

1

2 **Diet and activity patterns of Arsi geladas in low-elevation disturbed habitat**
3 **south of the Rift Valley at Indetu, Ethiopia**

4 **Kelil Abu¹, Addisu Mekonnen^{1,2}, Afework Bekele¹ and Peter J. Fashing^{2,3}**

5

6 ¹Department of Zoological Sciences, College of Natural Sciences, Addis Ababa University,
7 Addis Ababa, Ethiopia Email: rabiabudale@gmail.com Tel: +251910017179

8

9 ²Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University
10 of Oslo, P.O. Box 1066, Blindern, N-0316 Oslo, Norway Email:
11 addisumekonnen@gmail.com Tel: +4793987362

12

13 ³Department of Anthropology and Environmental Studies Program, California State
14 University Fullerton, Fullerton, CA 92834, USA

15

16

17

18

19 **Abstract** Understanding the basic natural history of threatened primate taxa is crucial to
20 developing and implementing successful conservation strategies for them. Data on feeding
21 ecology and activity patterns are particularly important for identifying the strategies through
22 which primates invest time and foraging effort towards survival and reproduction at a given
23 locale. Here, we report the results of the first study of the diet and activity budget of Arsi
24 geladas, a population of <1000 individuals endemic to a heavily disturbed region of the
25 southern Ethiopian Highlands and believed to represent a new taxon of geladas. We
26 conducted our research on a band of 34 individuals belonging to 5 one-male units at Indetu,
27 eastern Arsi, Ethiopia from August 2010 to May 2011 (excluding March 2011). Feeding
28 accounted for 41.7% of total scans, followed by moving (20.3%), resting (19.0%), and social
29 behavior (19.0%). Feeding and moving increased and resting and socializing decreased
30 during the dry season when food availability was probably lower than during the wet season.
31 Geladas ate mostly graminoid leaves (51.7% of feeding scans) though they also consumed
32 graminoid rhizomes (24.4%), forb tubers (7.1%), forb leaves (7.1%), cactus, shrub, and tree
33 fruits (3.6%), graminoid corms (1.7%), forb roots (1.6%), and unidentified items (3.0%).
34 Underground foods (corms, rhizomes, roots, and tubers) accounted for 22%-47% (mean =
35 35%) of the monthly (n=9) diet and were eaten slightly more during the wet season than
36 during the dry season. Contributions of human crops to the gelada diet could not be quantified
37 without creating conflict between farmers and researchers, though we did note that geladas
38 visited farms on 5-10% of study days. Threats from farmers, children, and dogs limited the
39 geladas' access to crops once they entered the farms. Further research involving
40 questionnaire surveys of farmers, direct observation of crop damage by geladas, and DNA

41 metabarcoding of gelada feces are crucial to the development of strategies to mitigate human-
42 gelada conflict in the densely populated Arsi Zone of Ethiopia.

43

44 **Keywords** Activity budget, anthropogenic disturbance, crop raiding, diet, Ethiopian
45 Highlands

46

47 **Introduction**

48

49 As primate habitats become increasingly fragmented by humans and their activities, the study
50 of isolated populations takes on increasing importance (Chapman et al. 2006; Irwin 2016).
51 Such studies are especially crucial when these isolated populations are taxonomically unique
52 (Oates et al. 2002; Fan et al. 2011). Understanding the basic natural history of all primate
53 taxa should be a fundamental goal of primatology, yet many of the rarest species and
54 subspecies remain largely unstudied (Rowe and Myers 2016). Data on the diet and activity
55 patterns of these little-known species are particularly important to understanding the
56 nutritional and energetic challenges they face, information that can contribute to the
57 development of more informed conservation strategies for them (Struhsaker 2010; Lambert
58 2011).

59 The country of Ethiopia is characterized by unusually high endemism, including for
60 primates (Yalden and Largen 1992). Despite facing high levels of habitat destruction and
61 degradation due to Ethiopia's rapidly growing human and livestock populations (Williams et
62 al. 2005), most of Ethiopia's unique primates remain little-studied. For example, two taxa,
63 Bale monkeys (*Chlorocebus djamdjamensis*) and Boutourlini's blue monkeys
64 (*Cercopithecus mitis boutourlini*), were only recently studied for the first time (Mekonnen et
65 al. 2010, 2012; Tesfaye et al. 2013). Of Ethiopia's endemic primates, only the gelada
66 (*Theropithecus gelada*) has been the subject of detailed research at multiple study sites (e.g.,
67 Dunbar and Dunbar 1975; Kawai 1979; Beehner and Bergman 2008; Nguyen et al. 2015).

68 Even among geladas, however, there is a rare, isolated, and little-studied population
69 known colloquially as the Arsi gelada, that represents the only gelada found south of the Rift
70 Valley. Recent genetic evidence suggests that Arsi geladas are different enough from their
71 northern counterparts (common and dusky geladas) to warrant their own taxonomic status
72 (Shotake et al. 2016) though it remains unresolved whether the different gelada clades
73 deserve subspecies (*T. gelada gelada*; *T. gelada obscurus*; Arsi gelada - proposed
74 nomenclature: *T. gelada arsi*: Shotake et al. 2016) or species status (C. Groves, pers. comm.),
75 an issue that requires further study. Though some details are known about its genetic
76 composition (Belay and Mori 2006; Shotake et al. 2016) and social structure (Mori et al.
77 1999, 2003), no studies of the Arsi gelada's basic natural history, including diet and activity
78 patterns, have been conducted. With fewer than 1000 individuals remaining and their
79 Afroalpine habitat experiencing intense disturbance (Belay and Shotake 1998; Abu 2011),
80 there is an urgent need for empirical data on their behavior and ecology, information that will
81 be useful to the development and implementation of a management plan for the Arsi gelada.

