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DIET AND FEEDING BEHAVIOUR OF GELADAS (*THEROPITHECUS GELADA*) AT THE GICH AREA OF THE SIMIEN MOUNTAINS NATIONAL PARK, ETHIOPIA

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ABSTRACT

The diet and feeding behaviour of geladas was studied at the Gich area of the Simien Mountains National Park from May 2013 to April 2014. The area is cold and wet, which is dominated by Afroalpine grasses and the endemic giant *Lobelia rhynchopetalum*. Data were collected during ten consecutive days each month for a year using continuous focal animal scan sampling method. Geladas fed on 27 different species of plants during the course of the study. The number of food plant species varied markedly between seasons, with dietary diversity being significantly more during the dry season. Grass blades formed a major dietary constituent throughout the year, contributing more than 78% of the feeding records.

Key words: food items, gelada, Gich, SMNP

INTRODUCTION

Theropithecus gelada is a primate species, which is endemic to the central and northwestern highlands of Ethiopia and is the only extant species of the genus *Theropithecus* (Dunbar, 1998). The geographical range of the species is narrowly restricted to the high-elevation montane grasslands of the country (Mori and Belay, 1990).

Geladas are almost entirely terrestrial quadrupeds (Fleagle, 1999) and have specialized morphological adaptations for feeding and moving on the ground (Dunbar, 1986; Krentz, 1993). They are the only known highly graminivorous primates, with grass forming the majority of the diet in most habitats (Dunbar and Dunbar, 1974; Dunbar, 1977).

Geladas feed by sitting upright, plucking grasses and other food items by hand. Their hands are characterized by a relatively long thumb, which is an adaptation for foraging grass leaves and seeds (Fleagle, 1999; Hunter, 2001). Although geladas primarily feed on grass blades, they seasonally consume fruit, seeds, roots, flowers and rarely on insects (Dunbar, 1978; Iwamoto, 1993).

Gelada habitats are characterized as wet and cool, but they may differ in geographic features, vegetation composition and climatic conditions (Hunter, 2001). The habitats are relatively rich in terms of food resource availability. At higher elevation, such as the Gich plateau, grasslands stay green for a longer period of time due to high rainfall and low temperature (Iwamoto and Dunbar, 1983; Puff and Nemomissa, 2005). This condition provides geladas with a better digestibility of grasses for a greater time span during the year. However, at very high altitude, grass protein content declines, which makes it hard for them to meet the nutritional requirements (Dunbar, 1998). Similarly, geladas face difficulty to cope with grasses at lower elevations, because the digestibility of grasses is too low (Demment and van Soest, 1985).

The objective of the study is to conduct the first detailed investigation on the diet and feeding behaviour of geladas at the Gich area of the Simien Mountains National Park (SMNP). We specifically aimed to: (1) examine the degree of flexibility in the feeding strategy of geladas by analyzing variations in diet between months, (2) examine if diet composition changes significantly between seasons and (3) elucidate how aspects of the spatio-temporal availability of food resources affect gelada feeding behaviour.

MATERIALS AND METHODS

Study Area

The SMNP is located in the North Gondar Zone of the Amhara National Regional State, Ethiopia. It is known for its high biodiversity and natural scenic beauty (Puff and Nemomissa, 2005). The National Park covers a surface area of approximately 412 km^2 of the Simien Mountains watershed (Gebremedhin *et al.*, 2009). It has become a World Heritage Site in 1978 (Julia, 2005), but was inscribed on the List of World Heritage in Danger in 1996 as a result of population decline in the highly endangered endemic walia ibex (*Capra ibex walie*) and habitat destruction (Falch and Keiner, 2000). The field study on which this research is based was conducted on the Gich plateau of the SMNP (Fig. 1). Gich consisted of an open plateau and is characterized as cold and wet (Iwamoto and Dunbar, 1983). The study area is dominated mainly by Afroalpine grasses and the endemic giant *Lobelia rhynchopetalum*.

