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Composition and Seasonality of Diet in Wild Hamadryas Baboons: Preliminary Findings from Filoha

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Key Words

Hamadryas baboon • Feeding ecology • Diet • Seasonality • Dietary breadth

Abstract

Here we report the first year-round quantitative data on dietary composition and seasonality in wild hamadryas baboons. Study subjects were adult male members of band 3 at the Filoha field site in central lowland Ethiopia. Data collection consisted of 10-min focal samples during all-day follows 4–6 days per month over the course of 1 year. The two largest contributors to the diet were *Hyphaene thebaica* and *Acacia senegal*, and these were the only plant species found in the diet during every month of the year. Other relatively major contributors to the diet, such as *Cyperus grandibulbosus*, *Seddera bagshawei*, *Tribulus cistoides* and *Typha latifolia*, showed a seasonal pattern. Fewer plant species were consumed during the dry months of the year compared to the wet months. During the hottest and driest months of the year, study subjects subsisted almost exclusively on *H. thebaica*, *A. senegal*, *C. grandibulbosus* and *T. latifolia*. Overall, these patterns suggest that this population of hamadryas baboons spends less time feeding and is able to subsist on a narrower array of plant foods compared to other baboons. This pattern may be driven by the presence at Filoha of the doum palm (*H. thebaica*), a high-quality food resource that is consumed year-round.

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Introduction

The hamadryas baboon (*Papio hamadryas hamadryas*) inhabits the Horn of Africa and the southwestern Arabian Peninsula, and is widely regarded to be the most divergent and specialized subspecies of *Papio* [Dunbar, 1988; Jolly, 1993; Kummer, 1995; Henzi and Barrett, 2003]. Its unusual multilevel social system and male-dominated social organization are commonly thought to be evolutionary adaptations to the semi-desert environment in which it likely evolved, either in the Horn of Africa

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or the Arabian Peninsula [Jolly, 1963; Crook and Aldrich-Blake, 1968; Nagel, 1973; Dunbar, 1988; Kummer, 1990; Jolly, 1993; Kummer, 1995]. Most areas inhabited by hamadryas baboons are dominated by *Acacia* thorn scrub and can be broadly described as semi-desert scrubland or *Acacia* woodland [Kummer, 1968; Sigg and Stolba, 1981; Biquand et al., 1992; Al-Safadi, 1994; Swedell, 2006]. In some areas of their distribution, in particular northern Ethiopia and Eritrea, hamadryas occupy a broader range of habitats, including moist highlands, moist lowlands and closed-canopy forests and woodlands [Zinner et al., 2001; Bergman and Beehner, pers. commun.]. However, the general pattern is that hamadryas habitat is drier and lower in altitude with higher year-round temperatures than found for other baboon subspecies, with the obvious exception of Namibian chacma baboons.

Like other baboons, hamadryas appear to be generalist omnivores, but the lower species richness and diversity of their habitats compared to those of other baboon subspecies suggest that they may subsist on a narrower array of plant species than other baboons. However, this notion has never been confirmed quantitatively, nor has there been any systematic assessment of hamadryas diets in any part of their range.

Previous studies suggest that hamadryas baboons subsist mainly on the fruits, flowers, leaves and seeds of *Acacia* trees and shrubs and a wide array of other semi-desert plants such as *Grewia* and *Dobera glabra* [Kummer, 1968; Al-Safadi, 1994; Swedell, 2002b, 2006]. Like other baboons, they also feed opportunistically on invertebrates, small mammals such as hares (*Lepus* spp.), agricultural crops and refuse from garbage dumps [DeVore and Hall, 1965; Altmann and Altmann, 1970; Ransom, 1981; Biquand et al., 1992; Al-Safadi, 1994]. In some parts of their range, specific food items only available in those areas are included in their diet, e.g. the fruit and young shoots of prickly pear (*Opuntia* spp.) [Kummer, 1968; Al-Safadi, 1994; Zinner et al., 2001] and the fruits of Egyptian doum palm (a.k.a. gingerbread palm) trees (*Hyphaene thebaica*) [Swedell, 2002b, 2006].

Previous studies also suggest that hamadryas baboon ecology may be influenced by seasonal patterns of rainfall. Both Boug et al. [1994] and Swedell [2002a, b] found that daily path lengths were longer during the wet season, when vegetation was more abundant, than during the dry season. This suggests the possibility that hamadryas baboons use a strategy of time minimization [Schoener, 1971] during the dry months, when food is scarce, but consume and expend more energy during the wet months when food is more abundant.

