

The Influence of Resource Distribution on the Social Structure and Travel Patterns of
Wild Hamadryas Baboons (*Papio hamadryas*) in Filoha, Awash National Park, Ethiopia

by

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Abstract

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Amy L. Schreier

Advisor: Larissa Swedell

Hamadryas baboons (*Papio hamadryas*) are well-known for the flexible, multi-level social structure distinguishing them from other species of the genus *Papio*. The evolution of this social structure has often been attributed to the scarce and widely dispersed distribution of resources in hamadryas habitats, but such an association between food availability and social structure in hamadryas baboons has never been shown quantitatively. Additionally, several studies suggest that hamadryas baboons use their home range unevenly, corresponding to the location of important resources. In this dissertation I quantified the distribution and abundance of resources in the home range of a band of hamadryas baboons at the Filoha site in Awash National Park, Ethiopia, and systematically investigated the relationship between resource availability and changes in the baboons' multilevel social structure, home range use, and travel patterns.

I surveyed the vegetation structure of the Filoha region, quantifying the density and distribution of resources in the home range of Band 1 of the Filoha hamadryas population. From March 2005 through February 2006, I conducted all-day follows of Band 1, during which I recorded the baboons' travel routes and quantified spatial cohesion at each level of hamadryas social structure.

Unlike other known hamadryas sites, the Filoha region includes permanent hot springs and doum palm fruit, a preferred food resource, in proximity to a commonly used sleeping cliff. Band 1 had a large home range of at least 38.6 km² and traveled an average of 8.3 km each day, despite both the high availability of doum palm fruit and the presence of a permanent water source near the Filoha cliff. The baboons at Filoha also still displayed the multilevel social structure typical of hamadryas even though resource distribution did not necessitate breaking up into smaller units to obtain sufficient food during most of the year. Band 1 at Filoha, however, exhibited greater plasticity with regard to its social system than its ranging patterns. The large band and clan sizes at Filoha compared with those at other hamadryas sites likely reflect the high abundance and availability of doum palm fruit.

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CHAPTER 1

INTRODUCTION

Hamadryas baboons (*Papio hamadryas*) are well-known for their flexible, multilevel social structure distinguishing them from other species of the genus *Papio*. The evolution of this social structure has often been attributed to the scarce and widely dispersed distribution of resources in hamadryas habitats (Kummer 1968a, 1971, 1995; Dunbar, 1988), with the assumption being that larger units of social structure break up into smaller units as food availability decreases and food distribution becomes patchier. However, an association between food availability and social structure in hamadryas baboons has never been shown quantitatively.

Additionally, several studies have suggested that hamadryas baboons travel as if they have knowledge of the spatial layout of their environment and use their home range unevenly, corresponding with the location of important resources (Kummer, 1968a, 1971; Sigg and Stolba, 1981; Sigg, 1986). Little work, however, has been conducted on hamadryas feeding ecology and foraging behavior, and how these vary with spatial and temporal variation in local food distribution.

The aims of this study are to quantify the distribution and abundance of resources in the home range of a band of hamadryas baboons at the Filoha site in Awash National Park, Ethiopia, and to systematically investigate the relationship between resource availability and changes in the baboons' multilevel social structure, home range use, and travel patterns.

1.1 Resource Distribution, Social Structure, and Travel Patterns in Primates

Animal ranging behavior tends to occur within the context of foraging, and travel patterns are thus closely tied to the distribution of food resources (Kinnaird and O'Brien, 2000; Milton, 2000). The foraging demands of primates in particular may exceed those of other mammals because primates tend to be large-bodied and social and therefore must choose food patches that are sizeable and abundant in order to feed the whole group and minimize feeding competition (Janson, 2000). When food and water resources are patchily distributed in both time and space, animals may need to structure their ranging and foraging strategies accordingly (Milton, 1981; Oates, 1987). One way for primates to ensure that they find sufficient food is to break up into smaller foraging parties when resources are sparse and widely dispersed. Foraging may also be enhanced by using strategies that increase the likelihood of encountering preferred feeding items, such as traveling in straight lines between them (Garber and Paciulli, 1997; Menzel, 1997; Milton, 2000). Successful travel decisions incorporate information about various ecological factors, such as the location and patterns of changing resource abundance (Garber and Dolins, 1996).