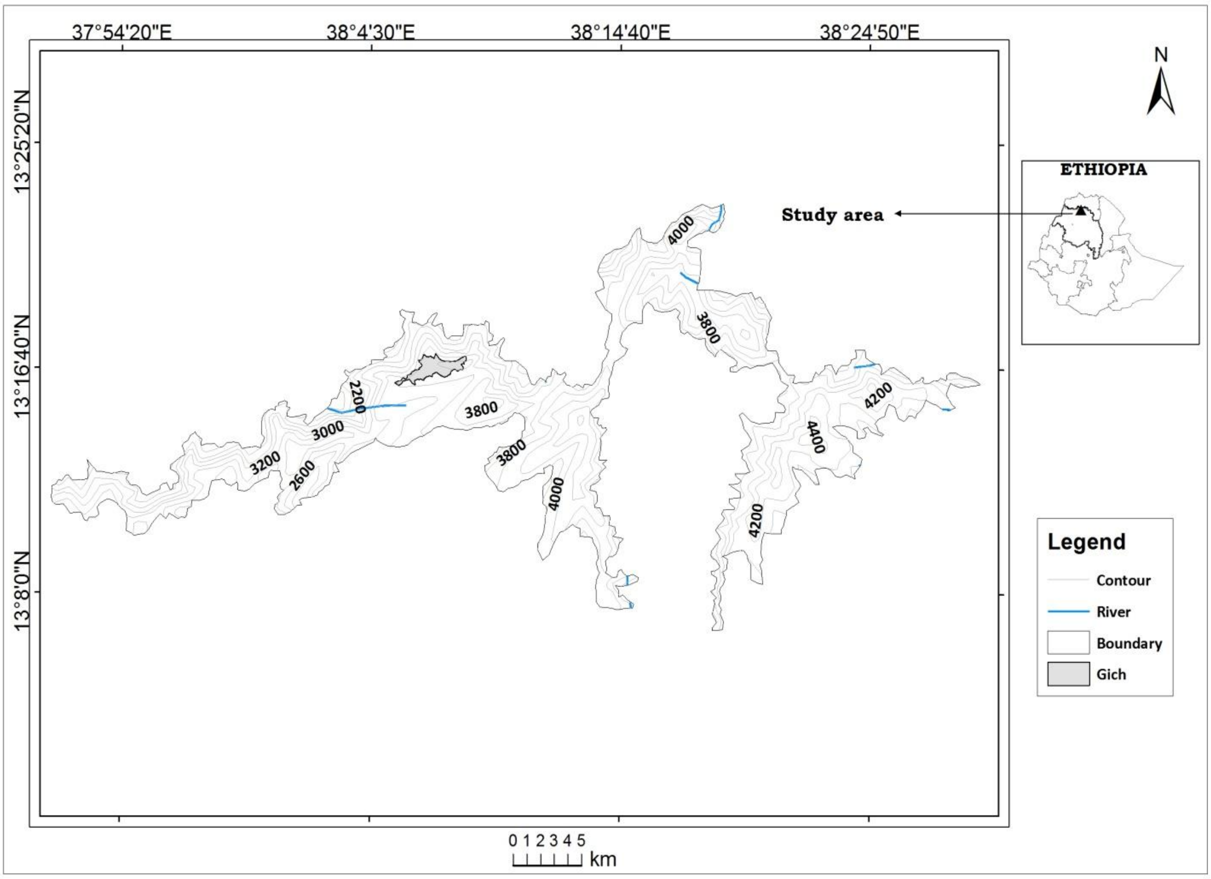

Figure 1. Map of the Simien Mountains National Park showing the study site

Methods

Four social bands of gelada inhabited various portions of Gich. The band that ranged into the major area of the plateau was the primary focus of the study. The band varied in size from 183 animals at the start of the study to 205 by the end, due to the birth of individuals. We began habituating members of the focal band to the presence of observers in April 2013. Geladas could be followed at a distance of <10 m and many individuals were easily identifiable based on natural markings.

Data were collected using continuous focal animal scan sampling method (Altmann, 1974) during ten consecutive days each month (from May 2013 through April 2014). Individual gelada was made the focus of dawn-to-dusk follows, from 7:00 a.m. to 18:00 p.m. Data were recorded for different age/sex classes, which were selected opportunistically. Age/sex classes were assigned to each individual based on physical size and development characteristics (Kawai *et al*., 1983). Feeding activity of focal individuals was recorded at 30 one-minute sequential scans following Hunter (2001). If contact with a focal animal was lost, the data collection process continued with another individual of the same age/sex class. Different species of plants on which geladas foraged were recorded, collected and identified. Plants that were not easily identified in the field were collected and preserved as specimens for identification in the National Herbarium of Addis Ababa University.