82 To address the paucity of knowledge about this taxon, we carried out the first study of
83 the diet and activity patterns of Arsi geladas. From August 2010-May 2011 (excluding
84 March), we studied a band of 34 individuals belonging to 5 one-male units at Indetu, a heavily
85 disturbed site in eastern Arsi. Here, we report our findings on the diet and activity patterns
86 of Arsi geladas and compare them with those from previous studies of *T. g. gelada* and *T. g.*
87 *obscurus* in northern and central Ethiopia, respectively. We also briefly discuss the
88 conservation implications of our results and suggest directions for further research on Arsi
89 geladas.

90

91 **Methods**

92

93 **Study site**

94

95 We carried out this study at Indetu (7°31'N, 39°60'E), an unprotected area experiencing
96 heavy usage by humans and their livestock, in Robe District, eastern Arsi, Ethiopia. Indetu
97 occurs at elevations ranging from 1180-2434 m asl and consists of ~30 km² of mixed
98 grassland, bushland, agricultural areas and forest near steep cliffs bisected by the Wabi River
99 (Mori et al. 1997; Abu 2011). Annual rainfall (~800 mm per year) at the nearest weather
100 station (50 km away at Robe) is only about half the amounts typical of gelada study sites
101 north of the Rift Valley (Hunter 2001; Fashing et al. 2014; Mekonnen et al. 2010; Abu 2011).
102 Rainfall in Arsi is seasonal with the wet season lasting from July-October (Abu 2011). The
103 short rainy season, low overall rainfall levels, and low elevation at Indetu result in there being
104 longer and more intense periods of drought and higher temperatures at Indetu (Abu 2011)
105 than at gelada study sites north of the Rift Valley (Hunter 2001; Fashing et al. 2014). Primates
106 present at Indetu include geladas (*Theropithecus gelada*), anubis baboons (*Papio anubis*),
107 hamadryas baboons (*Papio hamadryas*), and grivet monkeys (*Chlorocebus aethiops*).
108 Predators of geladas occurring at Indetu include leopards (*Panthera pardus*) and domestic
109 dogs (*Canis familiaris*) (Iwamoto et al. 1996; Mori et al. 1999; Abu 2011).

110

111 **Study animals**

112

113 We carried out our research on a gelada band of 34 individuals belonging to five one-male
114 units that often traveled together and shared a common home range (Abu 2011). Members of
115 the band were habituated to within 10 m of human observers. Several members of the study
116 band were easily identifiable by distinctive natural markings, coat colors, or facial features
117 though most members were not individually recognized. The study band occupied a W-
118 shaped valley with steep cliff faces descending to the east. During this study, they ranged at
119 elevations from 1800-2320 m asl (Abu 2011), at the low end of the elevational range for *T.*
120 *gelada* (1800-4400 m asl; Fashing and Nguyen 2016). Because of the challenging terrain and
121 tendency of geladas to spend much of their time on cliffsides at Indetu, many observations
122 had to be made through a telescope from near a cliff edge.

123

124 **Behavioral observation**

125

126 *Activity patterns*

127

128 Habituation of the study band was carried out for two months from June - July 2010. Over 9
129 of the next 10 months (August 2010 - May 2011, excluding March 2011), K.A. collected data
130 on activity budget and feeding ecology using instantaneous scan sampling (Altmann 1974)
131 at 15-minute intervals from 0700 to 1730 on an average of 10 consecutive days per month.
132 During each scan sample, the first activity that lasted for ≥ 3 seconds was recorded for up to
133 five adults, subadults or juveniles. Study animals were scanned consistently from left to right
134 to avoid biases towards eye-catching activities (Mekonnen et al 2010). Activities recorded
135 during scans consisted of 'feeding', 'moving', 'resting', or 'social'. Feeding was recorded

136 when a gelada manipulated or masticated a particular item of food. Moving was recorded
137 when a gelada changed its spatial position through locomotor behavior, including walking,
138 jumping or running. Resting was recorded when a gelada was inactive in a sitting or lying
139 position. Social was recorded when a gelada participated in grooming, play, sexual, or
140 agonistic behavior with another individual.

141 To calculate the proportion of time the study animals spent engaged in each activity, we
142 divided the number of records for each activity category by the total number of activity
143 records. We used the behavioral records of the group to calculate the activity budget for each
144 day and then averaged the daily values within each month to construct monthly activity
145 budgets. The grand mean proportions of the monthly budgets provided the overall activity
146 budgets for the entire study period (cf., Mekonnen et al. 2010).

