ORIGINAL ARTICLE



Feeding ecology of a highland population of hamadryas baboons (*Papio hamadryas*) at Borena-Sayint National Park, northern Ethiopia

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Abstract

Studying the diet and feeding behavior of primates is essential to understanding their ecology and designing effective conservation plans. Despite decades of study on the hamadryas baboon (*Papio hamadryas*) in lowland habitats, little is known about the feeding ecology of this species in highland ecosystems. To address this empirical gap, we tracked temporal changes in vegetation abundance and their relation to the dietary choices of hamadryas baboons in highland habitat at Borena-Sayint National Park (BSNP) in northern Ethiopia. We performed behavioral scan sampling on a focal study band of 21-37 hamadryas baboons over a 12-month period. We found that mature and young leaves were the most abundant plant parts throughout the year, while fruits and flowers were the least abundant, with significant seasonal variation that followed the bimodal pattern of rainfall characteristic of the Ethiopian highlands ecosystem. The annual diet of hamadryas baboons at BSNP consisted mostly of fruits (32.0%) and graminoid blades (21.2%), and included 52 food species across 22 families of plants and three families of animals. Food raided from nearby farms accounted for 8.8% of their diet. The availability of fruits and flowers was positively correlated with their consumption, suggesting that these are preferred foods, whereas graminoid blades, and other leaves, appeared to be less preferred foods. The feeding ecology of hamadryas baboons at BSNP differs considerably from that of lowland populations. The well-studied lowland hamadryas baboons in Awash National Park obtain much of their diet from Acacia species and palm fruit, whereas those at BSNP, where Acacia trees are rare and palms are absent, relied on Olinia rochetiana and Rosa abyssinica for a combined 27% of their annual diet. The reliance of hamadryas baboons at BSNP on cultivated crops for nearly one-tenth of their diet leads to conflict with humans and warrants more detailed study so that this issue can be addressed in conservation plans for the area.

Keywords Conflict · Conservation · Cultivated crops · Diet · Hamadryas baboon · Phenology

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Introduction

Primatologists have long been interested in how diet varies with spatiotemporal differences in food availability (Oates 1977, 1987; Kaplin and Moermond 2000; Lambert and Rothman 2015; Tesfaye et al. 2021). This line of inquiry provides insight into the preferred foods of primates as well as the foods they fall back on during times of scarcity (Marshall et al. 2009; Hanya and Chapman 2013). Primate diets often differ across space and time, with the same species sometimes having very dissimilar diets at different locations (Richard 1974; Gathua 2000; Chapman et al. 2002; Mekonnen et al. 2018). Species occurring across a wide elevational gradient can differ in diet because of variation in the foods available at different elevations. For example, Colobus angolensis in montane forest at Nyungwe National Park, Rwanda rely heavily on lichens, particularly as fallback foods (Miller et al. 2020), while conspecifics in low elevation habitats do not eat lichens, but are instead largely dependent on leaves (Dunham 2017) or seeds (Maisels et al. 1994). There are also instances where altitudinal variation influences the availability of food resources and dietary composition for primate species, including Macaca fuscata in Japan (Hanya et al. 2003), Macaca mulatta and Rhinopithecus bieti in China (Grueter et al. 2012; Zhang et al. 2022), Mandrillus leucophaeus in Equatorial Guinea (Owens et al. 2015), and Papio ursinus in South Africa (Byrne et al. 1993).

The hamadryas baboon (*Papio hamadryas*) is one of five species in the genus *Papio* and occurs mainly in the lowland habitats of the Horn of Africa, including parts of Ethiopia, Eritrea and the southwestern part of the Arabian Peninsula (Biquand et al. 1992; Al-Safadi 1994; Groves 2005; Kingdon 2015). Hamadryas baboons usually reside in arid and semi-desert areas, though they also sometimes occur in moist lowlands, including in closed canopy forests and woodlands (Kummer 1968; Zinner et al. 2001; Swedell 2013). Several populations occupy or utilize moist highland areas as well (Hunter 2001; Ibrahim 2019). Thus, though mostly known from long-term studies in arid regions (Kummer 1968; Swedell 2013), hamadryas baboons actually occur across a wide elevational gradient.

Hamadryas baboons are considered generalist omnivores and their multi-level social organization is thought to reflect low food availability and high levels of aridity within their habitats (Kummer 1968; Dunbar 1988; Swedell 2002; Henzi and Barrett 2003; Swedell et al. 2008). Hamadryas baboons rely mainly on the flowers, seeds, leaves and fresh shoots from *Acacia* (Fabaceae) trees as well as a wide array of semi-desert plants such as *Grewia* spp. (Malvaceae), *Dobera glabra* (Salvadoraceae) and *Hyphaene thebaica* (Arecaceae) (doum palm) (Kummer 1968; Nagel 1973; Al-Safadi 1994; Swedell et al. 2008; Schreier 2010; Admassu 2012). Studies suggest that fruits and flowers are preferred foods in lowland habitats of Ethiopia (Swedell et al. 2008; Schreier 2010). Like other baboons, they also feed opportunistically on invertebrates and small mammals such as hares (*Lepus* spp.) (Swedell 2013). Some hamadryas baboons also supplement their diet with human foods, via direct provisioning (Boug et al. 2017), or by consuming refuse from garbage dumps (Swedell 2013). Additionally, hamadryas baboons are known to occasionally raid crops and are considered pests in some areas (Nagel 1973; Admassu 2012; Abdela 2019).

Though the hamadryas baboon is classified as Least Concern in the International Union for Conservation of Nature (IUCN) Red List, the species is locally threatened as a result of the expansion of agricultural land and human settlements, as well as hunting in response to crop raiding and small domestic animal depredation (Admassu 2012; Gippoliti 2019). Unfortunately, the dietary requirements of hamadryas baboons have only been studied in a small proportion of the habitats where they occur, making it difficult to critically assess any dietary issues impacting the conservation prospects of the species across its range in Ethiopia and more widely across its distribution into Eritrea and the Arabian Peninsula (Swedell 2013). For example, although the feeding ecology of hamadryas baboons has been studied extensively in dry lowland habitat at Awash National Park (~900 m above sea level) in eastern Ethiopia (Swedell et al. 2008; Schreier 2010; Admassu 2012), little is known about hamadryas baboon populations residing in highland ecosystems.