ANALYSIS OF DATA

All statistical analysis was performed using SPSS statistical software (version 16.0) for windows. Prior to statistical analysis, all data were assessed to determine whether they were normally distributed. Where data did not follow a normal distribution, non-parametric tests were employed. All statistical tests are 2-tailed with a level of rejection set at p=0.05, although if trends are apparent in the data, precise p values may be listed.

RESULTS

During the course of the study, geladas foraged at least on 27 different species of plants, which belonged to 10 families. However, they concentrated heavily on a subset of this number. Food plants included at least 2 species of grasses, 21 species of herbs and 4 species of shrubs (Table 1). Only 6 species individually comprised more than 1% of the overall annual diet. The most frequently consumed plant species were *Festuca* spp., which accounted for 78.9 ± SD 10.2% (monthly range=62.6-91.1%) of the diet. *Merendera abyssinica* ranked second and *Lobelia rhynchopetalum* ranked third, accounting for 6.6 ± SD 5.6% (monthly range=0.9-18.3%) and 2.9 ± SD 4.8% (monthly range=2.0-13.1%) of the diet, respectively. Six plant species comprised more than 93% of the diet and 10 species comprised more than 96%.

Table 1. The proportions of the diet made up by each plant species during the study period

Family	Plant species	Habit	Items eaten	Percentage
Poaceae	*Festuca* spp.	Grass	L, S, R	78.9
Colchiaceae	*Merendera abyssinica*	Herb	C	6.6
Lobeliaceae	*Lobelia rhynchopetalum*	Herb	B, L	2.9
Rosaceae	*Alchemilla pedata*	Herb	L	1.8
Rosaceae	*Alchemilla abyssinica*	Herb	L	1.5
Crassulaceae	*Rosularia simiensis*	Herb	L	1.5
Lamiaceae	*Thymus schimperi*	Herb	R	1.0
Asteraceae	*Carduus schimperi*	Herb	F	1.0
Asteraceae	*Haplocarpha schimperi*	Herb	L, R	0.9
Asteraceae	*Dianthoseris schimperi*	Herb	S	0.8
Asteraceae	*Bidens macroptera*	Herb	L	0.05
Asteraceae	*Bidens pachyloma*	Herb	L	0.1
Asteraceae	*Bidens carinata*	Herb	L	0.1
Rubiaceae	*Galium simense*	Herb	L	0.3
Asteraceae	*Launaea rueppelii*	Herb	L	0.2
Apiaceae	*Pimpinella pimpinelloides*	Herb	L	0.1
Asteraceae	*Helichrysum citrispinum*	Shrub	F	0.1
Asteraceae	*Carduus macracanthus*	Herb	L	0.1
Asteraceae	*Carduus nyassanus*	Herb	F, L	0.1
Asphodelaceae	*Kniphofia foliosa*	Herb	F, N, P	0.05
Asphodelaceae	*Kniphofia uvaria*	Herb	L	0.1
Crassulaceae	*Aeonium leucoblepharum*	Shrub	L	0.05
Ericaceae	*Erica aerbora*	Shrub	P	0.04
Malvaceae	*Malva verticillata*	Herb	L	0.03
Ranunculaceae	*Ranunculus multifidus*	Herb	L	0.05
Asteraceae	*Sonchus oleraceus*	Herb	L	0.05
Rosaceae	*Rubus apetalus*	Shrub	L	0.04

Item key: B=Bud, C=Corm, F=Flower, L=Leaf, N=Nectar, R=Root, P=Pith, S=Stem

The inclusion of the 10 plant species that contributed more than 0.5% to the annual feeding budget was variable on a monthly basis (Table 2). Of the three most frequently consumed plant species, *Festuca* spp. contributed at least 62% to the feeding records each month. *Merendera abyssinica* made up at least 1.6% of the feeding records during 10 months. During August, the peak of the wet season, *Festuca* spp. contributed more than 90% to the feeding records. This is a significantly higher percentage than any other plant species' contribution to any month's feeding records. Some of the species were not consistently providing edible plant parts throughout the year and their inclusion in the diet on a month-by-month basis was highly variable. Only *Festuca* spp., *Merendera abyssinica* and *Lobelia rhynchopetalum* were consumed during every month of the study period. One-way ANOVA demonstrated that there were significant differences between months in the number of species used ($F_{[2,32]}=0.06$, $p<0.05$).