147

148 *Feeding ecology*

149

150 During activity scan sampling, when an individual gelada was observed feeding, we recorded
151 the type of food item – graminoid leaves (i.e., grass or sedge blades), forb leaves, graminoid
152 corms, graminoid rhizomes, forb roots, forb tubers, fruits from cacti, shrubs, or trees, or
153 unidentified - as well as the species consumed, if possible. Voucher specimens of species
154 consumed were collected for later taxonomic identification by a botanist in the National
155 Herbarium, Addis Ababa University. However, it was not possible to collect and identify all
156 the graminoid and forb species consumed by geladas because of the difficult terrain and large
157 distances from which geladas were observed when they occupied cliff sides. Geladas at
158 Indetu also raided the crops of local people on 5-10% of study days but we were unable to

159 follow them onto the farms because farmers were upset about these incursions and, in some
160 cases, believed researchers were leading geladas to the farms. Therefore, data on the
161 contribution of crops to gelada diets - and gelada activity patterns - while on the farms are
162 not available for this study. However, we should note here that several previous studies of
163 geladas have also described gelada crop raiding while also proving unable to collect data on
164 percentage crop consumption to incorporate into their estimates of overall gelada diet (e.g.,
165 Dunbar 1977; Hunter 2001).

166 We evaluated the diet of geladas by calculating the proportion of different food items
167 consumed by the geladas. We summed the daily food items consumed by geladas within each
168 month to construct a monthly proportion of food items consumed. We summarized the
169 monthly proportion of each food item in the scans by dividing the total number of monthly
170 individual scans for each food item by the total number of individual scans for all food items.
171 We then used the grand means of the monthly proportions of food items consumed to
172 calculate the overall diets of geladas for the entire study period (cf., Mekonnen et al., 2010).

173

174 **Results**

175

176 **Activity budget**

177

178 A total of 6,152 individual activity records were obtained during 1521 scans conducted on
179 87 study days. In these scans, geladas spent 41.7% ($SD\pm 5.3\%$) of their time feeding, 20.3%
180 ($SD\pm 5.5\%$) moving, 19.0% ($SD\pm 3.3\%$) resting, and 19.0% ($SD\pm 7.4$) engaging in social
181 activities. Percentage of time devoted to feeding (9.0% increase in dry season), moving (4.3%

182 increase in dry season), and socializing (12.3% increase in wet season) all differed markedly
183 between seasons (Figure 2). However, percentage of time spent resting (0.9% increase in wet
184 season) was relatively invariable between seasons (Fig. 2).

185

186 **Feeding ecology**

187

188 *Diet Composition* During scans, graminoid leaves accounted for 51.7% (SD \pm 12.5%) of the
189 overall diet (n=2481 feeding records). Graminoid rhizomes made the second largest
190 contribution to the diet at 24.4% (SD \pm 5.7%). Geladas also consumed forb tubers 7.1% (SD
191 \pm 5.8%), forb leaves 7.1% (SD \pm 7.0), fruit from cacti 2.0% (SD \pm 3.8%), fruit from shrubs
192 and trees 1.6% (SD \pm 2.2%), graminoid corms 1.7% (SD \pm 3.3), forb roots 1.6% (SD \pm 3.3),
193 and unidentified items 2.7% (SD \pm 5.3%). Geladas were never observed eating animal matter.

194 Graminoid leaves were the top food item during all months contributing between 38.1-
195 71.4% of the monthly diet (Table 1). Graminoid rhizomes were also consumed during all
196 months (range 16.9-32.4%). Forb tubers (0.0-17.1%) and forb roots (0.0-5.9%) were each
197 eaten in all but one month, as were forb leaves (0.0-15.0%). When combined into a single
198 category, underground foods (corms, rhizomes, roots, and tubers) accounted for 21.6-46.6%
199 of the monthly diet (mean=34.8%). Graminoid leaf consumption peaked towards the end of
200 the wet season (October) and the months immediately following it (November-January).
201 Underground items were eaten slightly more during the wet season (37.8% \pm 4.6) than during
202 the dry season (33.3% \pm 10.0).

203 Geladas consumed a minimum of 12 plant species during the study period, though this
204 number is undoubtedly an underestimate. The graminoids and forbs consumed by geladas

205 often could not be identified confidently to species because of the challenges inherent in
206 identifying these taxa from a distance. Geladas clearly fed on at least two species of
207 graminoid, *Hyparrhenia hirta* and *Hyparrhenia* sp. (Poaceae), and three species of forbs,
208 *Dodonaea angustifolia* (Sapindaceae, forb), *Euclea racemosa* (Ebenaceae, forb), and
209 *Ipomoea hildebrandtii* (Convolvulaceae). In addition, they fed on three species of shrubs,
210 *Balanites aegyptica* (Balanitaceae), *Rhus glutinosa* (Anacardiaceae), and *Opuntia stricta*
211 (Cactaceae) - the latter a cactus (i.e., an exotic succulent) - as well as on two species of trees,
212 *Ficus vasta* (Moraceae), and *Olea europaea* (Oleaceae). Lastly, geladas also consumed two
213 human crops, barley (*Hordeum vulgare*) and wheat (*Triticum* sp.), during their visits to
214 nearby farms on 5-10% of study days. However, threats from farmers, children, and dogs
215 undoubtedly limited gelada foraging on these crops.

