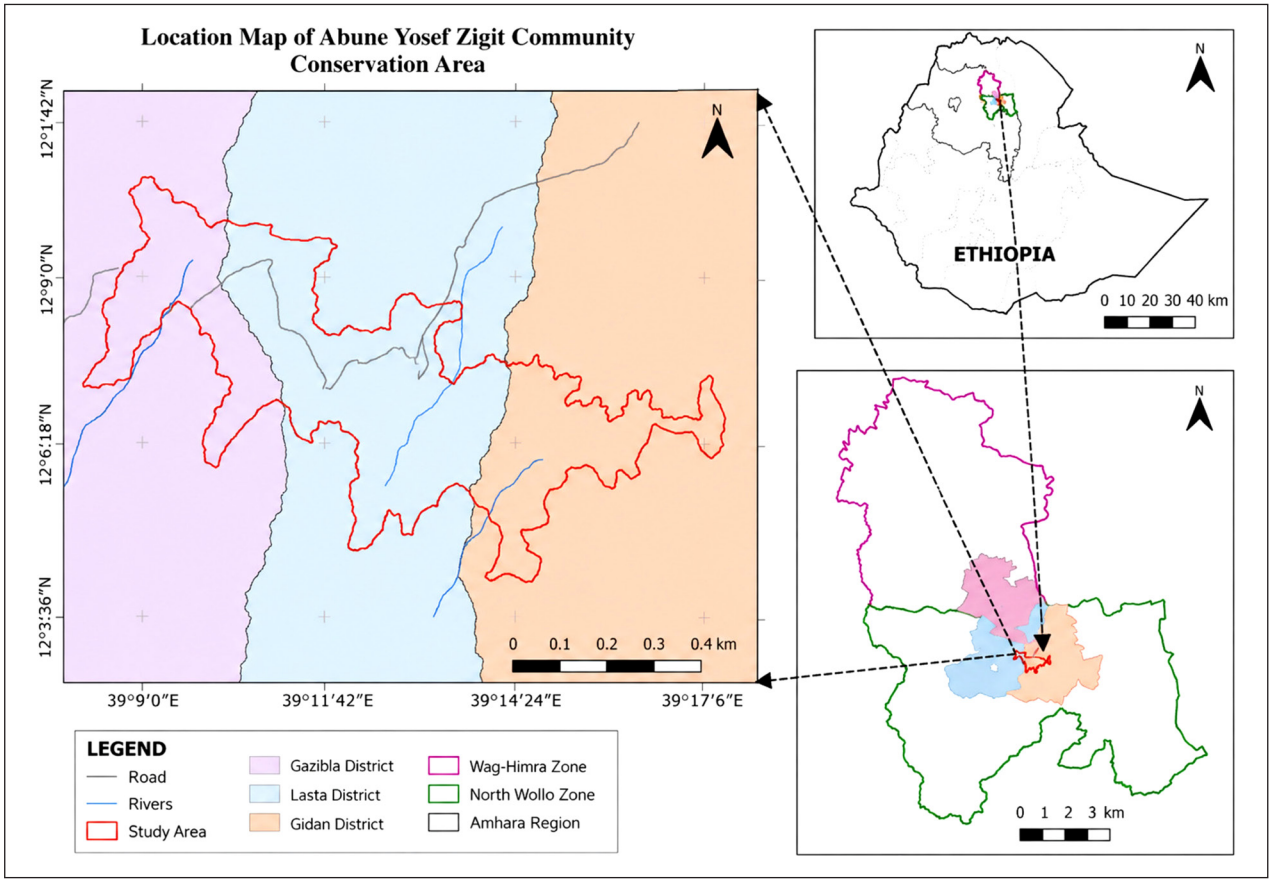

Figure 1. Location map of the study area.

areas. Moderately steep areas of the highlands of the Aremgarem are where the Giant Lobelias (*Lobelia rhynchopetalum*) are more abundant, with densities ranging from 800 to 2,500 plants per hectare (ACTPO 2014; AZACCA 2018).