Table 2. Contribution (%) of top 10 plant species to monthly feeding records

Plant species	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Festuca spp.	86.8	91.1	87.5	90.2	84.9	80.4	62.6	63.0	66.6	76.1	76.8	80.3
Merendera abyssinica	5.7	0.9	0.9	1.6	1.8	8.5	16.3	16.0	8.9	5.7	5.6	7.0
Lobelia rhynchopetalum	1.9	1.1	1.4	0.6	2.2	2.5	3.4	4.6	3.3	4.3	3.7	2.0
Alchemilla pedata	0.0	0.0	0.0	0.0	0.0	2.1	3.7	3.2	2.9	4.1	3.0	2.1
Alchemilla abyssinica	0.0	0.0	0.0	0.0	0.0	0.0	2.8	2.4	2.9	3.6	2.8	2.9
Rosularia simiensis	0.0	0.0	0.0	0.0	0.1	0.8	2.7	2.2	3.5	3.0	3.2	2.8
Thymus schimperi	0.0	0.0	0.0	0.0	0.0	0.8	1.5	0.4	2.9	1.3	1.8	3.0
Carduus schimperi	2.0	2.9	2.2	1.0	2.2	1.4	0.0	0.0	0.0	0.0	0.0	0.0
Haplocarpha schimperi	0.0	0.0	0.0	0.0	0.0	0.0	2.6	2.1	2.1	0.8	1.3	2.0
Dianthoseris schimperi	0.0	0.0	0.0	0.0	0.0	1.3	1.3	2.1	2.1	0.7	1.6	1.1

0.0=Species not consumed

When diets are considered in terms of the types of food that were utilized, there is an overall preference primarily for leaves (mostly of grasses) monthly and annually (Table 3). Grass blades accounted for 74.3 ± SD 12.9% (range=54-90%, n=12 mo) of the annual diet of geladas at Gich. Subterranean items were the second most dominant food, which contributed to 18.3 ± SD 11.6% (range=3.5-36.5%) of the overall diet. Herb leaves made the third largest contribution to the diet at 2.8 ± SD 1.8% (range=0.7-6.3%) of the diet. When subterranean food items are analyzed separately, grass roots made the largest contribution to the underground diet at 7.6 ± SD 4.7% (range=0.9-15.5%). Corms/bulbs made the second largest contribution to the subterranean diet at 6.7 ± SD 5.6% (range=1.1-18.3%). Herb roots accounted for 3.9 ± SD 2.9% (range=1-12%) of the diet. Geladas also consumed other food items, which made a very small contribution to the annual diet: flowers, 2.4 ± SD 2.2% (range=0-5%) and seeds, 0.6 ± SD 1.0% (range=0-3%).

Table 3. Monthly and annual diets as the percentage of feeding records spent on each food type

Month	Grass leaves	Grass roots*	Herb leaves	Herb roots*	Corms/ bulbs*	Seeds	Flowers	Others	(# records)
May	84.8	3.8	1.6	2.0	5.7	0.0	0.0	1.8	1,602
Jun	90.0	2.2	1.1	1.1	0.9	0.0	3.9	0.6	1,381
Jul	85.5	4.0	0.9	2.0	1.1	0.0	5.1	1.3	1,505
Aug	89.2	0.9	0.7	1.0	1.6	0.0	5.1	1.4	1,337
Sep	81.9	5.6	1.3	2.2	1.8	0.8	5.4	0.8	1,569
Oct	72.7	5.3	1.4	4.4	8.1	3.3	2.6	1.9	1,079
Nov	57.3	9.5	3.6	4.0	18.3	1.3	4.2	1.4	1,518
Dec	55.7	12.3	4.5	5.6	16.0	1.7	2.1	1.3	1,445
Jan	54.1	15.7	6.3	12.1	8.9	0.4	0.7	1.9	1,487
Feb	71.8	13.4	2.8	4.3	5.7	0.0	0.1	1.6	1,774
Mar	71.9	11.3	4.7	5.0	5.6	0.0	0.0	1.5	1,667
Apr	76.5	7.2	4.1	3.8	7.0	0.0	0.0	1.1	1,874
Mean	74.3	7.6	2.8	3.9	6.7	0.6	2.4	1.4	1,519.8

*=Subterranean food items

Animal prey was much less important sources of food, which accounted for less than 0.05% of the foraging time. It appeared that geladas do not usually plan for capturing them. However, on few occasions, they were seen turning herbivore dung over or scattering dried *Lobelia rhynchopetalum* bark around in search of insects, whilst feeding on plant food items.

