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Ranging Behavior, Group Size and Behavioral Flexibility in Ethiopian Hamadryas Baboons *(Papio hamadryas hamadryas)*

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Key Words
Hamadryas baboons · Behavioral ecology · Group size · Home range size · Daily path length · Seasonality · Diet

Abstract

This study reports group size, home range size, daily path lengths, seasonal effects on ranging behavior and qualitative information on diet for a population of hamadryas baboons inhabiting the lowlands of the northern Rift Valley in central Ethiopia. The minimum home range size and daily path length for this population are similar to those reported for other populations of hamadryas baboons in Ethiopia and Saudi Arabia. Group sizes, however, are much larger than those in most other hamadryas populations for which published data are available. The large group sizes in this area may be related to the abundance of one food resource in particular, doum palm nuts. Overall, this study suggests that hamadryas baboons may be more flexible in some aspects of their behavioral ecology (e.g. group size) than in others (e.g. ranging behavior).

Introduction

Hamadryas baboons *(Papio hamadryas hamadryas)* range throughout the semi-arid regions of the Horn of Africa, including parts of Ethiopia, Sudan, Somalia, Djibouti and Eritrea [1–3], as well as the southwestern tip of the Arabian peninsula in Yemen [4] and Saudi Arabia [5, 6]. Called ‘desert baboons’ to distinguish them ecologically from other *Papio* baboons (‘savanna baboons’ and ‘mountain

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baboons'), hamadryas baboons are unusual among primates with regard to their complex, multi-level social system (shared only by geladas) and their extreme male-dominated society, both of which have been interpreted as adaptations to a harsh semi-desert environment [1, 7, 8].

Three main levels of organization characterize hamadryas society [1, 9, 10]. *Troops* are large aggregations that assemble at sleeping sites but do not otherwise function as cohesive social groups. Each troop includes one or more *bands*, here referred to as *groups*, whose members are spatially cohesive and coordinate their movements. The band, or group, is the social unit analogous to the 'troop' or 'group' of other papionin monkeys [7]. Within each band are a number of *one-male units*, each consisting of one 'leader' male, one or more females, their dependent offspring and sometimes one or more 'follower' males. Cohesion of one-male units is maintained by aggressive herding behavior of leader males, who threaten and bite females that become spatially or socially separated from their unit. Also within bands are 'solitary' males, males who are not associated with any one-male unit in particular. Abegglen [10] observed a fourth level of social organization between that of bands and one-male units, the *clan*. Abegglen reported that members of each clan were spatially and socially distinct from other clans, both during daily travel and on the sleeping cliffs. The clan structure was also observed by Stolba [11] in other bands near Erer Gota.

Our understanding of hamadryas behavioral ecology comes largely from the work of Kummer and Kurt [1, 9], who surveyed several hamadryas groups, including the 'White Rock' group, near Erer Gota, Ethiopia, over a period of 12 months in 1960 and 1961. Subsequently, Nagel [12, 13] compared the behavioral ecology of a hamadryas group near Awash Station, about 170 km southwest of Erer Gota, with an anubis (*P. hamadryas anubis*) group in the same area. Additional data on hamadryas behavioral ecology were collected by Sigg and Stolba on the 'Cone Rock' group near Erer Gota in the mid-1970s [14, 15]. In this paper, I report results from a 14-month field study of a group of wild hamadryas baboons inhabiting a region in the far north of the Awash National Park, about 180 km southwest of Erer Gota, and compare these results to those from studies of wild hamadryas baboons in Ethiopia, Eritrea, Saudi Arabia and Yemen.

Methods

Study Site

Awash National Park is located in the semi-arid lowlands of the northern Rift Valley of Africa, about 150 km east of Addis Ababa, Ethiopia. The southern boundary of the park is formed by the Awash River, along which there is a zone of hybridization between hamadryas *(P. hamadryas hamadryas)* and anubis *(P. hamadryas anubis)* baboons that has been the subject of long-term investigation by the Awash National Park Baboon Research Project [16, 17]. The northern boundary of the park is formed by the Kesem River (a tributary of the Awash), the Awara Melka State Farm and the accompanying village of Sabure, and an area of hot springs known as Filoha ('fil woha' means 'hot water' in Amharic). At Filoha lies the northern-most outpost of Awash National Park and a cliff commonly used as a sleeping site by hamadryas baboons. An area of about 5 km^2 immediately surrounding the Filoha outpost consists largely of hot springs, doum palm trees *(Hyphaene thebaica)*, palm scrub and tall marsh grasses. The surrounding area resembles typical hamadryas habitat [1, 7] in that it is essentially a semi-arid thornscrub dominated by several species of shrubby *Acacia*.