1.1.1 Resource Distribution and Social Structure

The distribution of food resources is commonly thought to be a primary determinant of primate social structure and social organization (Crook and Gartlan, 1966; Eisenberg et al., 1972; Clutton-Brock and Harvey, 1974, 1977; Wrangham, 1980; van Schaik, 1983; Terborgh and Janson, 1986; Isbell, 1991; Sterck et al., 1997). Many primate species alter the size of their feeding parties in relation to the size and dispersion of food patches and these changes in party size appear to reduce intragroup feeding

competition (e.g., Chapman et al., 1995; Newton-Fisher et al., 2000). In fission-fusion social groups, members of a community split up when food patches are small and then come together when resources are abundant enough to accommodate more individuals (Wrangham, 1977, 1986; Isabirye-Basuta, 1988; Chapman, 1990a; Symington, 1990; Suarez, 2003). Thus, spatial cohesion of community members is reduced when patches are small and is greater in areas of higher resource abundance.

The fission-fusion system is most common in chimpanzees (*Pan troglodytes* spp.) and spider monkeys (*Ateles* spp.). For chimpanzees, it has been hypothesized that such a social system may minimize intragroup feeding competition, as their main resource, fruit, is generally patchily distributed (Wrangham, 1977, 1986). The abundance of fruit in each patch may constrain party size, with intragroup feeding competition forcing individuals into smaller parties. Previous studies have indicated that the size of chimpanzee foraging parties is correlated with food patch size (e.g., Isabirye-Basuta, 1988; Chapman et al., 1994; Boesch, 1996).

Spider monkeys also rely mainly on ripe fruit and display a fission-fusion social system across study sites (Chapman, 1990a; Symington, 1990; Suarez, 2003). As in chimpanzees, party size is positively related to patch size (Symington, 1990; Chapman et al., 1995; Robbins et al., 1991). A fission-fusion social system, thus, seems to be an effective means of adapting to a specific pattern of the spatial and temporal distribution of resources in both chimpanzees and spider monkeys.

1.1.2 Resource Distribution, Home Range Use, and Travel Patterns

Primate foraging efficiency may also be enhanced by using strategies that increase the likelihood of encountering preferred feeding items (Garber and Paciulli, 1997;

Menzel, 1997; Milton, 2000). Prior research suggests that primates are able to perceive and remember patterns of resource availability and incorporate them into their travel decisions. The majority of such support stems from experiments carried out in captive settings. Simulated foraging tasks have shown evidence for spatial memory in redbell monkeys (*Cercopithecus ascanius*: MacDonald and Wilkie, 1990), Japanese macaques (*Macaca fuscata*: Menzel, 1991), and long-tailed macaques (*M. fascicularis*: Menzel, 1996a,b). Experimental and naturalistic field studies of foraging behavior in natural conditions have suggested the use of spatial memory in moustached (*Saguinus mystax*) and saddle-back (*S. fuscicollis*) tamarins (Garber, 1989; Garber and Hannon, 1993; Garber and Dolins, 1996), white-faced capuchins (*Cebus capucinus*: Garber and Paciulli, 1997), and brown capuchins (*C. apella nigritus*: Janson, 1996, 1998). While much work on primate foraging and travel patterns has focused on arboreal frugivores, animals living in savanna environments, such as baboons, likely face similar foraging challenges.

In this study, home range refers to the area through which a group travels over a certain period of time, while travel patterns refers to distances traveled. Ranging behavior includes both home range use and travel patterns. Previous research has shown that home range use among baboons is affected by the spatial distribution of important resources (Barton et al., 1992), and that seasonal changes in their availability influence baboons' travel patterns (e.g., Kummer, 1968a; Altmann and Altmann, 1970; Whiten et al., 1987; Barton et al., 1992). The resources that play the largest roles in determining baboons' home range use and travel patterns are 1) *food* (e.g., Devore and Hall, 1965; Altmann and Altmann, 1970; Barton et al., 1992; Henzi et al., 1992; Altmann, 1998), 2) *water* (e.g., Altmann and Altmann, 1970; Barton et al., 1992; Altmann, 1974, 1998), and 3) *sleeping sites* (e.g., Devore and Hall, 1965; Altmann and Altmann, 1970; Anderson,

1984, 1998, 2000). Other factors that may influence baboons' ranging behavior include predation risk (Cowlishaw, 1997; Hill, 1999), as well as encounters with both conspecifics and local human populations.