How the diet of hamadryas differs from other baboons, whether it consists of a narrower set of food items and whether it varies seasonally are questions that have not been answerable to date due to a lack of sufficient quantitative data on dietary composition in hamadryas and its variation across seasons. In this paper, we make a preliminary attempt to fill this gap by providing data on dietary composition and seasonality from a band of hamadryas baboons in Ethiopia.

Methods

Study Site and Subjects

This study focused on a population of wild hamadryas baboons inhabiting the region surrounding the Filoha outpost of the Awash National Park of Ethiopia, both within and outside (north) the park [Swedell, 2002b, 2006]. The home range of this population encompasses sev-

eral habitat types but is predominantly a semi-desert scrubland dominated by shrubby *Acacia* and *Grewia* [Swedell, 2002b; Abule et al., 2007] broadly similar to the habitat of hamadryas baboons in other parts of their geographic range [Sigg and Stolba, 1981; Biquand et al., 1992]. Other habitat types within the range of the Filoha population include grasslands and swamps dominated by *Sporobolus* and *Cyperus* grasses and small forests of doum palm trees (*H. thebaica*). The region immediately surrounding the Filoha outpost (approx. 5 km²) can be characterized as an oasis or small wetland ecosystem with numerous hot springs, swamps, marshes and small forest patches of doum palms. Potential predators in the Filoha area include lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), jackals (*Canis* spp.), crocodiles (*Crocodylus niloticus*), birds of prey and snakes.

The Awash region is characterized by one long wet season, beginning in late June or early July and ending sometime in September, followed by a more sporadic set of short rains occurring intermittently between January and June. The two wettest months of the year are usually July and August, and the driest and hottest months of the year are usually May and June, just prior to the onset of the long rains [Swedell, 2002b, 2006]. The annual rainfall is 500–600 mm, with the vast majority of this falling during July and August (table 1).

This study focused on 'band 3' at Filoha, comprising about 400 individuals. The home range of band 3 lies slightly to the north of that of band 1 (formerly group 1), the focus of Swedell's [2000, 2002a, b, 2006] previous research. Both bands use the same two primary sleeping cliffs, the Filoha cliff and the Wasaro cliff about 4 km west of Filoha [Swedell, 2006; Schreier and Swedell, 2008]. The Filoha cliff is used as a sleeping site by band 3 at least 40% of the time and by band 1 at least 50% of the time [Swedell, 2006; Schreier and Swedell, 2008].

Study subjects consisted of adult male members of band 3. At the time of the study, band 3 included over 60 adult males. Because individual baboons were not identified, it is not known exactly how many study subjects contributed to these data, but we estimate that at least 30 adult males were sampled based on variation in one-male unit size and composition of focal subjects.

Data Collection

Observations took place over 12 sessions of 4–6 days each at approximately 1-month intervals from early August 2001 to early August 2002, totaling 52 days of observation (table 1). Data were collected during every month of the year, but the timing varied slightly from one month to the next so that two sessions began at the end of one month and ended at the beginning of the next.

On each observation day, band 3 was followed from just after dawn (approx. 6:00 in summer and 6:30 in winter) until about an hour before dusk (17:00 in winter and 17:30 in summer). Focal males were chosen sequentially at random, and 10-min focal samples were conducted. Samples were distributed relatively evenly throughout the daytime hours, with a total of 150–208 samples (mean 171; SD = 18.4) per hourly time block between the hours of 6:00 and 17:00 over the course of the study period. Morning samples (hourly mean 179; SD = 19.2) were slightly overrepresented compared to afternoon samples (hourly mean 160, SD = 11), a pattern that did not vary substantially across the year. Samples before 6:00 and after 17:00 were few in number, but this is unlikely to bias the results as this pattern was consistent across days and seasons, and the baboons are almost invariably resting and grooming on the sleeping cliff and not foraging or feeding during these times.

During focal samples, all behavior of the focal individual was recorded continuously using data sheets. Feeding was defined as harvesting food items from their source, putting food items into the mouth, chewing and swallowing. The beginning and end of each feeding bout was recorded, as well as the identity of the food item and, when visible, the plant part. We acknowledge that our sampling method overestimates time spent feeding on foods that take longer to process and underestimates time spent harvesting items such as seeds that can be obtained and ingested quickly. The latter are represented in our data as bouts of a few seconds' duration; we did not tabulate frequencies of these events.