Sampling design

Preliminary survey and focal group selection

A one-week preliminary reconnaissance survey was conducted in February 2021 to characterise habitat heterogeneity and identify gelada groups suitable for detailed dietary data collection during both the dry and wet seasons. Based on this assessment, two representative focal groups, one from Kechin Gedel and the other from Gimew Kitel, were selected for the study. These groups were strategically chosen because their combined home ranges encompassed the primary ecological gradients and vegetation communities, from extensive *Festuca* grasslands to mixed *Lobelia rhynchopetalum* communities (Fashing et al. 2014; Moges 2015). To ensure that differences in diet were driven by season rather than inter-group habitat disparities, we confirmed that the core foraging areas of these two groups did not differ in vegetation composition or plant availability. This design ensured the capture of essential behavioral and dietary variability associated with the major habitat types available to geladas in the region (Iwamoto and Dunbar 1983). The groups were reliably differentiated by distinctive phenotypic traits: the Kechin

Gedel group was identified by a unique scar and cut-off mane on the adult male leader, while the group at Gimew Kitel was recognized by its small, consistent population size (36 individuals) and isolated location.

Behavioral observations and dietary data collection

Dietary and behavioral data were collected using instantaneous scan sampling (Abie et al. 2017), supplemented by direct observation to record specific feeding behaviors (Yihune and Bekele 2012). Data were collected throughout the dry (February–April 2021) and wet (June–August 2021) seasons. A team of two observers (one researcher and one field assistant) followed the focal groups from a distance of 10–20 meters to minimize disturbance, positioning themselves downwind to avoid detection (Yazezew et al. 2011; Moges 2015). Sampling was conducted over an average of 8 days per month (2 days per week), yielding a total of 960 scans. Each scan lasted 5 minutes and scans were repeated at 10-minute intervals; the dominant activity of every visible individual was recorded, after a 2–3-minute settling period to ensure normal behavior (Jarvey et al. 2018). Food items were recorded at early morning (7:30–10:00 a.m.) and late afternoon (3:00–5:30 p.m.) (Fashing et al. 2007; Moges 2019). Insects consumed by geladas were identified using the insect identification field guide of Picker et al. (2018).

Vegetation survey

To quantify food availability and calculate feeding preference indices, a systematic vegetation survey was conducted within a 2.62 km^2 area, representing 20% of the potential gelada habitat in the AYZCCA (Yazezew et al. 2011). Because geladas may travel up to 2.3 km per day (preliminary survey observations), systematic random sampling was used, beginning at a random starting point and applying fixed intervals to ensure unbiased coverage. To minimize edge effects, transects were positioned 250 m from the boundary of the study area (Girma et al. 2012). Six transects were established at 400 m east–west intervals, with 20 plots (1 × 1 m) spaced at 200 m north–south intervals; transect lengths varied between 0.4 and 0.8 km depending on accessibility (Jatani et al. 2019). Transect lines were marked using painted stones and natural landmarks such as old Giant Lobelia stems and streams. Within each plot, all forage species were identified, and their phenological states (e.g., flowering, fruiting, new leaf growth) were recorded during both the dry and wet seasons to assess temporal fluctuations in resource availability (Fashing et al. 2007).

Data analysis

Diet composition and seasonal comparisons

Diet composition was quantified using two complementary approaches: frequency of occurrence and utilization percentage. Frequency of occurrence represented the percentage of feeding records in which a particular food item appeared, while utilization percentage reflected the proportion of total feeding records dedicated to each food item. Food items were categorized into four major groups: graminoids (grasses), underground roots, forbs, and insects.

To examine seasonal comparisons of diet composition, we employed a chi-square (x^2) test of independence to determine significant associations between season and food type consumption. Standardized residuals were calculated to identify which categories contributed to significant chi-square results, with absolute values greater than 2.0 indicating significant departures from expected frequencies. The chi-square (x^2) test was appropriate because the data were randomly sampled, categorical, expected frequencies were ≥ 5 in ≥ 80% of cells, and observations were mutually exclusive and exhaustive.

Dietary diversity indices

Dietary niche breadth was quantified using Levin's niche breadth index (B) and the Shannon Diversity Index (H'). To avoid inconsistent interpretation, we clearly distinguish their applications: Levin's index estimates the overall width of the dietary niche by quantifying the variety of broad food categories utilized, whereas Shannon's index accounts for both the richness and evenness of specific individual food items consumed. Because the study design involved repeated, non-independent measurements of the same focal groups across six study months, monthly feeding diversity was analysed using the Friedman test, a non-parametric test appropriate for repeated-measures data with more than two time points. To determine exactly which months differed from one another, Dunn's post-hoc tests with Bonferroni correction were applied. Consequently, seasonal differences in feeding diversity were not tested in an isolated two-season comparison but were inferred from these monthly pairwise contrasts (the three dry months against the three wet months), maintaining the appropriate statistical structure for our repeated-measures design.