In this study, we aimed to assess the feeding ecology of hamadryas baboons in and around Borena-Sayint National Park (BSNP) in the highlands of northern Ethiopia. Given the higher plant species diversity and composition in BSNP compared to the arid lowland ecosystem at Awash National Park (Friis et al. 2010; Adal 2014), we hypothesized that the diet of hamadryas baboons at BSNP would be more diverse and that the profile of its constituent plant species and plant parts would differ to that reported for hamadryas baboons at Awash National Park. In addition, due to the strong seasonality of rainfall in the Ethiopian highland ecosystem, we predicted seasonal differences in the consumption of the major food plant species and food items. By analyzing the consumption of food types in relation to their abundance, we also aimed to identify the preferred and fallback foods of hamadryas baboons at BSNP (Marshall and Wrangham 2007; Marshall et al. 2009). Given the proximity of BSNP to farms, we also anticipated hamadryas baboons there would engage in crop raiding and sought to quantify the percentage contribution of crops to their diet.



Fig. 1 Map of the study site, Borena-Sayint National Park (BSNP), northern Ethiopia

Methods

Description of the study area

BSNP is located in the South Wollo Zone of Amhara Regional State, northern Ethiopia, and covers an area of 4375 ha (10°50′45.4″–10°53′58.3″, 38°40′28.4″–38°54′49″; Fig. 1). Established as a National Park in 2009, BSNP is bordered by three districts: Borena and Sayint to the north and Mehal Sayint to the east. The study area is characterized by rough topography, including gorges, deeply incised valleys, steep escarpments, and strips of plateaus and cliffs (Ayalew et al. 2006) across a wide altitudinal range (2188–3732 m above sea level). BSNP is part of the Eastern Afromontane biodiversity hotspot, which is characterized by remarkable species richness and endemism, but also a high human population density (Williams et al. 2005; Fashing et al. 2022).

BSNP extends across two broad, agro-climatic zones known as Weina dega (cool, sub-humid) and Dega (cold, cold humid), as classified based on ambient heat intensity and moisture regimes (Adal 2014). Temperature and rainfall data (1998-2018) for the study area were obtained from Mekaneselam Meteorological Station (NMSA 2019), located 16 km from the National Park. The study area is characterized by a distinctive bimodal rainfall pattern, usually with a short rainy season from April to May and a main wet season from June to September (Ibrahim 2019). The average amount of rainfall per annum was 917 ± 39.78 mm $(\pm$ SD; range 655–1165 mm). The mean annual temperature was 16.7 ± 1.05 °C. The mean monthly minimum temperature ranged from 10.1 ± 0.85 (November) to 12.4 ± 1.74 °C (May), while the mean monthly maximum temperature ranged from 17.9 ± 0.67 (August) to 24.8 ± 0.79 °C (February) (Fig. 2).



Fig. 2 Mean monthly temperature [mean, mean minimum (*Min.*) and mean maximum (*Max.*)] and rainfall patterns at Mekaneselam town, 16 km southeast of BSNP, northern Ethiopia, 1998–2018

The study area consists of large areas of both natural forest and high altitude grassland, both containing rich floral and faunal communities (Adal 2014). The floristic composition of BSNP consists of 354 plant species belonging to 265 genera and 95 families, and includes trees, shrubs, graminoids and forbs (Adal 2014). In addition to the high diversity of plant species, BSNP also harbors many animal species. In particular, 23 species of medium- to large-sized mammals have been identified and recorded at BSNP, including the following nonhuman primates: hamadryas baboons, geladas, guerezas, and grivet monkeys (Chane 2010). BSNP is surrounded by human settlements and agrarian landscapes with little or no buffer zone (H. Ibrahim, personal observation).

Study subjects

From January to May 2016, we habituated a band of hamadryas baboons for study by following them from dawn, when they left their sleeping site, to dusk, when they returned to their sleeping site. Band size was small for the species (Kummer 1968; Schreier and Swedell 2012) and fluctuated between 21 and 37 individuals. Within the band, from four to seven individuals were adult males, from six to 15 were adult females and 11 to 15 were immatures. We identified the study band by individual members that had unique natural markings, coat color, or other identifiable features. During daily travel, the band sometimes separated into smaller foraging groups (i.e., one-male units with at least five individuals) (Kummer 1968; Swedell et al. 2008). On such occasions, we typically followed the subgrouping with the largest number of individuals. During our study, the study band ranged across elevations of 2341-3016 m (Ibrahim 2019).

Vegetation and food availability

Vegetation composition

We examined the vegetation composition of the study area by sampling plots/vegetation quadrats in the home range of the study band (e.g., Mekonnen et al. 2018; Tesfaye et al. 2021). Since deeply incised gorges and sharp cliffs posed obstacles to performing long transects, we employed a combination of stratified and systematic random sampling to select study plots. In particular, we sampled a total of 29 (20×20 m) vegetation quadrats in the range of the study band. Once we established the first sampling plot randomly, we laid subsequent independent sampling plots sideways ~ 0.5 km apart on a baseline projected along the long axis of the home range of the study band. We selected representative sampling plots on the basis of homogeneity of vegetation and visually checked for uniformity in floristic composition (Adal 2014).

In each quadrat, we counted trees ≥ 10 cm diameter at breast height (DBH) and measured and identified them to species (Swedell et al. 2008; Schreier 2010; Boug et al. 2017). Within these quadrats, we recorded all sampled plants, including the species and number of individuals. In addition, within each of the quadrats, we randomly placed one 5×5-m and one 1×1-m quadrat to quantify the available shrubs and forbs/graminoids, respectively. Considering the overall uniformity of the ground layer, we only placed and sampled one 1×1-m subplot in each nested plot where the vegetation appeared representative (Adal 2014). We collected, pressed, and dried unidentified plant species using a plant press. These samples were later identified to species level by professional botanists at the National Herbarium, Addis Ababa University.