216

217

218 **Discussion**

219

220 Here, we report the results of the first ever study of the feeding ecology and activity budget
221 of Arsi geladas south of the Rift Valley. Based on our research at Indetu, we found that Arsi
222 geladas fed mostly, but not exclusively, on graminoid parts to meet their daily energy needs.
223 Underground items from graminoids and forbs were substantial contributors (22%-47%) to
224 the monthly diet throughout the study. Geladas at Indetu increased time spent feeding and
225 moving in the dry season, perhaps to cope with reduced availability of preferred foods during
226 this time. The low elevation and intensive anthropogenic disturbance make Indetu the most
227 marginal habitat in which geladas have been studied to date. Given the taxonomic uniqueness,

228 restricted range, and small population size of Arsi geladas as well as the anthropogenic threats
229 they face, this little-known monkey urgently requires more detailed study and the
230 development and implementation of empirically-based conservation strategies to improve its
231 chances of long-term survival.

232

233 *Activity budget*

234

235 Animals occupying high elevation habitats typically have elevated energy requirements
236 because of the thermoregulatory demands of cold climates (Kleiber 1961; Grow et al. 2014).
237 As a result, Iwamoto and Dunbar (1983) predicted that, among geladas, percentage of time
238 spent feeding should be correlated with elevation. They described the activity budgets from
239 three gelada study sites at elevations ranging from 2300 m asl (Bole) to 3300 m asl (Sankaber)
240 to 3900 m asl (Gich) which fit this pattern. Geladas at Gich devoted a remarkable 62% of
241 their time to feeding while those at Bole only spent 36% of their time feeding (Iwamoto and
242 Dunbar 1983). Here, we add comparative data from a fourth site, Indetu (1800-2320 m asl),
243 at the lower elevational limit for geladas (Table 2). Though still lower than at the high
244 elevation sites of Gich (62%) and Sankaber (45%), percentage time spent feeding was higher
245 at Indetu (42%) than at Bole (36%) with a concomitant reduction in percentage time spent
246 resting at Indetu (19%) relative to Bole (26%). Thus, while the general pattern described by
247 Iwamoto and Dunbar (1983) seems robust, we suggest that the unexpected activity budget
248 differences between Indetu and Bole may result from the extremely degraded nature of Indetu
249 where human and livestock activity have made it an especially marginal site for occupancy
250 by geladas.

251 Geladas at Indetu also exhibited striking seasonal differences in activity patterns.
252 Increases in time spent feeding (9.0% increase) and moving (4.3% increase) during the dry
253 season are probably related to the lower availability of food for geladas at that time of year.
254 Studies of geladas at other sites have found that food availability, particularly of green
255 graminoids, is driven by rainfall (Iwamoto 1979; Hunter 2001; Fashing et al. 2014). Not only
256 is rainfall also strongly seasonal at Indetu, but annual rainfall totals in the region are half
257 those typical for geladas at study sites north of the Rift Valley (Hunter 2001; Mekonnen et
258 al. 2010; Fashing et al. 2014). Thus, a few months into the dry season at Indetu, most
259 graminoids have already turned brown and water sources have become scarce (K. Abu, pers.
260 observ.), compelling geladas to increase time spent feeding and traveling. Substantial
261 increases in feeding time during the dry season have also been noted for geladas at the high
262 elevation sites of Sankaber and Gich (Dunbar 1977; Iwamoto 1979, 1993), suggesting this is
263 a pattern that holds for geladas across sites and subspecies. It is also known to occur in some
264 baboon (*Papio* spp.) populations, particularly those that experience long dry seasons (Dunbar
265 1992).

266

267 *Feeding ecology*

268

269 The diet of geladas at Indetu was consistent with those of geladas studied at most other sites
270 (Table 3). For example, graminoid parts accounted for an average of 80% of the diet at other
271 sites and 78% of the diet at Indetu, supporting the long-held notion that geladas are mostly
272 graminivorous wherever they occur (Crook and Aldrich-Blake 1968; Iwamoto 1993; Swedell
273 2011; Bergman and Beehner 2013; Fashing and Nguyen, 2016). Further, forb parts

274 contributed an average of 17% of the diet at other sites versus 16% of the diet at Indetu.
275 Invertebrates were never consumed at Indetu, consistent with reports from other sites, where
276 invertebrates consistently account for $\leq 0.1\%$ of the diet with one exception (2.8% of the diet
277 at the most ecologically intact site, Guassa: Fashing et al. 2010, 2014).

278 On the other hand, reliance on underground foods (from both graminoids and forbs) was
279 higher at Indetu (35% of the diet) than elsewhere, with only geladas at Sankaber relying on
280 underground items nearly as much (32%: Hunter 2001; 26% Dunbar 1977). Furthermore,
281 whereas geladas elsewhere mostly consumed underground items during the dry season when
282 above-ground biomass was lower (Iwamoto 1979; Hunter 2001; Fashing et al. 2014), geladas
283 at Indetu consumed underground items consistently over time (never less than 22% of the
284 monthly diet), even eating them slightly more during the wet season (mean=38%) than during
285 the dry season (mean=33%). This result is consistent with our suggestion that Indetu is a
286 marginal habitat for geladas, where they must resort to excavating underground items across
287 all seasons to survive. The low overall species richness (n=12) of the gelada diet at Indetu,
288 though likely an underestimate, is also suggestive of a limited array of potential food species
289 being available there.