Sleeping sites are also key determinants of ranging behavior (Anderson, 1984, 1998, 2000), and this may be especially true for baboons because they tend to have large home ranges with limited suitable sleeping sites (Hamilton, 1982). Primates appear to prefer sleeping sites that limit predators' access and/or enable primates to detect approaching predators (Anderson, 1984, 1998). Primates may also select sleeping sites for their proximity to food and water sources (Anderson, 1984, 2000). Several studies have shown that the abundance and distribution of sleeping sites have a strong influence on baboons' home range use and travel patterns (Sigg and Stolba, 1981; Barton et al., 1992).

1.2 Hamadryas Baboons

1.2.1 Hamadryas Taxonomy and Distribution

Hamadryas baboons live in semi-desert habitats throughout the Horn of Africa (in parts of Ethiopia, Eritrea, Djibouti, Sudan, and Somalia) and the Arabian Peninsula in Yemen and Saudi Arabia (Kummer, 1968a; Kummer et al., 1981; Biquand et al., 1992; Al-Safadi, 1994; Zinner et al., 2001a; Swedell, 2002b, 2006). Hamadryas baboons are one of five major forms commonly recognized in the genus *Papio*: anubis (or olive), chacma, hamadryas, Guinea, and yellow baboons. These baboons have commonly been distinguished at the species level, alternatively classified as five species (e.g., Hill, 1967; Napier and Napier, 1967; Grubb et al., 2003) or two species (e.g., Kingdon, 1974; Smuts et al., 1987). Different forms of baboons, however, are known to hybridize where their

ranges meet (Jolly, 1993), and such hybridization has been extensively documented at the hamadryas-anubis hybrid zone in Ethiopia (e.g., Phillips-Conroy and Jolly, 1981, 1986; Phillips-Conroy et al., 1991, 1992). Consequently, many taxonomists have classified baboons as a single species (e.g., Disotell, 2000), distinguished at the subspecies level according to the phenotypic and geographic distinctions among them (e.g., Szalay and Delson, 1979; Groves, 1993; Jolly, 1993). Currently, the five-species classification of baboon taxonomy is becoming standard, and I will therefore follow it in this dissertation.

1.2.2 Hamadryas Social Structure and Organization

Hamadryas baboons have a complex, multilevel social structure. Its basic component is the *one-male unit* (OMU), consisting of one male, several females, their dependent offspring, and occasionally one or more ‘follower’ males. OMUs are socially and spatially cohesive (Kummer, 1968a, 1971; Swedell, 2006), and most social interaction among females occurs within these units rather than between them (Abegglen, 1984; Swedell 2002a, 2006). The next level of social structure in hamadryas society is the *clan*, comprising two or more OMUs that display spatial cohesion during both foraging and traveling (Abegglen, 1984). Two or more clans comprise the next level, the *band*, which is a stable social unit that travels and sleeps together, though its members often split up into OMUs and clans while foraging. Hamadryas social interaction as a whole occurs almost exclusively among members of the same band. Finally, a *troop* consists of two or more bands. Troops share a sleeping site, but do not otherwise behave as a unified social unit (Kummer, 1968a, 1971).

The cohesion of hamadryas social units at each level appears to be maintained by the aggressive behavior of males, male “respect of possession” of females, and learned

compliance by females. Males forcefully herd the females in their units, threatening and neck-biting those who stray too far from the group or interact with outsiders (Kummer, 1968a; Swedell, 2006; Swedell and Schreier, in press).

1.2.3 Resource Distribution and Hamadryas Social Structure

This male-dominated and rare multi-tiered social organization is thought to be related to the harsh environment that hamadryas baboons inhabit: breaking up into smaller groups presumably allows them to more efficiently exploit their patchy and sparse resources, while larger groups provide protection from predators (Kummer, 1968a, 1971; Stambach, 1987; Dunbar, 1988). An important distinction between the fission-fusion system typical of chimpanzees and spider monkeys and the multilevel social structure of hamadryas, however, is that in the former subgroups are variable in both size and composition over time. By contrast, the OMUs and clans of hamadryas baboons are consistent in their composition over time.