Phenology

We carried out phenological assessment of the trees in the home range of our hamadryas baboon study band to evaluate monthly changes in the availability of potential food resources (Mekonnen et al. 2018; Tesfaye et al. 2021). We collected phenological data on plant parts from ten randomly selected trees per species on a monthly basis. We chose and marked only trees ≥ 10 cm DBH for this monthly phenological monitoring (Mekonnen et al. 2018). We measured girth at breast height as circumference (in centimeters at a height of 1.3-1.4 m) and later converted this value to DBH using the standard conversion formula $DBH = circumference/\pi$. We collected phenological data for seven tree species frequently consumed by the study species during the habituation period: Olinia rochetiana (Oliniaceae), Dombeya torrida (Sterculiaceae), Olea europaea subsp. cuspidata (Oleaceae), Myrica salicifolia (Myricaceae), *Nuxia congesta* (Loganiaceae), *Scolopia theifolia* (Flacourtiaceae) and *Myrsine melanophloeos* (Myrsinaceae).

We inspected the availability of food items from the marked trees monthly for 1 or 2 days after completing the behavioral ecology data collection. We assessed each marked tree for the relative abundance score of potential food resources (mature leaves, young leaves, flowers, and fruits) by visual inspection and using binoculars, with a relative abundance score ranging from 0 to 8 at intervals of 1. A score of 0 corresponds to a complete absence of that plant part, and a score of 8 corresponds to the plant part comprising > 87.5% of the crown (Twinomugisha and Chapman 2008; Mekonnen et al. 2018). We calculated the proportion of monitored trees bearing each of the phenophases every month for each study species. We calculated the monthly and seasonal variability in the availability of the different potential food resources as in Mekonnen et al. (2017).

We also monitored the phenology of common and/ or dietarily important species of graminoids and forbs every month from the randomly selected permanent plots (each 1×1 m) in the home range area of the study band throughout the study period (Fashing et al. 2014; Jarvey et al. 2018). We monitored a total of 35 plots to assess the percentage of greenness and desiccation of graminoids and forbs. We selected and tagged these graminoid and forb plots at random. Depending upon their temporal changes in greenness, we assigned each plot a score of 0-3 at intervals of 1, where 0 (0%) indicates no graminoids or forbs in a plot, 1 (1-25%) indicates graminoids and forbs in plots that are entirely brown, 2 (26-50%) indicates graminoids and forbs in plots that are mixed green and brown), and 3 (> 50%) indicates graminoids and forbs in plots that are mostly or entirely green, using visual inspection (Moges 2018).

Feeding ecology

For 8 consecutive days per month from June 2016 to May 2017, we used the instantaneous scan sampling method (Altmann 1974) at 30-min intervals for up to 5-min duration (0600–1830 hours) to record the activities of hamadryas baboons. Activities were categorized as feeding, moving, resting, socializing and others (Ibrahim 2019). We recorded feeding when the baboons manipulated, masticated, or ingested a food item (food handling and processing) (Schreier 2010). During activity scans, when the baboons were feeding, we recorded the type of food item (as graminoids, roots, fruits, leaves, flowers, stem, bark, animal prey or unidentified items) and species consumed (Swedell et al. 2008; Schreier 2010). We identified and recorded most of the plant species consumed by hamadryas baboons in the field. However, for plant species that we were unable to identify, we recorded their local name (where possible), pressed them and transported them to the National Herbarium for taxonomic identification. We collected a total of 5293 individual behavioral records during 837 h of observation (Ibrahim 2019). Feeding accounted for 1807 (or 34.1%) of these records.

Data analyses

Vegetation composition and phenology

From the data collected on vegetation composition, we calculated the density of each plant species as the total number of individuals of each plant species divided by the total number of all plant species sampled per hectare in the home range of the study band (Mekonnen et al. 2010). We calculated plant species diversity in the home range of the study band using the Shannon-Wiener diversity index (H') and evenness using the evenness index (J) (Krebs 1999) to determine whether or not the dietary species were evenly distributed in the study band's home range. We calculated the basal area (BA) of each tree species to estimate the biomass of each tree within the home range of the hamadryas baboon band and to determine dominant tree species in the home range (Fashing 2001; Felton et al. 2008). BA for each tree was calculated from the measured DBH value using the following formula: $BA = [0.5 \times DBH]^2 \times \pi \text{ (Fashing 2001).}$

We obtained food availability index (FAI) (units per hectare) for young leaves, mature leaves, flowers and fruits from the monthly average phenology scores and the basal area per hectare value for trees in the vegetation sampling plots (Dasilva 1994). We computed FAI using the following formula: FAI*i* = PISp*i* × BA*i*, where FAI*i* is the FAI of species *i*, PISp*i* is the monthly phenological index for species *i*, and BA*i* is the basal area (cm²/ha) of species *i* obtained by using the vegetation survey data (Fashing 2001). The monthly total FAI for each phenophase was calculated by adding FAI*i* indices across plant food species (Fashing 2001).

We also assessed the level of greenness of graminoids and forbs in each month to determine phenology and availability of graminoid blades and forb leaves in the home range of the study band, and to estimate the availability of graminoid blades and forb leaves in each area. We calculated the proportion of greenness score of each month in each site by dividing the number of each plots assigned to a particular score by the total number of plots and then multiplying by 100.

Feeding ecology

The number of individuals we spotted in each scan was limited by the movement of the band amidst rough topography (mean 3.14, range 1–5). We divided the number of individuals feeding on a particular food item for each scan by the total number of individuals observed in the scan to prevent the overrepresentation of highly visible foods (Hanya and Bernard 2012). Using the proportion of the total number of records of feeding spent on each diet category, we determined the contribution of each food item and species to total diet. We summed the daily food item consumption within each month to obtain the monthly proportion of diet item composition. We then calculated mean seasonal and overall dietary composition by averaging the monthly percentages (Mekonnen et al. 2018; Kifle and Bekele 2021). To estimate the overall plant species richness of the diet, we pooled the data from all sampling months within the band. We calculated within-month and overall dietary diversity indices for the study band using H' and J (Krebs 1999) using the software PAST (Hammer et al. 2009).

We measured dietary selection ratio (relative dietary preferences) for different food species in the study band's diet by dividing the annual percentage of time spent feeding on species *i* by the percentage stem density that species *i* contributed to the total stem density in the study band's home range (Tesfaye et al. 2021). We could not include forbs and graminoids in this analysis given that they lack a comparably quantifiable stem density. A selected food species is consumed more frequently than expected based on its proportion in the home range of the study band. A selection ratio of 1 indicates no selectivity for that food plant species by baboons, <1 indicates a food species that is selected for.