The Awash region has two periods of seasonal rainfall: the long rains, occurring for 2–3 months between late June and September, and the short rains, occurring sporadically and intermittently between February and May. Of the 500–600 mm of annual rainfall reported by the park headquarters, 40 km south of Filoha [13, 18], the vast majority falls during the long rains, or wet season, of July and August. The drier months are generally about 2˚C warmer (average afternoon shade temperature 34.4˚C) than the rainy months (32.7˚C), with a peak of dryness and temperature (averaging 36˚C) in May and June, just before the beginning of the wet season.

Subjects

At least five groups (bands) of hamadryas baboons range throughout the Filoha area (both in and outside the park) and sleep on numerous cliffs, each 5–10 km apart. For the purposes of this study, three main groups (groups 1, 2 and 3) were identified, and group 1 was chosen as the main study group. In April 1998, group 1 consisted of about 175 individuals: 46 adult females, 10 subadult females, about 30 adult males (24 of whom were leader males of one-male units), about 10 subadult males and at least 80 adolescent males, juveniles and infants. The sex ratio of adult females to adult males ranged from 1.3 to 1.8 over the course of the study period. The two main sleeping cliffs of group 1 were the eastward-facing cliff at Filoha, about 200 m from the Filoha outpost, and a westward-facing cliff near the village of Wasaro, about 4.3 km from the Filoha cliff.

Behavioral Observations

Group 1 was observed on and off for a total of about 14 months between October 1996 and September 1998. Groups 2 and 3 were observed for a period of 2–3 weeks each during April and May 1997. Qualitative observations and data from groups 2 and 3 were used only to confirm that the broad patterns of behavior observed in group 1 were typical of this population of hamadryas baboons. A total of 986 h over 262 days were spent in contact with one or more baboon groups. Observation days and data collected, however, were not evenly distributed throughout the study period. No observations were conducted between May 29 and December 7, 1997, due to a field accident and the subsequent recovery period. Additionally, very few observation days were possible during the 1998 wet season (between late June and September) because observations and access to sleeping sites other than Filoha were hindered due to heavy rain and flooding. Therefore, most observations took place during the 1996–1997 dry season (November 1996 to May 1997) and the 1997–1998 dry season (December 1997 to June 1998).

Behavioral observations were made every day that group 1 had slept at the Filoha cliff the previous night, and also on some days that the group slept at the Wasaro cliff the previous night (depending on access to a vehicle and weather conditions). Follows began at dawn and lasted as long as possible each day, though the majority were cut short of a full day because the group was traveling too fast to keep up with it, the group traveled through an area of marshy swamp or hot springs that was not traversable by the human observer, or continuous heavy rain made observation impossible. When the group was traveling, the direction of travel and all changes in direction of travel (using a compass) were recorded as they occurred. Because the broader study (reported elsewhere) of which these results are a part did not focus on feeding ecology, systematic data on feeding behavior were not recorded. However, the identity, if known, of all food items that the baboons were observed eating was recorded ad libitum.

For analysis of ranging patterns, a map of the Filoha-Wasaro area was constructed using topographic maps based on satellite images obtained from the Ethiopian Mapping Authority in Addis Ababa. Landmark data were collected with a handheld Magellan 2000 GPS unit (with 100-meter error) and used to fit points on the map to known locations in the baboons' home range. Travel directions and durations recorded during daily follows were transcribed onto the map, and path lengths were calculated using a known scale.