Feeding preference indices

Feeding preferences of Southern Geladas were quantified using availability-based preference indices to distinguish true selection from consumption driven merely by resource abundance. The Forage Ratio (***FR***) was calculated as the proportion of a food item in the diet divided by its proportion in the environment:

$$\text{Foraging Ratio}(\boldsymbol{FR}) = \frac{\text{proportion of a specific food item in the diet (D)}}{\text{Total proportion of diet in the environment (A)}} \quad (1)$$

Additionally, two indices were applied to account for selectivity in a standardized manner:

$$\text{Electivity Index}(\boldsymbol{E}) = \frac{\text{D} - \text{A}}{\text{D} + \text{A}} \quad (2)$$

$$\text{Jacobs' index}(\boldsymbol{d}) = \frac{\text{D} - \text{A}}{\text{D} + \text{A} - 2\text{DA}} \quad (3)$$

Both indices range from -1 (total avoidance) to +1 (strong preference), with Jacobs' index providing improved sensitivity for rarely consumed items by correcting for biases associated with resource unevenness. High positive values indicate strong selection relative to availability, whereas negative values indicate avoidance. It is critically important to note that these indices quantify selection based purely on availability and consumption frequency; they do not

directly assess the nutritional value, energetic content, or chemical composition of the forage. Therefore, interpretations regarding the nutritional drivers of these preferences are made cautiously.

Correlation and temporal analyses

Spearman rank correlation coefficients (***rs***) were calculated to assess: (1) the relationship between plant availability and consumption patterns in each season, and (2) the consistency of preference rankings across seasons. Spearman correlation was used because the relationship between availability and consumption is not necessarily linear, and this method effectively identifies monotonic patterns in ranked data.

Seasonal differences in feeding preference indices were evaluated using the Wilcoxon signed-rank test, a non-parametric method suitable for paired and non-normally distributed data. This test accounts for repeated measurements of the same plant species across seasons and reduces the influence of extreme values. For temporal feeding patterns, we utilised kernel density estimation to identify peaks in feeding activity throughout the day. This non-parametric approach allowed visualization of feeding probability distributions without assuming a specific underlying distribution. Diurnal shifts in food preferences were assessed by comparing the percentage composition of feeding categories during morning (7:30–10:30 am) and afternoon (3:00–5:30 pm) periods.

All the data visualizations were created using ggplot2 package in R, and statistical significance was indicated using standard notation (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Results

Overall diet composition

Southern Geladas consumed a total of 25 food items including 22 plant species (Appendix 1) and three insect species, excluding unidentified tubers. The diet was dominated by forbs (roots, leaves, flowers, stems, and young shoots; 55.7%), followed by grasses (roots and blades; 42.7%) and insects (1.6%) (Table 1).

Table 1. Seasonal Variation in plant part composition of the diet of Southern Geladas (number of feeding records, % of the seasonal and total).

Plant Part	Dry Season (N = 408)	Wet Season (N = 353)	Total (N = 761)
GB (Grass Blades)	122 (29.9%)	132 (37.4%)	254 (33.4%)
HL (Herb Leaves)	35 (8.6%)	91 (25.8%)	126 (16.5%)
RTF (Roots of forb)	87 (21.3%)	30 (8.5%)	117 (15.3%)
RH (Rhizomes)	64 (15.7%)	36 (10.2%)	100 (13.0%)
RTG (Roots of grass)	56 (13.7%)	15 (4.2%)	71 (9.3%)
YS (Young Shoots)	12 (2.9%)	29 (8.2%)	41 (5.4%)
ST (Stems)	23 (5.6%)	12 (3.4%)	35 (4.5%)
FL (Flowers)	0 (0.0%)	5 (1.4%)	5 (0.7%)
LA (Larva Ants)	9 (2.2%)	3 (0.9%)	12 (1.6%)

Note: GB = Grass Blades, RTG = Roots of grass, RTF = Roots of forb, HL = Herb Leaves, RH = Rhizomes, YS = Young Shoots, ST = Stems, FL = Flowers, LA = Larva Ants.

Among individual plant species, *Festuca simensis* had the highest frequency of occurrence (17.82%) and utilization percentage (24.05%), indicating it was both abundant and frequently consumed. In contrast, *Helichrysum citrispinum* represented the smallest proportion (0.25%) of the diet (Appendix 1).

Diurnal and seasonal variation in diet composition

Diurnal feeding patterns

Analysis of 960 scan samples, yielding 761 feeding records, revealed a consistent bimodal feeding pattern in both the dry (N = 408) and wet (N = 353) seasons. Kernel density estimates identified distinct feeding peaks in the early morning (07:30–09:00) and late afternoon (15:00–16:30) (Fig. 2). While morning feeding was predominantly grass-based in both seasons, afternoon feeding incorporated a higher proportion of forbs and insects, reflecting a diurnal shift in foraging strategy. A consistent decline in feeding activity during midday (12:00–14:00) was observed across seasons. This pattern suggests a potential behavioral adaptation to daily environmental factors, such as ambient temperature or solar radiation, although direct thermoregulatory data were not collected.