In addition to foods consumed during focal samples, ad libitum observations of non-focal individuals also contributed to the list of plant species in table 2. All plants observed being

Table 1. Percentage of monthly feeding time spent on each plant species that contributed to at least 1% of total (annual) feeding time, with other relevant data for each month

a Percentage of monthly feeding time	Aug 2001	Sep 2001	Oct 2001	Nov 2001	Dec 2001	Jan–Feb 2002	March 2002	April 2002	May 2002	June 2002	July–Aug 2002	Total feeding time
<i>Acacia mellifera</i>	1.59	0.31	1.28	0.00	0.00	0.00	15.87	0.06	0.00	0.00	8.87	2.99
<i>Acacia senegal</i>	2.53	5.06	15.38	4.67	13.83	7.95	3.82	34.12	10.93	5.92	14.89	11.62
<i>Acacia tortilis</i>	0.00	1.30	0.00	0.03	27.46	0.00	4.06	0.00	0.00	0.00	0.00	3.68
<i>Balanites aegyptiaca</i>	0.00	2.65	3.13	0.33	3.13	0.00	2.43	0.00	0.00	0.00	5.32	1.68
<i>Barleria spinisepala</i>	0.00	2.99	15.87	0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.03
<i>Cyperus grandibulbosus</i>	0.00	0.00	0.00	0.00	0.00	9.15	0.00	10.15	28.02	13.10	0.00	6.21
<i>Hyphaene thebaica</i>	16.95	1.53	22.01	50.64	50.36	77.6	53.40	47.58	58.69	70.13	30.10	47.42
<i>Pentarrhinum insipidum</i>	0.00	0.23	0.00	0.00	2.25	1.10	15.86	0.00	0.00	0.00	5.56	2.78
<i>Psilotrichum gnaphalobryum</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.44	3.02
<i>Seddera bagshawei</i>	0.00	30.88	22.71	23.59	0.16	0.00	0.00	0.00	0.00	0.00	0.00	5.71
<i>Tribulus cistoides</i>	56.18	10.51	0.00	2.06	2.41	0.00	2.89	0.00	0.00	0.00	12.43	4.33
<i>Typha latifolia</i>	0.00	6.64	1.40	13.12	0.00	2.94	0.00	8.09	2.37	9.12	0.00	4.19
Total	77.25	62.10	81.78	95.00	99.60	98.74	98.34	100.00	100.00	98.27	99.61	94.64
b Observation details	Aug 2001	Sep 2001	Oct 2001	Nov 2001	Dec 2001	Jan–Feb 2002	March 2002	April 2002	May 2002	June 2002	July–Aug 2002	
Observation days	5	6	4	5	4	4	5	5	4	5	5	
10-min focal samples	72	143	125	192	166	159	178	224	197	217	237	
Minutes observed	592	1,287	1,216	1,883	1,630	1,575	1,762	2,216	1,955	2,163	2,362	
Time spent feeding, %	18.0	20.3	19.9	30.9	34.1	24.2	28.7	22.2	29	20.1	27.4	
Plant species in diet	10	22	18	12	8	7	8	5	4	4	10	
c Climatic conditions	Aug	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	June	July
Mean afternoon temperature, °C	29	34	36	33	31	34	33	35	34	36	38	33
Mean monthly rainfall, mm	117	59	38	4	6	15	37	44	47	39	26	133
Rainy days per month	13	7	5	1	1	2	3	5	6	5	5	14

Temperature data from January 1997 to October 1998, with averages for months for which data from both years are available (Jan–May); November data from 2003. Rainfall data from January 1990 to December 2000, recorded at Merti sugar plantation 40 km south of Filoha.

Table 2. Plant species consumed by band 3 at Filoha from August 2001 to August 2002, with total time spent feeding on that species, percentage of total feeding time and months in which that plant species was observed being consumed