290

291 *Conservation implications and recommendations for future research*

292

293 First discovered by scientists only three decades ago (Mori and Belay 1990) and identified
294 as genetically distinct from other geladas in 2016 (Shotake et al. 2016), Arsi geladas are
295 among the world's least known primates. Their extremely restricted distribution, small
296 remaining numbers (<1000 individuals), occurrence at the lower elevational limit for geladas,

297 and heavily anthropogenically-degraded habitat (Belay and Shotake 1998; Abu 2011;
298 Fashing and Nguyen 2016) may ultimately warrant listing them among the world's most
299 endangered primates (i.e., Schwitzer et al. 2015; IUCN 2017).

300 Future research that will be crucial to both filling a gap in our dietary study as well as to
301 the conservation of geladas involves quantifying levels and impacts of crop raiding by
302 geladas in Arsi. This research will require sustained efforts to gain the trust of local farmers,
303 questionnaire surveys of the farmers, and direct observation of crop damage by geladas (c.f.,
304 Yihune et al. 2009; Wallace and Hill 2012). The additional application of the more indirect
305 technique of conducting DNA metabarcoding analyses on feces (e.g., Kartzinell et al. 2015)
306 would also provide a thorough accounting of which crops are being eaten by geladas and in
307 what quantities. The issue of crop raiding at Indetu must be solved, not only to minimize the
308 potential for conflict between Arsi geladas and humans, but also because crop raiding by
309 local wildlife is a major factor driving human populations towards illegal resource
310 exploitation in natural environments (Harrison et al. 2015).

311

312 **Acknowledgements**

313

314 We thank Noel Rowe and Primate Conservation Incorporated, the Primate Action Fund of
315 Conservation International, Columbus Zoo and Aquarium, and the Mohamed bin Zayed
316 Species Conservation Fund for their financial support. In addition, we are grateful to Idea
317 Wild for donating equipment and to the World Association of Zoos and Aquariums (WAZA)
318 for branding this project. Peter Fashing thanks the U.S.-Norway Fulbright Foundation for
319 their support during the preparation of this manuscript. We also thank the Department of

320 Zoological Sciences of Addis Ababa University for logistical support. We are grateful to the
321 Ethiopian Wildlife Conservation Authority, Oromia Regional Forest and Wildlife Enterprise,
322 and District Agriculture Office for permission to conduct this research. We also thank Assefa
323 Hailu of the Natural Herbarium at Addis Ababa University for identification of plant
324 specimens. It would have been impossible to complete the fieldwork without the help of the
325 following field assistants, guides and camp attendants: Safi Ahimed, Abduraf Muhamed,
326 Abda Mama, Shamil Abda, Sada Safi, Ayub Ahimed, Sano Kabirhusen and Shekadir Gado.
327 Lastly, we thank John F. Oates and an anonymous reviewer for their helpful comments on
328 this manuscript and Colin P. Groves for sharing his insights into the complexities of gelada
329 taxonomy.

330

331 **References**

332

333 Abu, K (2011) Population census and ecology of a rare gelada population (*Theropithecus*
334 *gelada* unnamed subsp) in Indato, eastern Arsi, Ethiopia. MSc thesis, Addis Ababa
335 University

336 Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–
337 267

338 Beehner JC, Bergman, TJ (2008) Infant mortality following male takeovers in wild geladas.
339 Am J Primatol 70:1152-1159

340 Belay G, Shotake T (1998) Blood protein variation of a new population of gelada baboon
341 (*Theropithecus gelada*) in the southern Rift Valley, Arsi Region, Ethiopia. Primates
342 39:183–198

343 Belay G, Mori A (2006) Intraspecific phylogeographic mitochondrial DNA (D-loop)
344 variation of Gelada baboon, *Theropithecus gelada*, in Ethiopia. Biochem Syst Ecol
345 34:554–561

346 Bergman TJ, Beehner, JC (2013) *Theropithecus gelada*. In: Butynski TM, Kingdon J,
347 Kalina J (eds) Mammals of Africa: volume II Primates. Bloomsbury, London, pp
348 240-244

349 Chapman CA, Lawes MJ, Eeley HAC (2006) What hope for African primate diversity? Afr
350 J Ecol 44:116–133

351 Crook JH, Aldrich-Blake P (1968) Ecological and behavioural contrasts between sympatric
352 ground dwelling primates in Ethiopia. Folia Primatol 8:192-227

353 Dunbar RIM (1977) Feeding ecology of gelada baboons: a preliminary report. In: Clutton-
354 Brock TH (ed) Primate ecology: studies of feeding and ranging behavior in lemurs,
355 monkeys and apes. Academic Press, London, pp 251–273

356 Dunbar RIM (1992) Time: a hidden constraint on the behavioural ecology of baboons.
357 Behav Ecol Sociobiol 31:35-49

358 Dunbar RIM, Dunbar P (1974) Ecological relations and niche separate between sympatric
359 terrestrial primates in Ethiopia. Folia Primatol 21:36-60

360 Dunbar RIM, Dunbar P (1975) Social dynamics of gelada baboons. Karger, Basel

361 Fan PF, Fei HL, Scott MB, Zhang W, Ma CY (2011) Habitat and food choice of the
362 critically endangered cao vit gibbon (*Nomascus nasutus*) in China: implications for
363 conservation. Biol Conserv 144:2247–2254

364 Fashing, PJ, Nguyen (2016) *Theropithecus gelada*. In: Rowe N, Myers M (eds) All the
365 world's primates, Pogonias Press, Charlestown, RI, pp 447-449