There were significant differences in the average consumption of each food type between the wet and dry seasons. The proportion of the consumption of different food types by the geladas varied with season, except for herb roots and seeds as shown in Table 4. The diet depended mainly on the availability of plant types, with some plants clearly being preferred over others.

Table 4. Seasonal contribution of different food types to the diet

Food type	Wet season (%)	Dry season (%)	$F_{[1,58]}$	*P*
Grass leaves	84.0	64.5	17.900	0.001
Grass roots	3.6	11.6	5.162	0.027
Herbs	1.2	4.3	25.639	0.001
Herb roots	2.1	5.8	2.753	0.102
Corms/bulbs	3.2	10.3	9.523	0.003
Seeds	0.7	0.6	1.354	0.249
Flowers	3.7	1.2	11.700	0.001
Others	1.3	1.5	10.830	0.002

The mean monthly Shannon-Wiener' index for plant species diversity for the annual diet was 0.45 ± SD 0.1 (range=0.26-0.67, n=12 mo; Table 5). Dietary diversity was high during December and January and low in May. In general, the diet of gelada was relatively diverse and showed variation over the study period. However, the mean monthly dietary evenness index (*J*) was low at 0.67 ± SD 0.2, ranging from 0.39 in May to 0.83 in November. Gelada used a mean of 12 ± SD 3.0 plant species per month as sources of food (range=7-15 species, n=12 mo).

Table 5. Monthly food plant species diversity and evenness indices during the study period

Month	Diversity index, *H´*	Evenness index, *J*
May	0.26	0.39
Jun	0.44	0.67
Jul	0.40	0.61
Aug	0.37	0.55
Sep	0.52	0.78
Oct	0.41	0.61
Nov	0.56	0.84
Dec	0.67	0.81
Jan	0.54	0.83
Feb	0.52	0.78
Mar	0.33	0.50
Apr	0.37	0.55
Mean	0.45 ± SD 0.1	0.67 ± SD 0.2

Spearman's rank correlations demonstrated that across months, the consumption of grass leaves decreased as the consumption of grass roots, herbs, herb roots and corms/bulbs increased and these relationships were statistically significant (Table 6). However, there was a significantly positive correlation between the consumption of grass roots and herbs. Similarly, there were positive correlations between the consumption of grass roots and herb roots, and between herbs and herb roots. There was not significant correlation between the consumption of other food types.

Table 6. Spearman's rank correlations for different food types

Food type		Grass roots	Herbs	Herb roots	Corms/bulbs
Grass leaves	r_s	-0.433	-0.584	-0.306	-0.742
	p	0.001	0.001	0.017	0.001
Grass roots	r_s		0.289	0.271	0.233
	p		0.025	0.036	0.073
Herbs	r_s			0.289	0.215
	p			0.025	0.099
Herb roots	r_s				0.099
	p				0.452

DISCUSSION

Geladas are unique among the primates due to their high degree of specialization for a graminivorous diet (Dunbar and Bose, 1991; Mau *et al*., 2009). They have long been regarded as obligate graminivores (Dunbar and Dunbar, 1974; Dunbar, 1977; Iwamoto, 1993). In the present study, the overall diet of the geladas was highly dominated by grasses, with other food types, such as underground items, accounting for a considerable proportion to the diet. Geladas possess a number of behavioural and morphological adaptations, which enable them to utilize their specialized ecological niche (Crook, 1966; Jolly, 1972). Geladas at Gich exhibit higher degree of graminivory than what was previously reported in other habitats (e.g., Sankaber area: Hunter, 2001; Iwamoto and Dunbar, 1983; Guassa area: Fashing *et al.,* 2014). Further evidence for geladas' high degree of dietary specialization for grasses comes from the less-diverse nature of their diet, which comprised about 27 plant species from 10 families over the course of study. The study has shown that geladas feed on a relatively large spectrum of plant species, but a few correspond to the majority of the overall diet. For instance, the top 5 plant species alone accounted for more than 91% of the annual diet. Out of the top 5 species, grasses of *Festuca* spp. were the most dominant food plants contributing to more than 78% of the overall diet, the majority of it in the form of leaves. Iwamoto (1979) suggests that geladas appear to eat almost all the poaceae species available to them. Grasses were consumed over the entire period of the study, but different parts were eaten disproportionately in different seasons. For example, grass seeds and roots were foraged more during the dry season than in the wet season, while blades were eaten throughout the year.