Family	Species	Part eaten	Time spent feeding, min	Total feeding time, %	Months consumed
Acanthaceae	<i>Barleria spinisepala</i>	seeds	49.5	1.031	Sep–Nov
Acanthaceae	<i>Justicia odora</i>	young leaves	a.l.	a.l.	
Amaranthaceae	<i>Psilotrichum gnaphalobryum</i>	flowers, immature seeds	145.0	3.021	Jul–Aug
Amaranthaceae	<i>Pupalia lappacea</i>	roots	0.5	0.010	Sep
Apparidaceae	<i>Godoba rotundifolia</i>	fruit	8.4	0.175	Mar
Asclepiadaceae	<i>Pentarrhinum insipidum</i>	young leaves, stems, latex	133.3	2.778	Feb–Mar, Jul–Sep
Asclepiadaceae	<i>Sarcostemma viminalae</i>	stem, latex	a.l.	a.l.	a.l.
Balanitaceae	<i>Balanites aegyptiaca</i>	leaves, fruits	80.5	1.677	Mar, Jul, Sep–Dec
Boraginaceae	<i>Heliotropium strigosum</i>	young leaves	a.l.	a.l.	
Caesalpinioidae	<i>Delonix elata</i>	flowers, seeds	a.l.	a.l.	
Commelinaceae	<i>Commelina diffusa</i>	leaves	a.l.	a.l.	
Convolvulaceae	<i>Ipomoea blepharophylla</i>	immature fruits	13.4	0.279	Sept
Convolvulaceae	<i>Seddera bagshawei</i>	seeds	273.8	5.705	Sep–Dec
Convolvulaceae	<i>Seddera latifolia</i>	leaves	6.9	0.144	Oct
Cyperaceae	<i>Cyperus grandibulbosus</i>	flowers, stems	297.8	6.205	Jan–Feb, Apr–June
Cyperaceae	<i>Cyperus rotundus</i>	root bulb	21.3	0.444	Sep, Nov
Gramineae	<i>Sorghum arundinaceum</i>	seed heads	2.5	0.052	Oct
Gramineae	<i>Arundo donax</i>	stems	a.l.	a.l.	a.l.
Gramineae	<i>Brachiaria deflexa</i>	blades, flowers	13.7	0.285	Aug–Sep
Gramineae	<i>Chrysopogon plumulosus</i>	blades, stems	a.l.	a.l.	a.l.
Gramineae	<i>Coelachyrum poiflorum</i>	young leaves, flowers	18.3	0.381	Aug–Oct
Gramineae	<i>Sporobolus consimilis</i>	blades, stems	38.7	0.806	Jan–Feb, Aug–Dec
Gramineae	<i>Sporobolus ioclados</i>	flowers, seeds	19.2	0.400	Sept–Nov
Gramineae	<i>Sporobolus spicatus</i>	leaf blades	16.2	0.338	Oct–Nov
Gramineae	<i>Tetrapogon cenchriflorus</i>	blades	11.4	0.238	Sep
Labiatae	<i>Ocimum americanum</i>	leaves	5.0	0.104	Jul–Aug
Liliaceae	<i>Aloe</i> spp.	root sheath	a.l.	a.l.	a.l.
Malvaceae	<i>Abutilon figarianum</i>	fruit	a.l.	a.l.	a.l.
Malvaceae	<i>Hibiscus micranthus</i>	leaves	0.6	0.013	Oct
Mimosoideae	<i>Acacia mellifera</i>	young leaves, seeds	143.4	2.988	Mar–Apr, Aug–Oct
Mimosoideae	<i>Acacia nubica</i>	seeds	14.0	0.292	Aug–Oct
Mimosoideae	<i>Acacia senegal</i>	leaves, flowers, seeds, gum	557.5	11.617	all months
Mimosoideae	<i>Acacia tortilis</i>	young leaves	176.8	3.684	Mar, Sep, Nov–Dec
Palmae	<i>Hyphaene thebaica</i>	fruit epicarp and mesocarp	2,275.8	47.422	all months
Papilionoideae	<i>Tephrosia villosa</i>	immature fruit pods	1.0	0.021	Oct
Papilionoideae	<i>Tephrosia uniflora</i>	young leaves, fruit	a.l.	a.l.	a.l.
Solanaceae	<i>Solanum dubium</i>	flowers, immature fruits	a.l.	a.l.	a.l.
Tiliaceae	<i>Grewia erythraea</i>	fruit	10.6	0.221	Aug–Oct
Tiliaceae	<i>Grewia schweinfurthii</i>	fruit	a.l.	a.l.	a.l.
Tiliaceae	<i>Grewia tenax</i>	young leaves, fruit	4.2	0.088	Jan, Aug, Oct
Tiliaceae	<i>Grewia villosa</i>	fruit	0.1	0.002	Sep

Table 2 (continued)

Family	Species	Part eaten	Time spent feeding, min	Total feeding time, %	Months consumed
Typhaceae	<i>Typha latifolia</i>	root sheath	200.9	4.186	Jan, Apr–Jun, Sep–Nov
Verbenaceae	<i>Chaseanum laetum</i>	seeds	2.0	0.042	Sep
Zygophylloceae	<i>Tribulus cistoides</i>	young leaves, seeds	207.7	4.328	Mar, Jul–Sep, Nov–Dec
Unknown food item in ground			1.8	0.038	Oct
Invertebrates			12.2	0.254	Nov, Jun
Total feeding time, min			4,764		

a.l. = Observed ad libitum only, and field notes with ad libitum observations are no longer available so months of observation are unknown; months consumed = data reflect actual months in which these foods were eaten (disregarding whether data were collected during an observation session crossing two months).

eaten by baboons were collected, preserved and identified with the assistance of staff of the National Herbarium at Addis Ababa University. The total number of minutes spent feeding was tabulated from focal samples and the number of minutes spent eating each type of food item was divided by the total number of minutes spent feeding to obtain a percentage of time spent eating each food item. Unfortunately, the inconsistency with which the plant part was recorded in this study did not allow us to tabulate by plant part, only by species. We use the term ‘diet’ and ‘dietary composition’ here to refer to the plant species that compose an animal’s diet, not the parts of those plants. We use the term ‘dietary breadth’ to refer to the number of species that comprise the diet for a given time period. Data collection and plant identification were conducted by G.H. Data entry, tabulation and analysis were conducted by L.S. and a research assistant working under her supervision.