Statistical analyses

We mainly analyzed the data using SPSS 23.0 Software for Windows evaluation version. We used two-tailed statistical tests with 95% confidence intervals (the significance level was set at 0.05). We assumed that each of the observations was independent. We tested the data for normality using the Shapiro–Wilk test, and tested homogeneity of variances using the Levene test (P > 0.05). We compared phenological and feeding ecology data among seasons and months using statistical tests such as *t*-tests, one-way ANOVA, the Mann–Whitney *U*-test or Kruskal–Wallis *H*-test. Following ANOVA, we used the post hoc Tukey test to determine the difference between pairwise comparisons of overall food consumption. In addition, we computed Pearson rank correlation coefficients to determine the relationship between the availability of young leaves, mature leaves, flowers and fruits and their consumption.

Results

Vegetation composition and phenology

Our analysis of vegetation composition in the home range of the hamadryas baboon study band revealed a total of 18 tree, 27 shrub, 43 forb, nine graminoid, three liana and one fern species (Table S1). The stem densities for the tree, shrub and liana species and basal areas of tree species sampled in the home range of the study band are provided in Table S2. Plant species taller than 2 m in the home range of the study band occurred at a density of 610 stems/ha. The H' of plant species in the home range of the study band was 2.94 and the plant species J was 0.85. The mean number of plant species per hectare was 27.59. Mature leaves were the most abundant plant parts and were available in large quantities throughout the year, followed by young leaves (Table S3). However, a Pearson rank test revealed that there was no significant correlation in the FAI between young leaf and mature leaf availability ($r_{\rm p} = 0.52, P > 0.05$).

Flowers and fruits were the least abundant plant parts (Table S3). Flowers were most abundant from November 2016 to January 2017, and higher availability scores for fruits were recorded from June to September 2016. The Kruskal–Wallis *H*-test revealed that there was a statistically significant difference (P < 0.001) across months in the FAI scores of young leaves, mature leaves, flowers and fruits. Seasonal food item availability scores showed that young leaves (Z = -2.24, P < 0.05), mature leaves and fruits (Z = -2.25, P < 0.05) were more abundant during the wet season than the dry season (Fig. 3). On the other hand, FAI for flowers was significantly higher during the dry season than the wet season (Z = -2.25, P < 0.05). Green graminoid/ forb availability peaked from April to October (Table S4).



In the study plots, percentage of green graminoids/forbs was higher during the wet season than the dry season (Fig. 4).

Feeding ecology

Overall, we observed hamadryas baboons consume a total of 52 food species (including cultivated crops) from 22 families of plants and three families of animals (Table 1). The 49 plant species that were eaten included 12 species of trees, 13 species of shrubs, 14 species of graminoids and ten species of forbs (Table 1). Hamadryas baboons included in their diet five cultivated plants, wheat (Triticum spp.), maize (Zea mays), barley (Hordeum vulgare), sellalie (Avena abyssinica), and potatoes (Solanum tuberosum), from farmlands, which cumulatively accounted for 8.8% of their annual diet (Table 1). Hamadryas baboons were also observed to consume lichens by scraping them from the surface of rocks. Fruits comprised the largest proportion (32.0%) of food items consumed by hamadryas baboons, followed by graminoid blades (21.2%), young leaves (13.2%) and cereals (8.8%) (Fig. 5).

Other, less frequently consumed food items included flowers, forb leaves, stems, mature leaves, animal prey, graminoid roots, forb roots, bark and vegetables (Fig. 5). The proportion of time devoted to feeding on these food items differed significantly (Kruskal Wallis *H*-test, $\gamma^2 = 97.51$, df = 12, P < 0.05). Follow-up post hoc tests of pairwise comparisons indicated significant differences between the consumption of fruits and cereals (P = 0.025), flowers (P = 0.006), and forb leaves (P = 0.005); and between graminoid blades and forb leaves (P=0.004) and cereals (P=0.02). However, there were no significant differences in the consumption of fruits compared with young leaves (P=0.176), graminoid blades (P=0.934), and forb leaves (P=0.417). In addition, the availability of fruits was not correlated with the consumption of graminoid blades (r = -0.028, n = 12, P = 0.931), young leaves (r = -0.473, P = 0.931)n=12, P=0.121), forb leaves (r=-0.241, n=12, P=0.45),



Fig. 3 Seasonal food availability index (*FAI*) values of food items in the home range of the study band (FAI units/ha) at BSNP, northern Ethiopia, June 2016–May 2017

Fig. 4 Percentage of graminoids/forbs phenology during the wet and dry seasons at BSNP, northern Ethiopia, June 2016–May 2017