Kummer (1968a,b, 1995) suggested that the size and spatial cohesion of hamadryas groupings are related to resource density and distribution. Kummer's observations suggested that only sleeping cliffs supported troops; permanent water holes and *Acacia* forests with groundwater supported bands; patches of roots covering 500 square feet accommodated clans; and areas of bushes and trees separated by 100 meters or more accommodated only a few individuals, so in these areas the baboons split up into OMUs. Thus, both total band cohesion and individual OMU cohesion is expected to be greatest in areas with high resource density and lowest in less dense locales. In a study of captive hamadryas baboons at the Madrid Zoo, OMUs were more cohesive when food was clumped than when it was dispersed (Gil-Burmann et al., 2001). This general

pattern, however, had neither been explicitly tested nor described quantitatively in wild hamadryas populations prior to this study.

1.2.4 Resource Distribution and Hamadryas Travel Patterns

Hamadryas baboons have large home ranges (over 30 km²) and long daily path lengths (up to 16 km) compared with other primates, both of which are attributed to the sparse distribution of food and water in their habitats (Kummer, 1968a; Sigg and Stolba, 1981; Swedell, 2002b, 2006). Previous research suggests that this pattern of resource distribution influences hamadryas ranging behavior. Kummer (1968a, 1971) reported that the baboons spent a greater proportion of time in areas of their home range containing sleeping cliffs, water holes, and *Acacia* trees than in areas without these resources. The baboons seemed to remember specific locations in their natural environment and appeared to travel between them via the shortest route. When in search of water sources, the baboons appeared to use least-distance strategies to travel from one location to another, and they sped up as they approached a water source even before it was in view (Kummer, 1968a).

Similarly, Sigg and Stolba (1981) reported several lines of evidence suggesting that hamadryas baboons know the spatial layout of their home range. First, they found a strong correlation between departure direction (from the sleeping cliff) and the location (relative to the sleeping cliff) of the midday water hole. Members of bands often split up after leaving the sleeping cliff but reunited at midday water holes, arriving from an assortment of directions and morning travel sequences (Sigg, 1986). Second, the baboons reached frequently visited resources from a wider variety of departure directions than sites visited less commonly. In addition, the baboons' travel speed increased more

frequently before reaching such resources than would be expected by chance, even when those resources were not in sight (Sigg and Stolba, 1981).

1.2.5 Previous Research on Wild Hamadryas Baboons

Hans Kummer and Fred Kurt were the first to publish systematic observations of wild hamadryas baboons. They surveyed and collected behavioral data on several groups of hamadryas baboons near Erer Gota, Ethiopia. Their work was the first to describe the multilevel social structure unique to hamadryas (Kummer and Kurt, 1963, 1965; Kummer, 1968a). Kummer and his colleagues then conducted a series of field experiments in the Awash region of Ethiopia. By trapping anubis baboons and transplanting them into hamadryas groups, they documented and clarified aspects of male hamadryas herding behavior. Hamadryas males consistently herded both hamadryas and anubis females, and they quickly conditioned anubis females – who are not herded in their own troops – to an exclusive following response (Kummer et al., 1970). In another set of experiments, a male and a female were placed in an enclosure together, while another male looked on. When all three baboons were united, the second male did not fight over access to the female, even if he was the dominant male. Kummer and his colleagues termed this phenomenon “respect of possession” and suggested that this was the means by which the male-female pair-bond was maintained and protected (Kummer et al., 1974).

In 1971, several of Kummer’s students returned to Erer Gota and studied “Band 1” of the Cone Rock population until 1977, when they were forced to leave the country due to political reasons. Their work provided the first longitudinal study of wild hamadryas baboons. All members of the band were individually recognized, and this

allowed for detailed demographic and reproductive data to be collected, providing important information on life history parameters (Abegglen and Abegglen, 1976; Sigg et al., 1982). Research during this time also provided the first and most extensive study of hamadryas ranging behavior and travel patterns, quantifying their large home ranges and long daily paths and providing evidence that the baboons possess a “mental map” of their environment (Sigg 1980, 1986; Sigg and Stolba, 1981).

In 1996, Larissa Swedell began work on the Filoha population of hamadryas baboons in Awash National Park, Ethiopia, and research there has continued intermittently ever since (Swedell, 2000, 2002a, 2002b, 2006; Swedell and Tesfaye, 2003). Filoha differs from other hamadryas sites in that it is surrounded by doum palm forests, providing the baboons with access to a preferred food resource (Swedell, 2002b, 2006; Swedell et al., 2008). Swedell focused on the role of females in hamadryas society; she described female reproductive strategies and showed that females interacted with one another and exerted mate choice more commonly than previously assumed for hamadryas baboons (Swedell, 2000, 2002a, 2006; Swedell and Saunders, 2006). A year-long study by Getenet Hailemeskel of the Ethiopian Wildlife Conservation Department described the feeding ecology of “Band 3” at Filoha, and showed that the baboons most frequently consumed doum palm fruit (*Hyphaene thebaica*) and the seeds, leaves, and flowers of several *Acacia* species (Swedell et al., 2008). Current research at Filoha is investigating male reproductive strategies and the role of follower males in hamadryas society.