Geladas prefer to dig for roots and rhizomes when the grasses become dessicated and therefore less-digestible during the dry season (Braun, 1973; Iwamoto and Dunbar, 1983; Hunter, 2001). Other primates similarly respond to seasonal variations in food availability by shifting their diet (Hunter, 2001). In comparison to other gelada habitats (e.g., Sankaber area: Iwamoto and Dunbar, 1983; Hunter, 2001; Guassa area: Fashing *et al.,* 2014), the contribution of underground food to geladas' annual diet at Gich was significantly less. The small contribution of underground items to the diet may be due to an overall low availability of these food types in the study area. In general, geladas that live in different areas exhibit some differences in their feeding habits. For instance, the diet of gelada living in southern Ethiopia includes considerable amounts of fruits, which have rarely been used as food component by geladas in the study area (Iwamoto and Dunbar, 1983; Iwamoto, 1993; this study).

Geladas have shown seasonal variation in their foraging strategy, which is reflected by the increased time they spent feeding during a period of food scarcity during the dry season (Crook, 1966; Hunter, 2001). Changes in the foraging strategy of gelada were associated with seasonal variations in food availability. Similarly, some primates modify their foraging strategy in response to seasonal variations in the availability, relative abundance and distribution of food (Barton *et al.,* 1992; Hill, 1999). In temperate grasslands, such as the Afroalpine habitat of gelada at Gich, food resource availability fluctuates over time (Alberts *et al.,* 2005).

Braun (1973) stated that the digestibility of grass is reduced by half when it stops growing and dessicates during the dry season. At high-elevation gelada habitats, ambient temperatures are generally low (Iwamoto and Dunbar, 1983), and grasses dessicate less quickly and are more digestible for a longer time span (Dunbar and Bose, 1991). Furthermore, high amount of annual precipitation maintains the greenness of grasses for a longer period of the year. This may be one of the reasons why grasses contributed to more than half of the diet even at the height of the dry season. The result of this study gives support to previous studies that have shown gelada to feed preferably more on grasses than other food types so long as they remain green (Dunbar, 1977, 1978).

Hill and Dunbar (2002) suggest that some primates have remarkable abilities to modify their foraging behaviour and diet in response to the prevailing ecological conditions. Geladas have similar ability to change their foraging behaviour in response to variations in the availability of food. Seasonal patterns in their diet have shown that when preferable food types were less abundant during the dry season, diet choice becomes less selective and geladas broaden the diet by including less-desirable food items. For instance, geladas significantly consumed underground food as the habitat-wide availability of green grass decreased during the dry season. On the other hand, when desirable food types become abundant (e.g., green grass blades) geladas were more selective in food choice and diet tended to be narrow. Previous studies have shown a noticeable change in gelada diet as the preferred green grass leaves desiccate during the dry season (Crook, 1966; Dunbar, 1977; Iwamoto, 1979). Hughes (1993) suggests that diet choice in animals reflects the types of food that are most accessible in the habitat and can give maximum energy. Changes in foraging patterns and diet in gelada were directly associated with seasonal variations in resource availability. However, foraging behaviour is rarely influenced by one factor alone (e.g., Iwamoto and Dunbar, 1983), but is responsive to changing environmental and ecological factors, such as rainfall and temperature (Brownikowski and Altmann, 1996).

Animal prey was much less important source of food, which accounted for less than 0.05% of the overall diet. Similarly, geladas feed rarely on invertebrates in other habitats (Iwamoto and Dunbar, 1983; Iwamoto, 1993; Hunter, 2001, but see Fashing *et al.*, 2014). The reason for the apparently very small contribution of invertebrates to the diet may be due to low abundance of the animal prey in the study area and/or the less efficiency of geladas in finding or capturing them.

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