These methods were reviewed and approved by the Queens College Institutional Animal Care and Use Committee. All research reported here was conducted with permission of the Ethiopian Wildlife Conservation Organization, now known as the Wildlife Conservation Department of Ethiopia, and adhered to the legal requirements of Ethiopia.

Results

Dietary Composition

Table 2 lists the 44 plant species that were observed being consumed by members of band 3 at Filoha from August 2001 to early August 2002. Of the complete list, 32 were observed being eaten by focal males during the current study, and the others were observed being eaten only during ad libitum observations. Baboons in this study were also observed preying on guinea fowl (*Numida*), dik dik (*Madoqua*), hares (*Lepus*) and a variety of invertebrate animals, though these were rare events and occurred mainly during ad libitum observations. Doum palm fruits (*H. thebaica*), previously reported to be an important resource for this population [Swedell, 2002b, 2006], were both eaten off the ground and selected from terminal

branches of the aerial branching doum palm trees. Only the outer layer of the fruits is eaten by the baboons, who hold the fruit in their hands while scraping off the epicarp and mesocarp with their molar teeth, rotating the fruit between each bite.

Feeding Time

Adult males spent 25.6% of their time feeding, varying from 18 to 34% across monthly observation sessions (table 1). Of the total annual feeding time, 47.4% was spent eating doum palm fruits, and 11.6% was spent eating the leaves, flowers and seeds of *Acacia senegal* (table 1). Other plant species that contributed to at least 1% of the annual feeding time were *Cyperus grandibulbosus* (6.2%), *Seddera bagshawei* (5.7%), *Tribulus cistoides* (4.3%), *Typha latifolia* (4.2%), *Acacia tortilis* (3.7%), *Psilotrichum gnaphalobryum* (3.0%), *Acacia mellifera* (2.9%), *Pentarrhinum insipidum* (2.8%), *Balanites aegyptiaca* (1.7%), and *Barleria spinispala* (1.0%).

Dietary Seasonality

A comparison across observation sessions revealed a seasonal pattern in the number of plant species contributing to the monthly diet, which decreased gradually from the long rains of July and August to the peak dry months of May and June (table 1). The relationship between season and dietary breadth cannot be accounted for by a seasonal difference in observation time, as the number of observation days per month in the drier months of December to June (mean 4.5 days, SD = 0.54) was not significantly different from that in the wetter months of July to November (mean 5.0 days; SD = 0.70; Mann-Whitney rank sum test, $p = 0.26$).

The two species comprising the majority of annual feeding time, *H. thebaica* and *A. senegal*, were also the only two plant species that were consumed during every month of the year (fig. 1, table 1). Of the two, *H. thebaica* showed a seasonal pattern of use, whereas *A. senegal* did not. The third and fourth highest contributors to the annual diet, *C. grandibulbosus* and *S. bagshawei*, showed contrasting seasonal patterns, with the former contributing to the diet only from January to June and the latter only from September to December (fig. 2). The next two highest contributors to the annual diet, *T. cistoides* and *T. latifolia*, each showed weaker seasonal patterns, with *T. cistoides* being most commonly eaten during the wet months of the year and *T. latifolia* most commonly during the dry months (fig. 2).

Discussion

Dietary Composition and Seasonality

As measured by time spent in feeding bouts by focal males, doum palm fruits (*H. thebaica*) comprised the largest portion of the annual diet and were the most frequently consumed food during the 7 dry months of the year (fig. 1; tables 1, 2). Feeding time does not bear a direct relationship to caloric intake, however, particularly for doum palm fruit, which involves more manipulation than most other plant foods (see above). This process likely involves more handling time per unit of energy compared to fruits and flowers. There may be a higher payoff from doum palms, though, as nutritional analyses of two of its close relatives, *H. coriacea* and *H. compressa*, found that the mesocarp is high in carbohydrates and is also a good source of iron,

Fig. 1. Percentage of monthly feeding time devoted to *H. thebaica* and *A. senegal*.