| Scientific name | Vernacular name (Amharic) | Family | Category | Food item (%) | Frequency (%) |
|-----------------------------------|---------------------------|----------------|---------------|--|---------------|
| Olinia rochetiana | Tife | Oliniaceae | Tree | FL (0.15), FR (13.07), ML (0.37), YL (1.41) | 15.00 |
| Rosa abyssinica | Kega | Rosaceae | Shrub | FL (1.78), FR (10.59), YL (0.06) | 12.43 |
| Andropogon abyssinicus | Balamie | Poaceae | Graminoids | FL (0.04), GB (8.60), GR (0.75) | 9.39 |
| Unidentified species ^a | Fura | | Graminoids | GB (8.87), GR (0.09) | 8.96 |
| Triticum spp. ^b | Sinde | Poaceae | Graminoids | CER (5.09) | 5.09 |
| Acanthus sennii | Shekori | Acanthaceae | Shrub | B (0.03), FL (1.09), ML (0.31), S (1.92), YL (1.39) | 4.74 |
| Discopodium penninervium | Ameraro | Solanaceae | Shrub | B (0.55), FR (0.25), ML (0.9), S (0.72), YL (2.1) | 4.52 |
| Rubus steudneri | Gurarba | Rosaceae | Shrub | FL (0.07), FR (4.15), ML (0.29) | 4.51 |
| Dombeya torrida | Wulkefa | Sterculiaceae | Tree | FL (1.44), ML (0.40), YL (1.89) | 3.73 |
| Zea mays ^b | Bekolo | Poaceae | Graminoids | CER (3.1) | 3.10 |
| Haplocarpha schimperi | Getn | Asteraceae | Forbs | HL (2.82), HR (0.25) | 3.07 |
| Scolopia theifolia | Wanaye | Flacourtiaceae | Tree | FR (1.87), YL (0.03) | 1.90 |
| Rumex nervosus | Embuacho | Polygonaceae | Shrub | FL (0.15), ML (0.29), S (0.62), YL (0.58) | 1.64 |
| Nuxia congesta | Askuar | Loganiaceae | Tree | FL (0.16), ML (0.38), YL (1.03) | 1.57 |
| Ant | Chichuan | Formicidae | Invertebrates | AP (1.51) | 1.51 |
| Andropogon distachyos | Gaja | Poaceae | Graminoids | FL (0.04), GB (0.49), GR (0.83), S (0.04) | 1.40 |
| Trifolium polystachyum | Maget | Fabaceae | Forbs | HL (1.20), HR (0.11) | 1.31 |
| Cynodon aethiopicus | Serdo | Poaceae | Graminoids | GB (1.22), GR (0.07) | 1.29 |
| Cyperus sesquiflorus | Gicha | Cyperaceae | Graminoids | GB (1.29) | 1.29 |
| Urera hypselodendron | Lakuso | Urticaceae | Shrub | ML (0.2), YL (1.07) | 1.27 |
| Bidens prestinaria | Adey abeba | Asteraceae | Forbs | FL (0.76), HL (0.27), HR (0.08) | 1.11 |
| Ficus sur | Shola | Moraceae | Tree | FR (0.88) | 0.88 |
| Acacia decurrens | Dikerens | Fabaceae | Tree | ML (0.23), YL (0.63) | 0.86 |
| Vernonia myriantha | Buyte | Asteraceae | Shrub | FR (0.10), ML (0.26), YL (0.46) | 0.82 |
| Olea europaea subsp. cuspidate | Woira | Oleaceae | Tree | FR (0.56), ML (0.10), YL (0.13) | 0.79 |
| Maesa lanceolata | Akelaho | Myrsinaceae | Shrub | FL (0.32), FR (0.18), ML (0.04), YL (0.21) | 0.75 |
| Cyperus fischerianus | Gramta | Cyperaceae | Graminoids | GB (0.73) | 0.73 |
| Hordeum vulgare ^b | Gebs | Poaceae | Graminoids | CER (0.58) | 0.58 |
| Solanum dennekense | Emburi | Solanaceae | Shrub | S (0.52) | 0.52 |
| Dovyalis abyssinica | Koshim | Flacourtiaceae | Shrub | FR (0.51) | 0.51 |
| Phaulopsis imbricata | Derg | Acanthaceae | Forbs | HL (0.51) | 0.51 |
| Myrica salicifolia | Shinet | Myricaceae | Tree | B (0.03), FL (0.03), ML (0.14), YL (0.25) | 0.45 |
| Commelina benghalensis | Lalinch | Commelinaceae | Forbs | HL (0.42) | 0.42 |
| Myrsine melanophloeos | Gewra | Myrsinaceae | Tree | ML (0.10), YL (0.3) | 0.40 |
| Trifolium semipilosum | Chemekot | Fabaceae | Forbs | HL (0.4) | 0.40 |
| Arisaema schimperanum | Amoch | Araceae | Forbs | HR (04) | 0.40 |
| Hypericum revolutum | Amja | Hypericaceae | Shrub | FL (0.27), YL (0.13) | 0.40 |

Table 1Food species included in the diet of our study band of hamadryas baboons at Borena-Sayint National Park (BSNP), northern Ethiopia,June 2016–May 2017

Table 1 (continued)

| Scientific name | Vernacular name (Amharic) | Family | Category | Food item (%) | Frequency (%) |
|--------------------------------|---------------------------|--------------|-------------|----------------------|---------------|
| Prunus africana | Anje | Rosaceae | Tree | FR (0.37), ML (0.03) | 0.38 |
| Kalanchoe petitiana | Endawula | Crassulaceae | Forbs | S (0.23) | 0.23 |
| Carex bequaertii | Filla | Cyperaceae | Graminoids | GB (0.22) | 0.22 |
| Rumex abyssinicus | Mokmoko | Polygonaceae | Forbs | S (0.18) | 0.18 |
| Tragelaphus scriptus | Dekula | Bovidae | Vertebrates | AP (0.17) | 0.17 |
| Apodytes dimidiata | Dong | Icacinaceae | Tree | YL (0.16) | 0.16 |
| Schefflera abyssinica | Getem | Araliaceae | Tree | FR (0.13) | 0.13 |
| Laggera tomentosa | Alashume | Asteraceae | Shrub | YL (0.11) | 0.11 |
| Eleusine floccifolia | Akrma | Poaceae | Graminoids | GB (0.10) | 0.10 |
| Solanecio gigas | Yeshikoko gomen | Asteraceae | Shrub | S (0.08) | 0.08 |
| Hyparrhenia dichroa | Senbelet | Poaceae | Graminoids | GR (0.08) | 0.08 |
| Oplismenus compositus | Yekok sar | Poaceae | Graminoids | GB (0.07) | 0.07 |
| Lepus starcki | Tenchel | Leporidae | Vertebrates | AP (0.05) | 0.05 |
| Avena abyssinica ^b | Sellalie | Poaceae | Graminoids | CER (0.05) | 0.05 |
| Solanum tuberosum ^b | Dench | Solanaceae | Forbs | V (0.03) | 0.03 |

AP Animal prey, B bark, CER cereals, FL flowers, FR fruits, GB graminoid blade, GR graminoid root, HL forb leaves, HR forb root, ML mature leaves, S stem, YL young leaves, V vegetables

^aUnidentified graminoid

^bCultivated crops



Fig. 5 Overall percentage consumption of food items by hamadryas baboons at BSNP, northern Ethiopia, June 2016–May 2017

or mature leaves (r = -0.131, n = 12, P = 0.686). However, there were significant positive correlations between the availability of flowers and fruits and the consumption of flowers (r=0.743, n=12, P=0.006) and fruits (r=0.583, n=12, P=0.047), respectively. The availability of green graminoid plots correlated negatively with the consumption of graminoid blades (r=-0.669, n=12, P=0.030). We also found that the consumption of young leaves correlated negatively with their availability (r=-0.626, n=12, P=0.029).