In the dry season, morning feeding focused on grasses (72%), shifting toward more forbs (35%), and insects (12%) in the afternoon. In the wet season, morning feeding still favored grasses but at a lower proportion (65%), with forbs and insects comprising 30% and 5%, respectively. Wet-season afternoon feeding was the most diverse, with a more balanced distribution among grasses (45%), forbs (40%), and insects (15%).

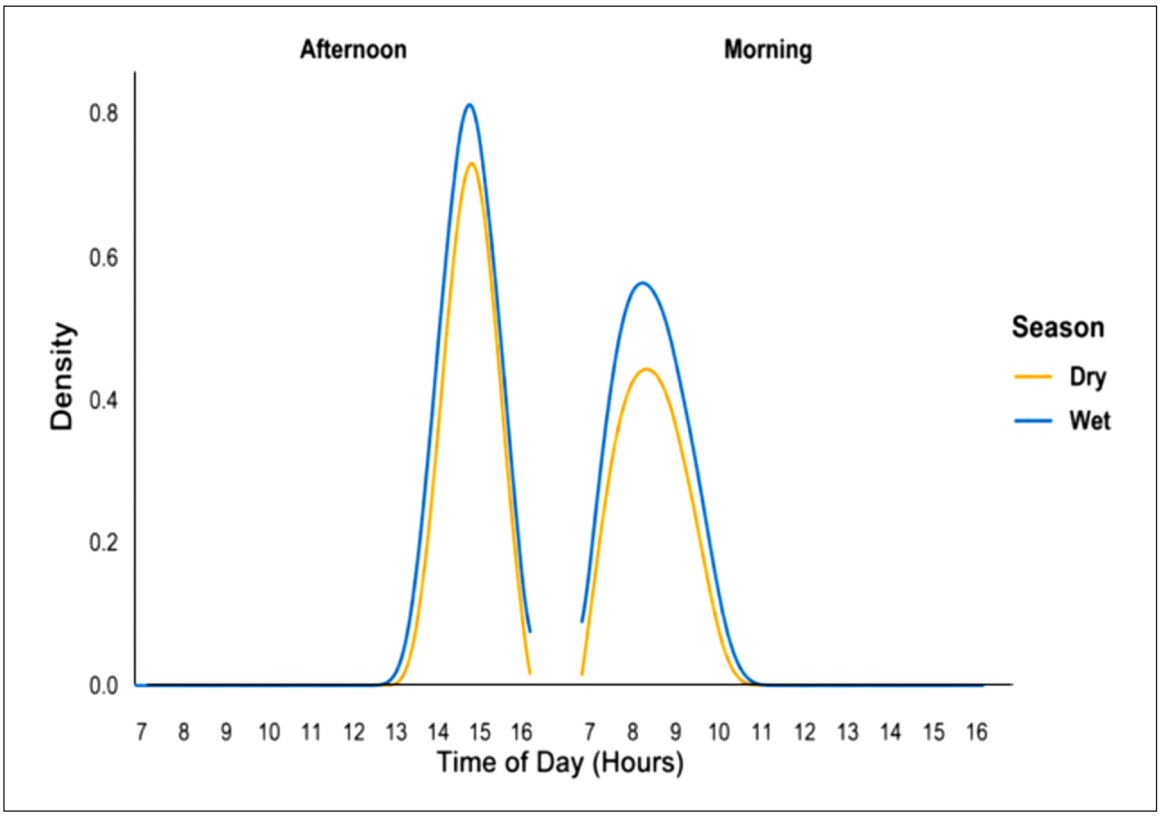

Figure 2. Seasonal kernel density feeding analysis.

Dietary shifts between seasons

Geladas consumed 19 and 17 food items in the dry and wet seasons, respectively. Although forbs remained the main food component in both seasons, diet composition differed significantly between seasons: a chi-square test of independence showed a highly significant association between season and plant part (x^2 = 65.29, p < 0.001). Some rare categories (flowers and unidentified items) had low expected frequencies, so these results should be interpreted with caution. The largest changes were in roots (RT) and forb leaves (LV), which showed opposite seasonal patterns. Standardized residuals indicated that grass-blade consumption was significantly higher in the wet season, whereas root consumption was significantly higher in the dry season (Table 1).