While most research on wild hamadryas baboons has been conducted in Ethiopia, several studies have been carried out in Eritrea and Saudi Arabia. Dietmar Zinner and his colleagues surveyed hamadryas baboons in Eritrea, documenting their distribution throughout the country and describing group composition (Zinner et al., 2001a,b). A

variety of studies have also surveyed hamadryas baboons in Saudi Arabia. This work has corroborated the existence of the multilevel social structure, and elucidated several differences in the spatial and social consistency of social groupings between Ethiopian and Saudi Arabian hamadryas baboons (Kummer et al., 1981, 1985; Al-Safadi, 1994; Mori et al., 2007).

Hamadryas baboons have also been studied as part of research examining the hybridization of hamadryas and anubis baboons at their hybrid zone in Awash National Park, Ethiopia. The first of these studies was carried out by Ueli Nagel, who compared aspects of ecology and social behavior among a hamadryas group, an anubis group, and a hamadryas-anubis hybrid group (Nagel, 1971, 1973). Hybrid groups and “mixed” groups of hamadryas and anubis baboons have since been studied extensively over the past several decades by members of the Awash National Park Baboon Research Project (Jolly and Brett, 1973; Phillips-Conroy and Jolly, 1981, 1986, 1988; Brett et al., 1982; Phillips-Conroy et al., 1991, 1992; Nystrom, 1992; Beyene, 1998; Bergman, 1999; Jolly and Phillips-Conroy, 1999, 2003; Beehner, 2003).

Overall, socioecological research on wild hamadryas baboons to date has focused on surveying their distribution, describing their multilevel social structure and patterns of social interaction, and investigating male and female reproductive strategies. Far less work, however, has been conducted on hamadryas feeding ecology and foraging behavior, and how they vary with spatial and temporal variation in food distribution.

1.3 Research Questions

The primary objective of this study was to investigate how the distribution and abundance of resources influence the social structure, home range use, and travel patterns of wild hamadryas baboons. The evolution of the flexible, multilevel social structure unique to hamadryas is thought to be related to the wide dispersion and low availability of resources in their habitat (Kummer 1968a,b, 1995), enabling the baboons to split up into individual OMUs when resource density and abundance is lowest. The ecological data needed to test this hypothesis, however, have been unavailable until this point. Furthermore, hamadryas home range use and travel patterns have only been quantified at one site to date (Sigg and Stolba, 1981), and that study did not explicitly examine the role of seasonality in ranging behavior.

I will address the following two main research questions and their accompanying hypotheses:

1. How do the distribution and abundance of resources influence hamadryas social structure? The main hypothesis to be tested is that cohesion at each level of hamadryas society (i.e., band, clan, and one-male unit) is a function of resource density and availability. I expect a direct relationship between cohesion and the density and availability of resources.

This study will explicitly test this association by comparing measures of group spread and social cohesion with measures of resource distribution and availability. The Filoha study site is an especially appropriate place to investigate this question as it is more heterogeneous (due to the presence of palm forests and swamp vegetation as well as arid bush and *Acacia* scrublands) than many other areas of the hamadryas geographic

range and will thus allow comparisons of the influence of various habitat types on hamadryas social groupings.

2. How do the distribution and abundance of resources influence hamadryas travel patterns? The first hypothesis to be tested is that the baboons' travel patterns will reflect the spatial distribution of environmental features. Namely, I expect the baboons to use their home range unevenly, corresponding with the availability of important resources such as food, water, and sleeping sites. The second hypothesis that I will test is that travel patterns will reflect other factors such as the presence of Afar nomads, predators, and conspecifics. I predict that the baboons will change directions and increase their travel speed when they are approached by Afar and that they alter their ranging patterns so as to avoid predators.

In addition to measuring changes in travel patterns over time in response to phenological changes in food and water availability, this study will examine the role of the heavily-used and highly available doum palm fruit on the travel patterns and foraging behavior of this population of hamadryas baboons. It will also provide basic quantitative data on hamadryas baboon feeding ecology and the distribution and availability of resources in their home range, filling a large gap in the baboon literature.