Results

Group Size

Group 1 consisted of about 150 individuals in November 1996 and about 170 in September 1998. Groups 2 and 3 consisted of about 200 and 220 individuals, respectively. A fourth group consisted of at least 100 individuals, and a fifth group consisted of about 50 individuals. Smaller groups of fewer than 30 individuals were observed on two occasions, but it is not known whether these were the same group. As such smaller groupings were observed only twice over a period of 14 months, it is likely that they were temporary foraging parties (e.g. clans) of a larger group (band).

Home Range Size

The estimated minimum home range size for group 1 is 30 km^2. Group 1's home range is undoubtedly much larger than this, however, because the group was often lost or left while traveling towards, and presumably beyond, the edges of the mapped area. There were also several periods, including a 25-day period during the 1998 wet season, when group 1 could not be found at any of its known sleeping sites and was probably ranging southwest of Wasaro, closer to Mt. Fantalle and outside of the estimated home range area.

Daily Path Length

Of the 30 days for which a complete daily path for group 1 was mapped (i.e. those days for which their starting and ending points were known and they were followed for most or all of their route), path lengths varied from 3.2 to 11.2 km, with an average of 7.5 km. Some daily path lengths are minimum figures because the group was not followed all the way to its sleeping site (because dusk was approaching and the observer had to return to the base camp before dark) but its final destination was confirmed by driving to the sleeping site the next morning. On these days, it was assumed that the baboons followed the shortest path from where they were left to their sleeping site, but they may have followed a more circuitous route instead. Therefore, a mean daily path length of 7.5 km is probably a slight underestimate.

Seasonality

While observations during the dry season far outnumbered those during the wet season, some preliminary results with respect to seasonality can be reported. The 7 wet season routes that were mapped averaged 8.1 km and ranged from 5.0 to 10.0 km. The 23 dry season routes that were mapped averaged 7.3 km and ranged from 3.0 to 11.2 km. The dry season routes were, on average, slightly (though not statistically significantly) shorter than the wet season routes. There was a greater range for the dry season routes (8.2 km) than for the wet season routes (5.0), however, and the longest routes occurred during the dry season, not the wet season. The only routes that were greater than 10 km (n = 3) occurred during the dry season, and the only routes that were less than 5 km (n = 4) also occurred during the dry season. A greater range for wet season routes (similar to that for dry season routes) would most likely result from a larger sample size, as it is unlikely that my sample of 7 wet season routes is representative for this population.

Table 1. Group size, home range size and daily path length of Filoha hamadryas baboons compared to Erer Gota, Ethiopia, Awash Station, Ethiopia, Saudi Arabia and Yemen

Filoha (this study)	Erer Gota, Ethiopia [1]	Erer Gota, Ethiopia [15]	Erer Gota, Ethiopia [10]	Awash Station Ethiopia [13]	Saudi Arabia [5]	Saudi Arabia [20, 23]	Yemen [4]
Group (band) sizes observed							
50–220	30–90	62–95	52–90	51–57	13–70	9–102	22–89
Estimated home range size, km^2							
30	n.r.	28	n.r.	n.r.	n.r.	9.31	n.r.
Daily path lengths, km							
3.2–11.2 mean 7.5 (n = 27)	4.1–19.2 mean 13.2 (n = 9)	mean 8.6 (band I; n = 57) mean 10.4 (band II; n = 13)	n.r.	mean 6.5 (n = 7)	n.r.	1.04–14.03 (mean n.r.)	n.r.

n.r. = Not reported.

During the 1998 wet season, group 1 spent a greater percentage of time away from Filoha than during either dry season. For a period of 25 days from August 4 to August 28, 1998, group 1 did not sleep at either the Filoha cliff or the Wasaro cliff. During this time it was suspected, but not confirmed, that group 1 was using a sleeping site several kilometers to the southwest of the Wasaro cliff.

Diet

The main food items eaten year-round were the nuts of doum palm trees *(Hyphaene thebaica)* and the leaves, flowers, pods and seeds of *Acacia senegal* and *A. mellifera*. Other common food items were grass seeds, blades and flowers, *A. nubica* leaves and seeds, and *Grewia tenax* berries. Grass roots, *A. tortilis* seeds and sap from *A. senegal* were also occasionally eaten. Both the doum palms and most *Acacia* species appeared to be variable enough in their reproductive cycles so that there were ripe palm nuts as well as *Acacia* flowers and young leaves available year-round. On three occasions, I observed baboons (2 adult males and 1 adult female) eating Abyssinian hares *(Lepus capensis habessinicus)*, which are common in the region.