Dietary diversity varied seasonally. Levins' index indicated a broader dietary niche (greater variety of food categories) in the dry season. The Shannon diversity index, which accounts for richness and evenness of individual food items, was higher in the dry season (H' = 2.31) than in the wet season (H' = 1.92), a difference supported by the monthly contrasts below. This increase in diversity suggests that geladas broaden their diet in the dry season, including a wider variety of items such as underground roots, to compensate for reduced availability of high-quality forage.

Monthly changes in feeding diversity

Monthly feeding diversity was analyzed with the Friedman test to account for repeated measures across the six study months. Feeding diversity varied significantly among months (Friedman x^2 = 42.37, p < 0.001), decreasing from February (H' = 2.38) to August (H' = 1.82). Dunn's post-hoc tests showed significantly higher feeding diversity in the early dry months (February, March, April) than in the later wet months (June, July, August). Mean feeding diversity was therefore higher in the dry season (mean H' = 2.31) than in the wet season (mean H' = 1.92). This monthly trajectory confirms the seasonal pattern shown by Levins' index: geladas progressively narrowed their dietary niche as the wet season advanced and high-quality grasses became abundant, in contrast to the broad, generalized foraging of the dry months.

Dietary selectivity and foraging strategies

Synthesizing the electivity indices (Table 2) showed that Southern Geladas demonstrated strong, context-dependent selectivity.

Overall, *Haplocarpha schimperi* (FR = 5.87, E = 0.71) and *Lobelia rhynchopetalum* (FR = 5.26, E = 0.68) were the most preferred species, consumed disproportionately to their availability. Other preferred species included *Rumex nepalensis* (FR = 1.54) and *Thymus schimperi* (FR = 1.54). In contrast, *Festuca richardii* (FR = 0.18, E = –0.69) and *Bidens macroptera* (FR = 0.20, E = –0.66) were avoided, indicating active selection against these species despite their presence in the environment. *Festuca simensis*, the most frequently consumed species overall, was consumed approximately in proportion to its availability (FR = 1.25, E = 0.11), indicating that it served as a staple, neutral resource.

Table 2. Dietary selectivity of Southern Geladas for the most frequently recorded plant species (overall, dry season, and wet season).

Species	Taxonomic Authority	Type	Season	D	A	FR	E	d
Haplocarpha schimperi	Beauverd, 1915	Forb	Entire	0.71	0.12	5.87	0.71	0.89
L. rhynchopetalum	Hemsl., 1877	Forb	Entire	0.77	0.15	5.26	0.68	0.90
Rumex nepalensis	Spreng., 1825	Forb	Entire	0.63	0.41	1.54	0.21	0.42
Thymus schimperi	Ronniger, 1932	Forb	Entire	0.95	0.62	1.54	0.21	0.84
Delosperma abyssinicum	(Regel) Schwantes, 1928	Forb	Entire	0.80	0.57	1.42	0.17	0.51
Festuca simensis	Hochst. ex A.Rich., 1850	Grass	Entire	0.25	0.20	1.25	0.11	0.14
Cyperus bulbosus	Vahl, 1805	Forb	Entire	0.38	0.32	1.19	0.09	0.14
Salvia tiliifolia	Vahl, 1794	Forb	Entire	0.20	0.19	1.04	0.02	0.03
Utica simensis	Hochst. ex A.Rich., 1850	Forb	Entire	0.15	0.15	0.97	-0.01	-0.02
Kniphofia foliosa	Hochst., 1844	Forb	Entire	0.05	0.128	0.4	-0.41	-0.45
Bidens macroptera	(Sch.Bip. ex Chiov.) Mesfin, 1984	Forb	Entire	0.09	0.449	0.2	-0.66	-0.78
Festuca richardii	E.B.Alexeev, 1986	Grass	Entire	0.17	0.91	0.18	-0.69	-0.96
Festuca abyssinica	Hochst. ex A.Rich., 1850	Grass	Entire	0.11	0.62	0.18	-0.7	-0.75
Trifolium acaule	Steud. ex A.Rich., 1848	Forb	Entire	0.10	0.99	0.1	-0.81	-1.00
Rumex nepalensis			Dry	5.15	3.08	1.67	0.25	0.26
Festuca richardii			Dry	13.24	9.23	1.43	0.18	-0.02
Festuca simensis			Dry	20.83	21.54	0.97	-0.02	0.00
Utica simensis			Dry	2.7	3.08	0.88	-0.07	0.04
Thymus schimperi			Dry	3.92	4.62	0.85	-0.08	0.03
Delosperma abyssinicum			Dry	4.9	6.16	0.8	-0.11	0.03
Trifolium acaule			Dry	8.33	10.77	0.77	-0.13	0.02
L. rhynchopetalum			Dry	10.29	15.38	0.67	-0.2	0.02
H. schimperi			Dry	8.5	13.85	0.61	-0.24	0.03
Festuca abyssinica			Dry	1.96	12.31	0.16	-0.73	0.30
Delosperma abyssinicum			Wet	9.51	5.13	1.85	0.3	-0.05
Festuca richardii			Wet	16.4	8.97	1.83	0.29	-0.03
Thymus schimperi			Wet	13.12	7.69	1.71	0.26	-0.03
Festuca simensis			Wet	23.61	17.95	1.32	0.14	-0.01
Rumex nepalensis			Wet	6.23	5.13	1.21	0.1	-0.02
Trifolium acaule			Wet	10.16	8.97	1.13	0.06	-0.01
Cyperus bulbosus			Wet	6.89	6.41	1.07	0.04	-0.01
Salvia tiliifolia			Wet	3.61	3.85	0.94	-0.03	0.01
H. schimperi			Wet	4.26	10.26	0.42	-0.41	0.08
Kniphofia foliosa			Wet	0.98	2.56	0.38	-0.45	1.07
L. rhynchopetalum			Wet	3.61	14.1	0.26	-0.59	0.12
Bidens macroptera			Wet	1.64	8.97	0.18	-0.69	0.39