Fig. 2. Percentage of monthly feeding time devoted to *C. grandibulbosus*, *S. bagshawei*, *T. cistoides* and *T. latifolia*.

zinc, calcium, and several essential and non-essential amino acids [Hoebekke, 1989; Lokuruka, 2007]. Regardless of how energy-efficient the fruits are to harvest, it is clear that *H. thebaica* is a crucial food resource for this population, especially during the dry months of the year when fewer other foods are available.

The second highest contributor to the diet was *A. senegal*, the dominant vegetation in most of the Filoha region and an important resource for this population during every month of the year (fig. 1, table 1). Unlike *H. thebaica*, in which only the fruit is consumed, *A. senegal* flowers, leaves, seeds and gum are all eaten by baboons to varying degrees [Swedell, 2002b, 2006, pers. observation]. Preliminary results from band 1 at Filoha suggest that the contribution of each of these parts of *A. senegal* varies seasonally according to both its abundance and the availability of other preferred food items [Schreier, in preparation].

The top 2 contributors to the annual diet were also the only 2 plant species that were consumed during every month of the year. By contrast, the next 4 highest contributors to the diet – *C. grandibulbosus*, *S. bagshawei*, *T. cistoides* and *T. latifolia* – each showed a stronger seasonal pattern, some more pronounced than others (fig. 2). As shown in table 1, the number of plant species contributing to the diet from December to June, the driest months of the year, ranged from 4 to 8. By contrast, anywhere from 10 to 22 plant species contributed to the monthly diet during the long rains of July and August, and a high number of plant foods remained in the diet through November. Seventeen of the 44 species contributing to the annual diet were consumed exclusively in August, September, October, November or some combination of these months during and just after the long rains, and did not contribute to the diet in any other month of the year (table 2). If food abundance bears a predictable relationship to dietary breadth, then the above pattern makes sense in light of the fact that the wet season usually extends into September, and a high abundance and diversity of plant life persists for at least a month or two afterwards. November and December are thus the ‘driest’ months of the year in terms of rainfall (table 1), but there is still an abundance of ground water and a relatively high diversity of plant foods during these months compared to May and June after several months of more sporadic, less frequent rainfall.

One of the most striking results from this study is the low number of plant taxa consumed during the months of the year that are most removed temporally from the long rains of July and August. From January through June, males in this study appeared to subsist almost entirely on four main foods: *H. thebaica* palm fruits; the leaves, flowers and seeds of *A. senegal*; the flowers and stems of the grass-like herb *C. grandibulbosus*, and the root sheaths of the grass *T. latifolia*. Interestingly, *Cyperus* was not consumed at all during the wettest months, despite it being a staple food during the dry season. It is likely that the reliance of this population on doum palm fruit, combined with the permanent water supply at Filoha, allows them to reduce their dietary breadth in the dry season while still obtaining sufficient nutrients. As mentioned above, the fruit mesocarp of *H. coriacea*, a close relative of *H. thebaica*, is not only high in carbohydrates and minerals, but also contains several essential and non-essential amino acids. Two of these are methionine and cystine, the only two amino acids that contain sulfur, and quantities of which are generally low in most plant foods [Lokuruka, 2007].

During the wet season, by contrast, diets were far more varied. The majority of plant foods appeared in the diet solely during the wet months or shortly thereafter,

most likely because they were only available during that time (tables 1, 2). For example, the herb *S. bagshawei* comprises over 22% of the diet in the months following the long rains but is completely absent from the diet during the remainder of the year (fig. 2, tables 1, 2).

It is likely that a higher number of plant taxa are encountered during the wet months not only because more water is available (producing a higher diversity of plant species), but also because the baboons travel farther each day during this time compared to the dry months of the year [Swedell, 2002b, 2006]. Longer daily paths during the wet months may be a consequence of forays into areas that contain foods only available during these times. Alternatively, longer paths during these months may simply result from a relaxation of the normal geographic limitations imposed by the restricted distribution of drinking water [Swedell, 2002b], which, during the driest months of the year, is limited to the Filoha hot springs and a few other areas. Unfortunately, we cannot assess a seasonal effect on daily path lengths for this study because simultaneous ranging data were not collected. A more robust analysis of the interaction of food distribution and ranging behavior in band 1 promises to shed further light on this question [Schreier, in preparation].

Because this study was conducted for only 1 week per month, we have almost certainly underestimated the number of plant taxa consumed by males in band 3 at Filoha. Observations were relatively equally distributed across the year, however, suggesting that the seasonal pattern shown by these results is not an artifact of observer bias. Undoubtedly, seasonal differences in diet are largely determined by annual patterns of rainfall leading to seasonal leaf production, flowering and fruiting patterns. While we cannot examine the details of these relationships here as we do not have phenological data for the home range of band 3, we plan to do so for band 1 in a more detailed analysis of habitat use and foraging behavior currently under way [Schreier, in preparation].