366 Fashing PJ, Nguyen N, Fashing NJ (2010) Behavior of geladas and other endemic wildlife
367 during a desert locust outbreak at Guassa, Ethiopia: ecological and conservation
368 implications. Primates 51:193–197

369 Fashing PJ, Nguyen N, Kerby JT, Venkataraman VV (2014) Gelada feeding ecology in an
370 intact ecosystem at Guassa, Ethiopia: Variability over time and implications for
371 hominin and theropith dietary evolution. Am J Phys Anthropol 155:1-16

372 Grow NB, Gursky-Doyen S, Krzton A (2014) High altitude primates. Springer, New York

373 Harrison M, Baker J, Twinamatsiko M, Milner-Gulland EJ. (2015) Profiling unauthorized
374 natural resource users for better targeting of conservation interventions. Conserv Biol
375 29:1636-1646

376 Hunter CP (2001) Ecological determinants of gelada ranging patterns (*Theropithecus*
377 *gelada*). Dissertation, University of Liverpool

378 Irwin M (2016) Habitat change: loss, fragmentation, and degradation. In: Wich, SA,
379 Marshall AJ (eds). An introduction to primate conservation. Oxford University Press,
380 Oxford, pp 111-128

381 IUCN (2017) IUCN Red List of Threatened Species. Version 2017-1.
382 <www.iucnredlist.org>. Downloaded on 30 June 2017.

383 Iwamoto T, Mori A, Kawai M, Bekele A (1996) Anti-predator behavior of gelada baboons.
384 *Primates* 37:389–397

385 Iwamoto T (1993) The ecology of *Theropithecus gelada*. In: Jablonski, NG (ed) The rise
386 and fall of a primate genus. Cambridge University Press, Cambridge, pp 441–552

387 Iwamoto T, Dunbar RIM (1983) Thermoregulation, habitat quality and the behavioural
388 ecology in gelada baboons. *J Anim Ecol* 53:357–366

389 Iwamoto T (1979) Feeding ecology. In: Kawai (ed), Ecological and sociological studies of
390 gelada baboons. Karger, Basel, pp 279–330

391 Kartzinel TR, Chen PA, Coverdale TC, Erickson DL, Kress WJ, Kuzmina ML, Rubenstein
392 DI, Wang W, Pringle RM (2015) DNA metabarcoding illuminates dietary niche
393 partitioning between African large herbivores. *Proc Nat Acad Sci USA* 112:8019-
394 8024

395 Kleiber M (1961) The fire of life: An introduction to animal energetics. Wiley, New York

396 Lambert JA (2011) Primate nutritional ecology: Feeding biology and diet at ecological and
397 evolutionary scales. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK,

398 Stumpf (eds), *Primates in perspective*, 2nd edn. Oxford University Press, Oxford, pp
399 512-522

400 Mekonnen A, Bekele A, Fashing PJ, Lernould J, Atickem A, Stenseth NC (2012) Newly
401 discovered Bale monkey populations in forest fragments in southern Ethiopia:
402 Evidence of crop raiding, hybridization with grivets, and other conservation threats.
403 *Am J Primatol* 74:423–432

404 Mekonnen A, Bekele A, Fashing PJ, Hemson G, Atickem A (2010) Diet, activity patterns,
405 and ranging ecology of the Bale monkey (*Chlorocebus djamdjamentis*) in Odobullu
406 Forest, Ethiopia. *Int J Primatol* 31:339–362

407 Mori A, Belay G, Iwamoto T (2003) Changes in unit structures and infanticide observed in
408 Arsi geladas. *Primates* 44:217–223

409 Mori A, Iwamoto T, Bekele A (1997) A case of infanticide in a recently found population
410 in Arsi, Ethiopia. *Primates* 38:79-88

411 Mori A, Iwamoto T, Mori U, Bekele A (1999) Sociological and demographic
412 characteristics of a recently found Arsi gelada population in Ethiopia. *Primates*
413 40:365–381

414 Mori A, Belay G (1990) The distribution of baboon species and a new population of Gelada
415 baboons along the Wabi-Shebeli River, Ethiopia. *Primates* 31:495–508

416 Nguyen N, Fashing PJ, Boyd DA, Barry TS, Burke RJ, Goodale, CB, Jones, SCZ, Kerby
417 JT, Kellogg BS, Lee LM, Miller CM, Nurmi NO, Ramsay MS, Reynolds JD, Stewart
418 KM, Turner TJ, Venkataraman VV, Knauf Y, Roos C, Knauf S. (2015). Fitness
419 impacts of tapeworm parasitism on wild gelada monkeys at Guassa, Ethiopia. *Am J*
420 *Primatol* 77:579-594.