Monthly consumption of fruits ranged from 1.4% in November 2016 to 58.3% in March 2017 (Table S5). Kruskal–Wallis *H*-test revealed that there were significant differences across months in percentage of time devoted to feeding on all of the seven main food items: fruits $(\chi^2 = 66.78, df = 11, P < 0.05)$, graminoid blades $(\chi^2 = 30.12, df = 11, P < 0.05)$, young leaves $(\chi^2 = 26.59, df = 11, P < 0.05)$, cereals $(\chi^2 = 50.33, df = 11, P < 0.05)$, flowers $(\chi^2 = 48.55, df = 11, P < 0.05)$, forb leaves $(\chi^2 = 42.17, df = 11, P < 0.05)$, and stems $(\chi^2 = 22.67, df = 11, P < 0.05)$.

Fruits were the most consumed food items during both the wet (38.3%) and dry seasons (25.6%), followed by graminoid blades (wet 16.4%, dry 22.8%) (Table 2). There were no statistically significant differences between seasons in the time spent feeding on flowers (Student's *t*-test, t=-2.06, df=10, P=0.066), fruits (t=1.167, df=10, P=0.27), graminoid blades (t=-0.72, df=10, P=0.48), young leaves (t=-1.176, df=10, P=0.267), mature leaves (t=0.443, df=10, P=0.667), stems (t=0.82, df=10, P=0.432), cereals (t=-0.739, df=10, P=0.477), or forb leaves (t=1.74, df=10, P=0.112).

The 20 most frequently consumed plant species comprised 79.2% of the overall diet. Each of these plant species accounted for > 1% of the diet except *Ficus sur*, which accounted for 0.9%. Out of the top 20 diet species, five were trees that accounted for 23.1% of the overall diet, six were shrubs (29.1%), four were forbs (6.8%) and five were graminoids (20.3%).

The monthly consumption of each plant species is listed in Table S6. Mean monthly food plant species richness was 16.75 (range 6–30 species) (Table S7). We recorded the highest dietary diversity during June and July 2016 (H'=2.84 for both months) and the lowest in March 2017

| Food items | Seasonal food items (%) | | | | |
|------------------|-------------------------|------------|---------|--|--|
| | Wet season | Dry season | Average | | |
| Fruits | 38.32 | 25.64 | 31.98 | | |
| Graminoid blades | 19.64 | 22.76 | 21.20 | | |
| Young leaves | 10.65 | 15.74 | 13.20 | | |
| Cereals | 6.97 | 10.67 | 8.82 | | |
| Forb leaves | 8.04 | 3.50 | 5.77 | | |
| Flowers | 2.34 | 10.36 | 6.35 | | |
| Stem | 5.86 | 4.16 | 5.01 | | |
| Mature leaves | 3.23 | 2.30 | 2.77 | | |
| Animal prey | 2.11 | 1.35 | 1.73 | | |
| Graminoid roots | 1.00 | 2.24 | 1.62 | | |
| Forb roots | 1.01 | 0.28 | 0.64 | | |
| Bark | 0.78 | 0.23 | 0.51 | | |
| Vegetables | 0.05 | 0.00 | 0.03 | | |

Table 2 Seasonal variation in the diet of hamadryas baboons atBSNP, northern Ethiopia, June 2016–May 2017

(*H*'=1.27). The mean monthly dietary *J* was 0.59. Dietary *J* was highest in January 2017 (0.78) and lowest in October 2016 (0.42). There were significant differences across months in food plant species diversity (F = 23.9, df = 11, P < 0.05) and evenness indices (F = 3.7, df = 11, P < 0.05).

Hamadryas baboons consumed a higher mean number of food plant species per month during the wet season (n = 19.67) than the dry season (n = 13.83), though the difference did not reach statistical significance (*t*-test, t=1.429, df=10, P=0.184). There was a higher diversity of food plant species during the wet season (H'=2.30) compared to the dry season (H'=2.05) but this difference was not significant (*t*-test, t=0.942, df=10, P=0.368). Mean dietary evenness index was higher during the dry season (J=0.63) than the wet season (J=0.55), though this difference was also not significant (*t*-test, t=-1.347, df=10, P=0.208). Scolopia theifolia was by far the most selected for food plant species, with a selection ratio of 11.88. The second and third highest selection ratios were for Olinia rochetiana at 1.79, and Dombeya torrida at 1.75 (Table 3).

Discussion

We conducted, to the best of our knowledge, the first-ever study on the feeding ecology of hamadryas baboons at a high-elevation site, BSNP, in northern Ethiopia. The highland habitat of BSNP has a different vegetation composition than the arid lowland field sites where hamadryas baboons have been studied, including at Awash [Filoha, Ethiopia (Swedell et al. 2008; Schreier 2010); Erer-Gota, Ethiopia (Kummer 1968)] and in Saudi Arabia and Yemen (Biquand et al. 1992; Al-Safadi 1994; Boug et al. 2017). Generally, young leaves and fruits were more abundant during the wet season than the dry season at BSNP. These plant parts were also more abundant during wetter months at hamadryas

 Table 3
 Dietary preference of hamadryas baboons based on stem density and percentage of feeding time for plant species consumed at BSNP, northern Ethiopia, June 2016–May 2017

| Scientific name | Family | Category | Stem density (%) | Annual diet (%) | Selection ratio |
|--------------------------------|----------------|----------|------------------|-----------------|-----------------|
| Olinia rochetiana | Oliniaceae | Tree | 8.36 | 15.00 | 1.79 |
| Rosa abyssinica | Rosaceae | Shrub | 8.2 | 12.43 | 1.52 |
| Acanthus sennii | Acanthaceae | Shrub | 10.16 | 4.74 | 0.47 |
| Discopodium penninervium | Solanaceae | Shrub | 7.05 | 4.52 | 0.64 |
| Rubus steudneri | Rosaceae | Shrub | 5.08 | 4.51 | 0.89 |
| Dombeya torrida | Sterculiaceae | Tree | 2.13 | 3.73 | 1.75 |
| Scolopia theifolia | Flacourtiaceae | Tree | 0.16 | 1.90 | 11.88 |
| Rumex nervosus | Polygonaceae | Shrub | 4.26 | 1.64 | 0.38 |
| Nuxia congesta | Loganiaceae | Tree | 1.48 | 1.57 | 1.06 |
| Urera hypselodendron | Urticaceae | Shrub | 1.97 | 1.27 | 0.64 |
| Vernonia myriantha | Asteraceae | Shrub | 5.74 | 0.82 | 0.14 |
| Olea europaea subsp. Cuspidate | Oleaceae | Tree | 3.11 | 0.79 | 0.25 |
| Maesa lanceolate | Myrsinaceae | Shrub | 2.62 | 0.75 | 0.28 |
| Dovyalis abyssinica | Flacourtiaceae | Shrub | 0.49 | 0.51 | 1.03 |
| Myrica salicifolia | Myricaceae | Tree | 0.33 | 0.45 | 1.36 |
| Myrsine melanophloeos | Myrsinaceae | Tree | 0.49 | 0.40 | 0.82 |
| Prunus africana | Rosaceae | Tree | 0.98 | 0.38 | 0.38 |
| Apodytes dimidiata | Icacinaceae | Tree | 0.82 | 0.16 | 0.19 |
| Solanecio gigas | Asteraceae | Shrub | 1.64 | 0.08 | 0.05 |