Hamadryas Feeding Ecology in Comparative Perspective

An initial comparison of these results with those from other sites suggests that hamadryas at Filoha spend less time feeding than other baboons. The hamadryas males in this study spent about 26% of their daytime feeding, varying from 18 to 34% across the months of the year (table 1). By comparison, 45–48% of daylight hours are spent feeding by yellow baboons at Amboseli in Kenya [Bronikowski and Altmann, 1996], about 50% by chacma baboons in the Drakensberg Mountains of South Africa [Whiten et al., 1987], 36% in summer and 50% in winter [Hill et al., 2003], or about 43% overall [Gaynor, 1994] by chacma baboons at De Hoop, 80% by chacma baboons in the Western Cape Peninsula of South Africa [Hall, 1962], 33% by the same population 15 years later [Davidge, 1978a] and about 70% by the desert chacmas of the Kuiseb River Canyon in Namibia [Hamilton et al., 1978]. Ransom [1981] reported for anubis baboons at Gombe Stream in Tanzania that ‘except for three periods of heightened social activity ... [early morning, an hour around midday and early evenings], food-gathering was the dominant activity of a troop throughout the day’.

In a comparative analysis of 12 baboon (*Papio hamadryas anubis*, *P. h. cynocephalus*, *P. h. papio* and *P. h. ursinus*) populations, Hill and Dunbar [2002] found a negative correlation between overall time spent feeding and the proportion of feeding time devoted to fruit and seeds. They noted that previous research has in-

licated that the two most important food components for baboons are carbohydrates and protein [Hamilton et al., 1978; Altmann, 1991, 1998; Barton and Whiten, 1994], and suggested that a diet higher in these two food components – predominant in fruit and seeds, respectively – enables baboons to reduce time spent feeding. Their reliance on doum palm fruit – high in carbohydrates, iron and amino acids – may thus enable this population to reduce their overall feeding time compared to baboon populations living in semi-arid habitats without palms. We would expect that hamadryas in other parts of their range, where habitats are drier and of poorer quality in general, would spend a far greater proportion of their time feeding than those at Filoha. That the greatest proportions of time spent feeding, across baboon populations, have been found among the Kuiseb River and Cape Peninsula chacmas (at least in one study) supports the idea of a general association between low habitat quality and greater time spent foraging, as Kuiseb River is far more arid than other baboon habitats (18 mm of annual rainfall compared to 500 mm at Filoha [Hamilton et al., 1976; Swedell, 2006]), and the Cape Peninsula is dominated by the locally endemic fynbos, a low-quality food resource [Davidge, 1978b; Cowling et al., 1996].

Overall, hamadryas appear to resemble other baboons in their wide dietary breadth and apparent selectivity (table 2). A comparison across populations, however, suggests that hamadryas may consume a narrower array of plant species than other baboons. While many baboon populations appear to subsist largely on *Acacia* trees and shrubs where they occur [DeVore and Hall, 1965; Hamilton et al., 1978; Ransom, 1981; Norton et al., 1987; Barton et al., 1993], the number and types of other plants included in the diet vary widely across sites. Similar to the 44 plant species observed being eaten by baboons in this study (32 of which were observed being eaten by focal males during focal samples), 45 plant species contribute to the diet of olive baboons at Laikipia Plateau, Kenya, where *Acacia* species comprise almost a third (29%) of the total diet [Barton et al., 1993]. By contrast, anubis baboons at Gombe consume at least 75 (62 identified) plant species [Ransom, 1981], chacma baboons of the Cape Peninsula consume at least 94 plant species [DeVore and Hall, 1965; Davidge, 1978b], and yellow baboons in Mikumi National Park, Tanzania, consume at least 185 plant species [Norton et al., 1987]. Such comparisons must be made with caution, however, as floral diversity varies widely across baboon sites. Laikipia and Filoha, for example, likely share a lower plant species richness than Gombe and Mikumi in Tanzania and the Cape Peninsula of South Africa, where baboon dietary breadth is correspondingly higher. Moreover, the length of a study will inevitably increase the number of food items recorded; for example, it is likely that the 185 plant food species of yellow baboons in Mikumi National Park, Tanzania, are due to the lengthy study period (5 years) rather than a substantially broader diet by this population compared to other baboons [Norton et al., 1987].