421 Oates JF, McFarland KL, Groves JL, Bergl RA, Linder JM, Disotell TR (2002) The Cross
422 River gorilla: natural history of a neglected and critically endangered subspecies. In:
423 Taylor AB, Goldsmith ML (eds). Gorilla biology: A multidisciplinary perspective.
424 Cambridge University Press, Cambridge, pp 472-497

425 Rowe N, Myers M (2016) All the world's primates. Pogonias Press, Charlestown, RI

426 Schwitzer C, Mittermeier RA, Rylands AB, Chiozza F, Williamson EA, Wallis J, Cotton A.
427 (2015) Primates in peril: the world's 25 most endangered primates 2014–2016. IUCN
428 SSC Primate Specialist Group, International Primatological Society, Conservation
429 International, Bristol Zoological Society, Arlington, VA

430 Shotake T, Saijuntha W, Agatsuma T, Kawamoto Y (2016) Genetic diversity within and
431 among gelada (*Theropithecus gelada*) populations based on mitochondrial DNA
432 analysis. *Anthropol Sci* 124:157-167

433 Struhsaker TT (2010) The red colobus monkeys: variation in demography, behavior, and
434 ecology of endangered species. Oxford University Press, Oxford

435 Swedell L. 2011. African papionins: diversity of social organization and ecological
436 flexibility. In: Campbell CJ, Fuentes A, Mackinnon KC, Bearder SK, Stumpf RM
437 (eds) *Primates in perspective*, 2nd edn. Oxford University Press, New York, pp 241-
438 277

439 Tesfaye D, Fashing PJ, Bekele A, Mekonnen A, Atickem A (2013) Ecological flexibility in
440 Boutourlini's blue monkeys (*Cercopithecus mitis boutourlinii*) in Jibat Forest,
441 Ethiopia: A comparison of habitat use, ranging behavior, and diet in intact and
442 fragmented forest. *Int J Primatol* 34:615-640

- 443 Wallace GE, Hill CM (2012) Crop damage by primates: quantifying the key parameters of
444 crop-raiding events. PLoS ONE 7:e46636
- 445 Williams S, Pol JLV, Spawls S, Shimelis A, and Kelbessa E. 2005. Ethiopian Highlands.
446 In: Mittermeier RA, Gil PR, Hoffman M, Pilgrim J, Brooks T, Goettsch Mittermeier
447 C, Lamoreux J, da Fonseca GAB, (eds) Hotspots revisited: Earth's biologically richest
448 and most endangered terrestrial ecoregions. Conservation International, Washington,
449 pp 262-273.
- 450 Yalden DW, Largen MJ (1992) The endemic mammals of Ethiopia. Mammal Rev 22:115–
451 150
- 452 Yihune M, Bekele A, Tefera Z (2008) Human–gelada baboon conflict in and around the
453 Simien Mountains National Park, Ethiopia. Afr J Ecol 47:276–282
- 454

455 **Figure Legends**

456

457 **Fig. 1** The locations of *Theropithecus gelada* study sites across the Ethiopian Highlands,
458 including our site, Indetu, where the rare Arsi gelada is found.

459 **Fig. 2** Comparison of the activity budgets of Arsi geladas during the dry season and the wet
460 season at Indetu, Ethiopia.

461

462

463

464

465

466

467

468

469

470

471

472

473

474 **Table 1** Monthly variation in percentage contribution of different food items to the diet of
 475 geladas at Indetu

Months	% of diet							
	Graminoid leaves	Graminoid rhizomes	Graminoid corms	Forb leaves	Forb roots	Forb tubers	Fruit	Unidentified
Aug	39.1	16.9	0.8	1.5	1.5	15.0	12.0	13.2
Sept	38.1	32.4	0.0	0.4	0.0	10.6	7.8	10.7
Oct	63.2	23.7	0.0	0.0	0.5	12.2	0.0	0.5
Nov	71.4	25.5	0.0	0.5	0.8	1.3	0.5	0.0
Dec	65.2	17.8	0.0	8.1	1.2	2.8	4.9	0.0
Jan	56.1	19.3	0.0	13.2	0.5	4.7	6.1	0.0
Feb	44.6	26.5	0.0	7.4	5.9	14.2	1.5	0.0
Apr	40.8	25.2	9.5	18.4	2.7	3.4	0.0	0.0
May	46.8	32.2	4.7	14.6	1.8	0.0	0.0	0.0
Mean	51.7	24.4	1.7	7.1	1.6	7.1	3.6	2.7

476

477

478 **Table 2** Activity budgets of geladas at different study sites across Ethiopia

Subspecies	Study site	Elevation (m)	Activity budget (%)					Reference
			F	M	R	S	O	
Arsi gelada	Indetu	2060	41.7	20.3	19.0	19.0	0.0	This study
<i>T. g. gelada</i>	Bole	2300	35.7	17.4	26.3	18.5	2.1	Iwamoto and Dunbar 1983
<i>T. g. gelada</i>	Sankaber	3250	45.2	20.4	13.8	20.5	0.0	Iwamoto and Dunbar 1983
<i>T. g. gelada</i>	Gich	3900	62.3	14.7	5.2	16.0	1.8	Iwamoto and Dunbar 1983