D = Proportion of a specific diet frequency, A = Total proportion of diet in the environment, FR = Forage Ratio, E = Electivity Index, d = Jacobs' index.

The seasonal electivity indices reveal dynamic, context-dependent foraging strategies rather than fixed dietary preferences. In the dry season, geladas selected *R. nepalensis* (FR = 1.67, E = 0.25) and *F. richardii* (FR = 1.43, E = 0.18), although, without direct nutritional analyses, it cannot be confirmed whether this reflects high energetic value or simply greater palatability relative to desiccated

alternatives. Meanwhile, species that were highly preferred overall, *H. schimperi* and *L. rhynchopetalum*, were avoided (FR < 1, E < 0), while *F. simensis* remained a neutral staple consumed in near-proportion to its availability (FR = 0.97, E = –0.02). The onset of the wet season brought a distinct reorganization of selectivity. *Delosperma abyssinicum* (FR = 1.85, E = 0.30), *F. richardii* (FR = 1.83, E = 0.29) and *T. schimperi* (FR = 1.71, E = 0.26) became the primary targets, while avoidance of *H. schimperi* (FR = 0.42, E = –0.41) and *L. rhynchopetalum* (FR = 0.26, E = –0.59) intensified. This seasonal shift in preference rankings indicates that plant selection is closely tied to shifting phenological states or relative seasonal abundance, rather than to intrinsic, year-round nutritional superiority of particular species.

Discussion

Overall diet composition

This study provides the first comprehensive data on the feeding ecology of the Southern Gelada (*Theropithecus gelada obscurus*) in AYZCCA. Consistent with the classification of the gelada as the most graminivorous primate in the world (Dunbar and Dunbar 1974; Fashing et al. 2014), the diet in AYZCCA was dominated by grasses and forbs. However, the high proportion of forbs (55.7%) relative to grasses (42.7%) deviates notably from populations in Borena Sayint National Park, where grasses constitute nearly 80% of the diet (Kifle and Bekele 2021). This variation underscores the ecological plasticity of the species and shows how local habitat structure and floristic composition shape foraging strategies. The AYZCCA is a purely Afro-alpine ecosystem with steep slopes and potentially high grazing pressure from livestock, factors that might limit the availability or palatability of high-quality grasses, thereby necessitating a greater reliance on forbs (Gebrehiwot et al. 2018).

The 22 plant species recorded in the AYZCCA are fewer than those reported for geladas elsewhere in Ethiopia: 56 plant species at Guassa Community Conservation Area (Fashing et al. 2014), 74 plant species at Borena Sayint National Park (Kifle and Bekele 2021), 61 at Arsi (Moges 2019), and 41 at Abo Gedam (Yazezew et al. 2020). Primate dietary diversity is often reduced in heavily disturbed habitats compared with intact ecosystems (Fashing et al. 2014; Moges 2015), but the lower richness observed here most likely reflects the extreme altitudinal constraints of the area. As a purely Afro-alpine ecosystem between 3,505 and 4,284 m a.s.l. (Gebrehiwot et al. 2018), the AYZCCA inherently supports lower floristic diversity than the sub-Afro-alpine or transitional ecosystems at those other sites (Sklenář et al. 2016). The physical limitation of available forage species at this altitude, rather than behavioral rigidity, therefore most likely explains the narrower dietary breadth of Southern Geladas at Abune Yosef.