The seasonal patterns observed in this study are broadly similar to those at Mikumi, where only 7 of the 185 plant species in the baboons' diet were eaten across all 12 months of the year. Similar to Filoha, the greatest number of plant species at Mikumi was consumed at the end of the wet season in April and May, while the fewest species were consumed at the end of the dry season in October [Norton et al., 1987]. There were no seasonal patterns in plant food species, however, for yellow baboons in gallery forests along the Tana River in Kenya. At Tana River, the number of plant food species ranged from 11 to 38 over 7 months; when rainfall was highest in Janu-

ary and February, 17 and 27 species, respectively, contributed to the diet [Wahungu, 1998]. It is possible, however, that this study took place over too short a period (7 months) for seasonal patterns to emerge.

With the obvious exception of desert chacmas in Namibia, hamadryas have been traditionally described as living in poorer-quality habitats than most other baboon populations. The scarce and widely dispersed resources in their characteristic habitat have often been drawn on as a causal factor in the evolution of their unusual social system in which one-male units disperse from one another during foraging, presumably in order to avoid feeding competition. Indeed, hamadryas habitats consist largely of scrubland and, as such, are generally hotter and drier with a lower floral abundance and diversity than the habitats of other baboons. Hamadryas travel for greater portions of their day than other baboons, suggesting that they may need to do so, either in their current or past habitats, in order to obtain enough food [Swedell, 2002b, 2006].

The reduced time that hamadryas spent feeding in this study, however, belies their apparent need to expend more effort to obtain sufficient food resources. This can likely be explained by the presence of doum palms within the home range of this population, which may obviate the need for these baboons to expend as much energy as other baboon populations to reach the same energy intake.

Optimal foraging theory predicts that animals will travel and forage in a way that maximizes energy return for effort expended, and Schoener [1971] proposed a dichotomy between 'time minimizing' and 'energy maximizing' as two strategies to achieve this goal. The longer wet season path lengths found in a previous study at Filoha [Swedell, 2002b] suggest, at first, that this population of hamadryas may be characterized as 'time minimizers' in the dry season but 'energy maximizers' in the wet season [Schoener, 1971]. However, the subjects of this study did not spend more time feeding in the wet season, and feeding time did not vary across the months of the year in a way that was predictably associated with rainfall or temperature (table 1).

One way to reconcile the inconsistency in patterns of seasonality between path lengths and time spent feeding is to consider time spent *searching* for food, a behavioral category that was not included as feeding time in this study. Swedell [2006] found that band 1 at Filoha, as a whole, spent only 6% of its time exclusively foraging, but at least some members of the band were foraging during about half of all scan samples: the band as a whole spent 16% of their time traveling and foraging; 19% resting, grooming and foraging, and 5% resting, grooming, traveling and foraging. This suggests that band 1 spends up to 46% of its time acquiring food, a figure that is well within the range of feeding time for all other baboon populations except the desert chacmas of Namibia. Unfortunately, Swedell [2006] did not compare activity budgets across seasons, so we cannot yet assess possible seasonal variation in food acquisition time as measured above, but it does seem likely that feeding-related behavior comprises a larger proportion of hamadryas activity budgets than suggested by the results of the present study. Future analyses using a more robust data set will be crucial to elucidate further the relationship between seasonality, food abundance, travel patterns, feeding time and food intake in hamadryas baboons at Filoha and how their seasonal patterns of behavior compare to those of other populations.

Conclusions

In summary, the main plant food components of the diet of adult male hamadryas baboons, as measured by time spent in feeding bouts, were doum palm fruits and various parts of *A. senegal* (depending on the time of year). Dietary breadth, defined as the number of plant foods contributing to the diet, was reduced during the dry months of the year, and 4 plant species in particular comprised the diet almost exclusively during some of these months. Overall, it appears that hamadryas baboons consume fewer plant taxa compared to other baboon subspecies and that this difference is most pronounced during the dry season. The high abundance of doum palms, a high-quality and preferred food resource, may underlie the lack of dietary breadth and the reduced feeding time of the study subjects compared to other baboons.

Generalizations from this study and comparisons to other taxa must be made with caution, however, for several reasons. First, this study took place over only a 1-year period, an insufficient amount of time to fully characterize baboon diets, which can vary widely from one year to the next [Norton et al., 1987]. Second, these data derive from only 1 week of observation per month and are thus underestimates of dietary breadth. Third, this study focused on only adult males, which are less constrained by food intake than females because they do not undergo the costs of gestation and lactation. For these reasons, diets often differ between the sexes [Bercovitch, 1987; Barton, 1990; Muruthi et al., 1991], and further study of females in this population may yield a different pattern. Finally, this study did not take into account food availability or variation in use of parts of plant species and is thus limited in its ability to characterize dietary diversity and selectivity. More detailed study of the diet of females in addition to that of males, as well as the relationship between food availability and diet should enable more robust comparisons between hamadryas diets and those of other baboons as well as other savanna- and semi-desert-dwelling primates.

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