479 *F* feeding and foraging, *M* moving, *R* resting; *S* socializing *O* other

480

481 **Table 3** Comparison of gelada diets across study sites in Ethiopia

Subspecies	Site	Elevation (m)	Study length (month)	% of diet									# of species	Reference
				GLV	GUG	GS	FLV	FUG	FLO	FR	IN	OT		
<i>Arsi gelada</i>	Indetu, Arsi	2060	9 ^a	51.7	26.1	0.0	7.1	8.7	0.0	3.6	0.0	3.0	≥10	This study
<i>T. g. obscurus</i>	Bole, Debre Libanos	2300	6 ^b	91.4	0.5	5.0	0.3	0.0	0.3	2.0	0.0	0.5	≥14	Dunbar and Dunbar (1974)
<i>T. g. gelada</i>	Sankaber, Simien Mts.	3300	6 ^c	55.2	11.9	1.8	5.6	20.5	0.6	3.3	0.1	1.1	---	Hunter (2001)
<i>T. g. gelada</i>	Sankaber, Simien Mts.	3300	5 ^d	45.0	24.5	23.2	1.4	1.4	1.1	1.0	0.1	2.3	---	Dunbar (1977)
<i>T. g. obscurus</i>	Guassa, Menz	3450	15 ^e	50.6	4.0	2.2	28.7	7.5	0.4	0.0	2.8	3.8	≥78 ^g	Fashing et al. (2014)
<i>T. g. gelada</i>	Gich, Simien Mts.	3900	3 ^f	68.8	8.0	5.1	15.7	2.5	0.0	0.0	0.0	0.0	≥35 ^h	Iwamoto (1979, 1993)

482 *GLV* Graminoid leaves, *GUG* Graminoid under-ground, *GS* Graminoid seeds, *FLV* Forb leaves, *FUG* Forb under-ground, *FLO* Flowers, *FR* Fruit, *IN*

483 Invertebrates, *OT* Other

484 ^a study conducted over 10-month period (Aug10-May11) though no data were collected in Mar10

485 ^b mean diet from 82 hours of observation during 3 non-contiguous periods of 1-3 months

486 ^c mean diet from 3 wet season and 3 dry season months

487 ^d mean diet from 3 several day to two-week periods during 5 months

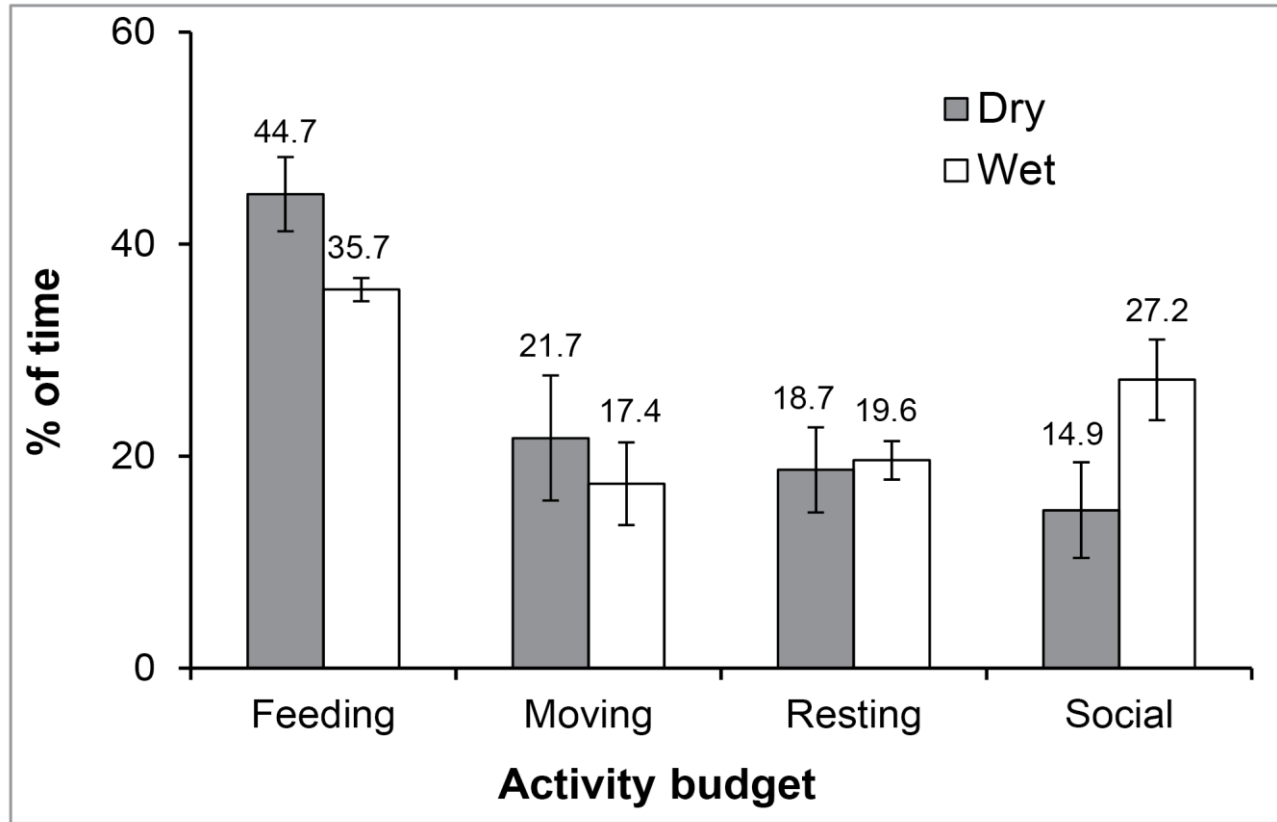
488 ^e study conducted over 15 contiguous months (Feb07-Apr08), though values here represent the mean of the 4 possible annual diets (Feb 07 - Jan 08, Mar
489 07 - Feb 08, Apr 07 - Mar 08, May 07 - Apr 08)

490 ^f mean diet from 3 non-contiguous months (1 wet season and 2 dry season months)

491 ^g dietary species richness data collected over a 7-year period, ^h dietary species richness data collected over an 8-month period

492

493



494