The dominance of *Festuca simensis* (24.05% of the diet) underscores its role as a staple resource in this region. This agrees with observations from other gelada habitats, where specific grass species form the dietary core, probably because of their high abundance and relatively high digestibility (Fashing et al. 2014; Barton et al. 2019). The minimal consumption of animal matter (insects) suggests that, unlike some cercopithecines that hunt actively, geladas in the AYZCCA ingest insects mainly incidentally while foraging on vegetation, supporting the view that animal protein is not a critical dietary component for this species (Gippoliti and Hunter 2018).

Diurnal feeding patterns

The bimodal feeding pattern, with peaks in the early morning and late afternoon, is consistent with gelada populations across Ethiopia (Iwamoto and Dunbar 1983; Fashing et al. 2014). The midday decline in feeding activity is often attributed to thermoregulatory constraints that minimize heat stress during peak solar radiation (Hill 2006; Korstjens et al. 2010). This schedule probably allows geladas to synchronize their most energetically demanding activities with cooler ambient temperatures, thereby reducing the risk of hyperthermia in the high-altitude environment (Hill et al. 2003).

The diurnal shift in diet composition might reflect a strategy for managing digestive constraints. Fashing et al. (2014) suggested that geladas maximize fiber digestion by consuming grasses earlier in the day, allowing longer retention times in the gut. The subsequent increase in forb and insect consumption in the afternoon might represent an attempt to balance nutrient intake, although direct nutritional analysis is required to confirm this mechanism (Rothman et al. 2014).

Seasonal variation and feeding strategies

The marked seasonal dietary shifts observed here highlight the behavioral adaptability of geladas to the harsh, variable conditions of the Afro-alpine zone. The increase in underground root consumption in the dry season (65.93% vs 22.09% in the wet season) represents a critical survival strategy (Appendix 1). According to OFT and the FFH, primates broaden their diet during periods of scarcity by incorporating less preferred but accessible resources (Marshall and Wrangham 2007; Fashing et al. 2014). In the AYZCCA, as above-ground biomass desiccates and loses nutritional quality in the dry season, geladas switch to excavating roots and rhizomes. This behavior is energetically costly but provides essential water and carbohydrates when other resources are limited (Jarvey et al. 2018; Kifle and Bekele 2021).

The higher Shannon diversity in the dry season further supports niche expansion. In the wet season, selective feeding on high-quality grass blades and young shoots leads to dominance by a few preferred items, whereas the dry season requires more even use of the available resource base to meet energy requirements. This pattern matches findings from Guassa, where geladas also expanded their dietary niche during resource-poor periods (Fashing et al. 2014).

Dietary selectivity and preference

The selectivity indices showed that geladas do not feed randomly but exercise distinct selectivity, often decoupling consumption from availability. The strong preference for *H. schimperi* and *L. rhynchopetalum*, despite their varying abundance, suggests that these species possess traits that make them highly attractive. *Lobelia rhynchopetalum*, for instance, is known to have high water content, which could be crucial for hydration in the arid Afro-alpine environment (Yihune and Bekele 2012). Similarly, the preference for *H. schimperi* might be driven by nutrient density or low concentrations of secondary compounds such as tannins or phenolics (Cork and Foley 1991).

Conversely, the avoidance of *Festuca abyssinica* and *B. macroptera*, despite their presence in the environment, points to possible defensive mechanisms. *Bidens* species, for example, often bear hooked bristles that might cause physical irritation, and *F. abyssinica* might be physically tougher or chemically defended, making it less profitable than softer grasses such as *F. simensis* (Barca et al. 2020; Truppa et al. 2024). Although the indices used (FR, Jacobs' index) effectively quantify selection, the underlying drivers, whether nutritional quality, secondary metabolites, or handling time, remain speculative in the absence of phytochemical analyses. Nonetheless, the strong correlation between availability and consumption (rs > 0.8) indicates that, while selectivity is present, it operates within the boundaries of what the environment offers, a core tenet of Optimal Foraging Theory (Pyke et al. 1977).

The weak correlation in preference rankings between seasons (r_s = 0.36) indicates that foraging strategies are not static. Species such as *R. nepalensis* became important preferred items in the dry season, probably serving as high-quality fallback resources when preferred grasses were scarce (Fashing et al. 2014). This dynamic shifting of preferences underscores the ability of geladas to adapt behaviorally to the temporal heterogeneity of their habitat, a key factor in their resilience to environmental fluctuations.