baboon study sites in Saudi Arabia (Boug et al. 2017) and Yemen (Al-Safadi 1994). There was a scarcity of fruits from November to January, which were among the drier months at BSNP. Shrubs such as Myrsine africana, Clutia lanceolata, Acanthus sennii, Rosa abyssinica, Discopodium penninervium and Rubus steudneri were common in the home range of the study band, in addition to many species of trees, forbs and graminoids. In other parts of Ethiopia (Erer-Gota and Awash National Park), Acacia species are common trees in the habitat of hamadryas baboons (Kummer 1968; Sigg and Stolba 1981; Schreier 2010), but they are rare in the highland environment at BSNP. Hamadryas baboons in Saudi Arabia mainly relied on wadi vegetation and figs (Ficus sp.) because they were abundant in the area (Biguand et al. 1992). In their survey undertaken in Eritrea, Zinner et al. (2001) reported that the exotic succulent Opuntia ficus-indica was a dominant species in the range of hamadryas baboons there. Taken together, these findings indicate that hamadryas baboons inhabit varied habitats across a large geographic area and wide elevational gradient.

We documented several qualitatively similar patterns of feeding ecology for hamadryas baboons at BSNP and the Filoha site at Awash National Park, where the most extensive research on hamadryas baboons has been conducted to date (Swedell et al. 2008; Schreier 2010; Admassu 2012; Swedell 2013). At BSNP, hamadryas baboons largely relied on fruits, as they did at Filoha (Swedell et al. 2008; Schreier 2010). Given the significant positive correlation between the availability and consumption of fruits, and their disproportionate consumption compared to other food items, we suggest that fruits are a preferred food item for the hamadryas baboons at BSNP (Fashing et al. 2007; Marshall and Wrangham 2007; Mekonnen et al. 2018). However, the absence of correlations between the availability of fruits and the consumption of graminoid leaves, young leaves, and mature leaves suggests that these are not fallback foods (Marshall and Wrangham 2007; Marshall et al. 2009), but rather less preferred food items for hamadryas baboons at BSNP.

In contrast to results from Filoha (Swedell et al. 2008; Schreier 2010), hamadryas baboons at BSNP did not exhibit major dietary changes between seasons. Moreover, the profile of plant species and plant parts consumed by hamadryas baboons at BSNP differed from those reported for Filoha (Swedell et al. 2008; Schreier 2010; Admassu 2012), in line with our hypothesis that dietary strategies would differ between populations of hamadryas baboons inhabiting lowland versus highland habitats, though both populations consumed cultivated crops (Admassu 2012; Ibrahim et al. 2023). In addition, hamadryas baboons in BSNP were unusual in their frequent consumption of graminoid blades (21.2% of annual diet), a food item rarely consumed by conspecifics in the lowlands of Awash (Swedell et al. 2008; Shreier 2010). Highland graminoids are considered of higher nutritional quality than those growing in the lowlands of Ethiopia (Dunbar and Bose 1991), and represent the main food item of geladas (Fashing et al. 2014; Jarvey et al. 2018; Kifle and Bekele 2021). The potential for feeding competition between hamadryas baboons and geladas where they co-occur, like at BSNP, is a topic worthy of investigation. Hamadryas baboons at BSNP showed significant variation across months in their consumption of their major food items, similarly to hamadryas baboons at Awash National Park (Swedell et al. 2008; Shreier 2010). For instance, the low consumption of fruits from November to January (Table S5) coincided with their scarcity (Table S3) and the high consumption of cultivated crops (Table S5). This indicates that the diet of hamadryas baboons at BSNP changes over short time scales.

Seasonality is an important factor that influences the dietary composition of many baboons (Hill and Dunbar 2002) and other primates (Brockman and van Schaik 2005). When the most preferred food items of baboons are scarce, they typically show a shift in their diet by eating other food items (Kummer 1968; Whiten et al. 1987; Hill and Dunbar 2002). Hamadryas baboons at Erer-Gota and Filoha consumed fruits, flowers and young leaves when they were available, but switched to less preferred items like roots and stems during the dry season (Kummer 1968; Swedell et al. 2008; Schreier 2010). Conversely, although hamadryas baboons at BSNP spent somewhat more time feeding on fruits during the wet season and on graminoid blades during the dry season, significant seasonal differences in the consumption of food items existed only for forb leaves, which comprised a relatively small proportion of the annual diet. Fruits, which are the most often consumed and most preferred food at BSNP, were fed on throughout the year. For example, fruit of Olinia rochetiana, which was largely available during the wet season, and fruits of Rosa abyssinica, Rubus steudneri and Discopodium penninervium, which were available for a few months during both the wet and dry seasons.

Fruit is the most important component of the diet of baboons across their range (Kummer 1968; Dunbar and Dunbar 1974; Davidge 1978; Sharman 1981; Norton et al. 1987). Leaves represented 24% of the diet of hamadryas baboons in BSNP. Leaves are also important components of the diet of hamadryas baboons at Erer-Gota [28% (Kummer 1968)] and of the diets of some populations of *Papio anubis* [41% (Dunbar and Dunbar 1974)] and *Papio ursinus* [25% (Davidge 1978)]. Hamadryas baboons in BSNP also consumed flowers and subterranean items, consistent with reports for hamadryas baboons at Erer-Gota (Kummer 1968) and Filoha (Swedell et al. 2008; Schreier 2010). Like many other hamadryas baboon populations (Biquand et al. 1992; Al-Safadi 1994; Admassu 2012; Bough et al. 2017; Abdela

2019), hamadryas baboons in BSNP supplement their diet by consuming crops grown on farms near their habitat.