Discussion

Table 1 shows the group size, home range size and daily path length of group 1 at Filoha compared to other populations of wild hamadryas baboons for which published data are available. The group sizes at Filoha are considerably larger overall than those reported for most other hamadryas populations. However, stable groups of 120–190 baboons, similar to group sizes observed at Filoha, have been observed on cliffs along the Wabi-Shebeli River, south of Awash [A. Mori, pers. commun.], and bands of over 200 baboons have been observed at Durfo, Eritrea [19]. Filoha is therefore not the only site where hamadryas baboons form groups of 200 individuals or more.

While the estimated home range size for group 1 at Filoha is clearly an underestimate and reflects mainly the dry season only, some comparative statements can be made. Not only is the home range for this population much larger than Saudi Arabian populations for which home range data are available (9.3 km^2 in the Alhada Mountains of Saudi Arabia [20]), but it is as large *or larger* than home ranges for other hamadryas populations in Ethiopia (28 km^2 at Erer Gota [15]). A larger home range size for the Filoha population would not be surprising, as group sizes at Filoha are larger as well and socioecological theory would predict a positive relationship between group size and home range size, a pattern that generally holds among primates [21]. Unfortunately, comparative data from other hamadryas sites are currently limited to the above two, as Kummer [1] and Nagel [13] did not report home range sizes; Abegglen [10] did not follow his study group away from the sleeping sites; and Kummer et al. [5], Biquand et al. [22, 23], Al-Safadi [4] and Zinner et al. [3, 19] conducted only surveys and so did not report ranging data (table 1).

On average, daily path lengths of the Filoha hamadryas baboons are shorter than those reported by Kummer [1] for the White Rock troop near Erer Gota, who ranged from 4.1 to 19.2 km a day, averaging 13.2 km for the 9 daily routes that Kummer and Kurt [9] were able to map. The Filoha path lengths are comparable, however, to those of Nagel's hamadryas study group near Awash Station (which averaged 6.5 km over 7 routes), Sigg and Stolba's study groups at Erer Gota (which averaged 8.6 km over 57 routes for band I and 10.4 km over 13 routes for band II) and Boug's population in the Alhada Mountains of Saudi Arabia (which ranged from 1.04 to 14.03 km; no average or number of routes reported).

Results from Filoha show a slight, but not statistically significant, effect of seasonality in that wet season daily path lengths were slightly longer than dry season daily path lengths. Boug et al. [20] found a similar relationship between seasonality and daily path length for the hamadryas baboons at Alhada Mountain in Saudi Arabia. There, the baboons had the smallest home range and shortest daily path length in August, the driest month, and the longest daily path lengths in April, when vegetation was more abundant. Both of these studies suggest a pattern of longer daily path lengths during periods of resource abundance and shorter path lengths during periods of resource scarcity, a pattern opposite to that predicted by socioecological theory [21]. At Filoha, this pattern may be explained by the fact that the Filoha hot springs are a reliable year-round source of water for baboons. During the dry season, the baboons may need to come to Filoha if only to obtain drinking water, whereas during the wet season there is standing water available elsewhere. Although the baboons clearly use other resources in the Filoha area besides the water (e.g. doum palm nuts), they are not as dependent on Filoha as a water source during the wet season and may be more flexible in their ranging behavior during this time than during the drier months. Whether the baboons actually travel farther per day during the wet season or simply range in a slightly different area is not yet clear. Further observations of the Filoha population during the wet season will add to this data set and help to clarify the relationship between seasonality and ranging patterns in this population.

Aside from the larger group sizes and probable larger home range sizes, the main ecological difference between the Filoha hamadryas and other hamadryas populations was the apparently high frequency with which baboons at Filoha ate

doum palm nuts. Palm nuts are presumably high in fat and probably satisfy a large portion of a baboon's daily caloric requirements. The high abundance of palm nuts in the Filoha area may be one factor allowing the large group sizes there compared to other areas where hamadryas have been studied. Further studies focusing on the feeding ecology of this population, ongoing at the present time, will provide quantitative data on patterns of feeding behavior and should further elucidate the relationship between resource availability and social structure in hamadryas baboons.