Conclusion

This study provides the first comprehensive assessment of Southern Gelada feeding ecology in the AYZCCA. The results show high behavioral plasticity: geladas employ flexible foraging strategies that respond to seasonal fluctuations. They maintain a consistent bimodal schedule but significantly alter diet composition, expanding their niche to rely on underground roots in the dry season while relying more on grass blades and young shoots in the wet season. Although *Festuca simensis* serves as a staple, preferences for secondary species shift dynamically. Conservation efforts should therefore prioritize habitat heterogeneity to ensure access to both staple grasses and critical seasonal forbs.

This study provides a behavioral foundation and opens several opportunities for future research. The context-dependent selectivity observed here underscores a gap in our understanding of gelada nutritional ecology. Future studies should combine phytochemical and proximate analyses of key forage species and seasonal roots to determine whether the preference shifts are driven by fluctuating protein content, specific mineral requirements, or changes in plant secondary metabolites. The persistent midday decline in feeding activity also warrants targeted investigation: combining fine-scale microclimatic data with physiological measures (e.g., body temperature, respiration rate) during resting periods would test whether this rhythm is strictly thermoregulatory or driven by other ecological constraints. Finally, although our two focal groups captured the dietary variability across the dominant habitat gradients of the area, comparing multiple social units across varying degrees of human disturbance will be essential to quantify the behavioral limits of the Southern Gelada's ecological plasticity.

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Appendix 1

Table A1. Dietary composition, edible parts, and mean frequency of occurrence of food items consumed by Southern Geladas.

Family	Scientific Name	Local name (Amharic)	Type	Edible part	Mean freq. (%)
Poaceae	*Festuca simensis*	Guassa/lisha	G	GB	19.52
Poaceae	*Festuca richardii*	Key sar	G	GB, GR	13.70
Fabaceae	*Trifolium acaule*	Chemekote	F	RT	8.56
Lamiaceae	*Thymus schimperi*	Tosign	F	LV	8.19
Aizoaceae	*Delosperma abyssinicum*	Yelam tut	F	HR	7.66
Campanulaceae	*Lobelia rhynchopetalum*	Jibera	F	YS, ST	6.71
Polygonaceae	*Rumex nepalensis*	Tult	F	LV, RT	5.32
Asteraceae	*Haplocarpha schimperi*	Getin	F	RH	5.15
Polygonaceae	*Rumex abyssinicus*	Mekmeko	F	HR, ST	4.17
Asphodelaceae	*Kniphofia foliosa*	Ashendye	F	RT, ST	4.09
Cypreae	*Cyperus bulbosus*	Yezenejoro kolo	G	GB	2.98
Poaceae	*Pennisetum mezianum*	Kirtan	G	GB, GR	2.82
Asteraceae	*Carduus schimperi*	Dendero	F	RT	1.96
Poaceae	*Festuca macrophylla*	Chima	G	GB	1.72
Lamiaceae	*Salvia tiliifolia*	Yezenjoro zekakibe	F	LV	1.56
Utricaceae	*Utica simensis*	Sama	F	RT	1.35
Scrophulariaceae	*Hebenstretia angolensis*	Wetet matebia	F	LV	0.99
Poaceae	*Festuca abyssinica*	Kundo chima	G	GB	0.98
Asteraceae	*Bidens macroptera*	Adey abeba	F	FL	0.71
Formicidae	*Pogonomyrmex barbatus*	Kunchach	I	I	0.62
Termitidae	*Macrotermes carbonarius*	Kiremt Agba	I	I	0.57
Asteraceae	*Senecio schultzii*	Koilo	F	LV	0.57
Lepidoptera	*Perigaea capensis*	Til	I	I	0.43
Asteraceae	*Echinops macrochaetus*	Kushele	F	FL	0.25
Asteraceae	*Helichrysum citrispinum*	Tonchi	F	FL	0.13

Grasses = G, Forbs = F, Insects = I, Grass Blades = GB, Grass Roots = GR, Forb Flowers = FL, Forb Fruits = FR, Forb Roots = RT, Forb Rhizomes = RH, Forb Leaves = LV, Forb Stems = ST, Forb Young Shoots = YS.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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Author contributions

Conceptualization: SE, ZG. Data curation: SE. Formal analysis: SE. Methodology: SE. Supervision: ZG. Validation: SE, ZG. Writing – original draft: SE, ZG. Writing – review and editing: ZG. Both authors approved the final version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.