Hamadryas baboons in BSNP obtained food from 49 plant species, which is within the range of the number of species of plants consumed by hamadryas baboons at Filoha in Awash National Park [40 species (Schreier 2010); 45 species (Swedell et al. 2008); 73 species (Admassu 2012)] and Alhada in Saudi Arabia [42 species (Boug et al. 2017)]. Hamadryas baboons at BSNP exploited only one species of Acacia (Acacia decurrens), which comprised < 1% of the total diet, whereas five Acacia species provided 39% of the diet of hamadryas baboons at Filoha (Schreier 2010). Acacia species are also important to the diets of several other hamadryas populations, as well as other baboon species (Norton et al. 1987; Barton et al. 1993; Al-Safadi 1994; Swedell et al. 2008; Boug et al. 2017). Acacia has a very limited distribution and low abundance in BSNP, however, which may be due to the area's high elevation and climatic patterns, which differ to those at lower altitudes. The incorporation of animals (Tragelaphus scriptus, Lepus starcki, and one species of ant) in the diet of hamadryas baboons at BSNP is consistent with the diets of some other populations of hamadryas baboons, which also exploit mammals and invertebrates for food (Admassu 2012; Schreier et al. 2019).

The three most consumed plant food species together accounted for 36.8% of the diet of hamadryas baboons, and the 20 most consumed species of plants accounted for 79.2% of their feeding time at BSNP. In comparison, just three plant species consumed by Band 1 of hamadryas baboons at Filoha accounted for 50.3% of their annual feeding budget (Schreier 2010). Band 1 relied most frequently on the fruit of H. thebaica and the seeds, leaves and flowers of Acacia senegal (Schreier 2010). Additionally, Band 3 at Filoha spent 47.4% of their total annual feeding time eating H. thebaica fruit and 11.6% on the leaves, flowers and seeds of A. senegal (Swedell et al. 2008). Notably, the focus of the baboons at Filoha was on the fruit of H. thebaica when it was available (Swedell et al. 2008; Schreier 2010). The high energy density of this fruit apparently enabled the baboons at Filoha to devote a relatively low percentage of their activity budget to feeding (Swedell et al. 2008; Schreier 2010). There was no such highly prized food item for the hamadryas baboons in our study at BSNP. Taken together, these comparisons suggest that hamadryas baboons have a more eclectic diet at BSNP than at lowland sites, where a single or a few prized food items comprise a larger proportion of their diet.

In BSNP, there was no single food plant species that was consumed throughout the year. Still, the top ranked food plant species (*Olinia rochetiana*) was consumed during all of the months except for March. This absence of *Olinia rochetiana* from the diet during March might be related to the high consumption of *R. abyssinica* during the same month. On the other hand, Band 3 at Filoha consumed *H. thebaica* and *A. senegal* during every month of the year (Swedell et al. 2008). In addition, Band 1 in Filoha consumed food items from *Acacia senegal*, *Tribulus cistoides*, *Acacia tortilis* and *Acacia mellifera* throughout the year (Schreier 2010). These patterns suggest that, unlike hamadryas baboons at Filoha, those at BSNP did not rely on specific plant species throughout the year. However, like Band 3 at Filoha (Swedell et al. 2008), hamadryas baboons in BSNP consumed more food plant species during the wet season than the dry season.

The availability of cultivated crops along the boundaries of protected areas often compels primates to forage outside the boundaries (Seiler and Robbins 2016; Mekonnen et al. 2020; Kifle 2021). Crop foraging behavior is a common response by some primates to a reduction of their preferred wild food resources (McLennan et al. 2017; Mekonnen et al. 2020). Hamadryas baboons in BSNP spent more time feeding on cultivated crops, particularly during November and December when there was low availability of fruit (the preferred food item). Similar tendencies have been observed in hamadryas baboons at Awash National Park (Admassu 2012) as well as in several other primates, including ring-tailed lemurs (Lemur catta) (LaFleur and Gould 2009), chimpanzees (Pan troglodytes) (McLennan 2013), tufted capuchin monkeys (Sapajus nigritus) (Mikich and Liebsch 2014), Bale monkeys (Chlorocebus djamdjamensis) (Mekonnen et al. 2020), and olive baboons (*P. anubis*) (Kifle 2021).

At BSNP, the crop foraging behavior of hamadryas baboons elicited retaliation from some local people, which posed a risk to the baboons' survival (Ibrahim et al. 2023). In some instances, people injured or killed the hamadryas baboons by throwing spears, stones, sticks, and long knives (Ibrahim et al. 2023), as reported previously for olive baboons in Wollo area, Ethiopia (Kifle 2021). To ensure the long-term survival of hamadryas baboons in habitats like BSNP where there is conflict with nearby communities, it is essential to include nearby farmlands in management plans. For example, monocultures of unpalatable plant species can be grown in a buffer zone to discourage crop foraging by hamadryas baboons (Ibrahim et al. 2023). The role of local people is crucial in such participatory conservation programs, as we cannot hope to conserve non-human primates without considering the wider political, socioeconomic, ecological, and cultural conditions under which their coexistence with humans is possible (McLennan et al. 2017).

Our results show that the diet and feeding behavior of hamadryas baboons in highland habitat at BSNP differ from those of well-studied bands in lowland habitat at Filoha. However, fruit comprised the largest proportion of the diet of hamadryas baboons at both locations. Contrary to our prediction, there was no significant difference in the consumption of the major food items and food plant species between seasons. However, the hamadryas baboons preferred fruits and flowers when these food items were available in their habitat. Hamadryas baboons raided cultivated land throughout the year, and cultivated crops accounted for 8.8% of their annual diet at BSNP. This crop foraging behavior creates conflict with the surrounding local community (who are subsistence farmers), and represents a risk for the future conservation of the species that should be addressed in the development of conservation and management plans for BSNP.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Permission to conduct this research project was granted by the Ethiopian Wildlife Conservation Authority. This project adhered to the legal requirements of Ethiopia and complied with the American Society of Primatologists' Principles for the Ethical Treatment of Non-human Primates.

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