Although palm nuts appeared to be an important resource for this population and were available within a short distance of one of their primary sleeping cliffs, the baboons still traveled up to 11 km (or more) each day. There may have been some critical nutrient, not available in palm nuts, that the baboons were seeking in these other areas. Although the baboons were not directly observed eating anything in these other areas that was obviously unavailable at Filoha, systematic data on feeding behavior were not collected and so other food resources may have been easily overlooked. Alternatively, the Filoha hamadryas population may be to some degree constrained by its phylogenetic history in that it need not travel more than a couple of kilometers each day in order to satisfy its caloric and nutritional requirements and yet it does so anyway. Hamadryas baboons, due to their presumable evolution in a semi-arid environment where food resources are scarce [8], may be to some extent genetically predisposed to range a certain minimum distance per day, or at least a minimum distance over a several-day period, even if food resources are relatively abundant. Many aspects of hamadryas behavior, such as male herding and 'notifying' (whereby one male quickly approaches, looks at, presents to and then leaves another male), appear to be invariable under a wide array of environmental conditions [24, 25], and hamadryas ranging behavior may be no exception to this pattern. Lackman-Ancrenaz [26] found that a group of hamadryas baboons in Taif, Saudi Arabia, still traveled long distances each day and exhibited a multi-level social system typical of wild hamadryas even though they could probably meet all of their food requirements by feeding at the city garbage dump. This observation suggests that the hamadryas multi-level social system and ranging patterns, although they may have originally evolved for ecological reasons, do not readily revert back to a social system with more cohesive groups and shorter travel lengths even when ecological conditions are favorable.

On the other hand, Nagel [13] found that his hamadryas study group near Awash Station had a significantly shorter mean daily path length than the hamadryas groups near Erer Gota. Compared to Erer Gota, a semi-arid region more characteristic of typical hamadryas habitat, Nagel's group inhabited an area of gallery forest along the Awash River, and its home range probably also included the Awash Station garbage dump, a site at which baboons have often been observed foraging [C. Jolly and J. Phillips-Conroy, pers. commun.]. Nagel's results suggest, therefore, because the habitat near Awash Station appears to be richer in resources than that around Erer Gota, that there may in fact be a relationship between local environmental conditions and hamadryas ranging patterns. The mean daily path length of Filoha hamadryas baboons (7.5 km) is intermediate between that shown by the Awash Station (6.5 km) and the Erer Gota hamadryas baboons (8.6 km, 10.4 km and 13.2 km; table 1). If Filoha is also intermediate in habitat quality between Awash Station and Erer Gota, then the relationship between habitat quality and daily path length among these 3 sites suggests that hamadryas baboons may be

somewhat flexible in their ability to adjust their ranging patterns to resource availability. Although rainfall data for these 3 sites are not available, qualitative observations suggest that Filoha is indeed intermediate in habitat quality due to its being generally drier than the riverine forest of Awash Station but richer than Erer Gota due to the presence of hot springs and doum palms as additional resources.

In summary, the main ecological traits distinguishing the Filoha population from other hamadryas populations are the large group sizes, the probable larger home range sizes, and the apparent importance of doum palm nuts as a food resource. Despite the year-round availability and exploitation of palm nuts, however, the Filoha hamadryas baboons were similar in their daily path lengths to other hamadryas populations, and their home range sizes may in fact be larger than those reported for other sites. At Filoha, the availability of an abundant, year-round food resource such as doum palm nuts results in larger group sizes but not reduced home ranges and daily path lengths. This suggests the possibility that hamadryas ranging patterns, like some aspects of hamadryas male behavior [24, 25], may be less flexible and somewhat independent of local environmental conditions, whereas hamadryas group size may vary depending on the distribution and abundance of local resources. Further studies of wild hamadryas, both in the Horn of Africa and the Arabian peninsula, will undoubtedly shed further light on the relationship between ecology and behavior in hamadryas baboons.

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