1.4 Outline of Dissertation

Following this introduction, in Chapter 2, I provide information on the study site and study population, as well as a description of my general behavioral observation methods. In Chapter 3, I describe the vegetation structure of the Filoha region in detail, as well as the phenology of important food species. In Chapter 4, I describe the study band's diet by food species and plant type. I also depict the temporal variation in food

consumption and its relation to the abundance of food items in the baboons' home range. In addition, I describe the overall characteristics and temporal variation in the baboons' activity patterns. In Chapter 5, I illustrate the study band's home range use and travel patterns. In Chapter 6, I describe and discuss the social structure and social organization of the Filoha hamadryas population. Having shown that the baboons at Filoha display the multilevel social structure typical of hamadryas baboons, in Chapter 7, I describe variation in spatial cohesion at the OMU, clan, and band levels of hamadryas social organization in relation to resource distribution and availability. Finally, in Chapter 8, I summarize my findings and review the conclusions reached in this dissertation, and discuss how they impact current models of the evolution of baboon social organization.

CHAPTER 2

STUDY SITE, STUDY POPULATION, and METHODS

I conducted research on hamadryas baboons at the Filoha outpost of Awash National Park, Ethiopia (9°6'27"N, 40°0'50"E). Several bands of hamadryas baboons populate the Filoha region. Band 1 has been studied intermittently since 1996 (Swedell, 2000, 2002a, 2002b, 2006; Swedell and Tesfaye, 2003), and was the focus of this study.

In January and July 2004, I constructed an initial map of the Filoha region and began ecological sampling of habitats. The main study period took place from March 2005 through February 2006, during which I collected behavioral data on feeding ecology, habitat use, ranging patterns, social behavior, and spatial cohesion. I also collected phenological data and continued ecological sampling of habitats. In this chapter, I describe the study subjects and my general behavioral sampling methods. Methods specific to analyses of feeding ecology and activity patterns, home range use, social structure and social organization, and spatial cohesion are described in greater detail in chapters 4, 5, 6, and 7, respectively.

2.1 Study Site

Awash National Park is located in the lowlands of the northern Rift Valley in central Ethiopia, about 150 km east of Addis Ababa (Figure 2.1). Filoha is the northernmost outpost of Awash National Park (Figure 2.2), and is surrounded by approximately 2 km² of natural hot springs, doum palm trees (*Hyphaene thebaica*), swamp vegetation, and a 1.5 km-long cliff (Swedell, 2002b, 2006). The outlying area of *Acacia* scrubland and open grassland is characteristic of hamadryas habitat in many other

areas of their range (Kummer, 1968a; Sigg and Stolba, 1981; Biquand et al., 1992; Al-Safadi, 1994; Swedell, 2006). Mt. Fantalle, a dormant volcano about 20 km southwest of Filoha, is the source of the permanent hot springs and other features of the Filoha landscape. The altitude throughout the Filoha region ranges from 750 to 832 meters a.s.l.

2.1.1 Sleeping Sites

Most primate populations, including many baboons, sleep in trees (Altmann & Altmann, 1970; Anderson, 1984, 1998; Anderson & McGrew, 1984; Hamilton, 1982). Unlike other baboons, however, hamadryas baboons (*Papio hamadryas hamadryas*) habitually sleep on cliff faces, presumably because their habitat differs from that of most other baboon populations in containing few trees appropriate for sleeping or aggregations of tall trees that would support a whole group (Kummer, 1968a).

There are at least four cliffs in the Filoha vicinity (Figure 2.3). Band 1 slept on both the Filoha and Wasaro cliffs over the main study period (section 5.3.3). (Descriptions of each of these cliffs are provided in section 3.1.6.) Previously, the baboons were observed sleeping on the cliff 4 km west of the Wasaro cliff (Swedell, 2006). No baboons in the Filoha population, however, have been observed using the cliff 3 km east of the Filoha cliff as a sleeping site.

2.1.2 Climate and Seasonality

The Filoha region is characterized by year-round high temperatures. At the Filoha camp, I recorded the daily mean, maximum, and minimum shade temperatures. The mean daily temperature from March 2005 through February 2006 was 31.5° C. The mean

daily temperature did not vary extensively across months, peaking at 34.9° C in June and dipping to 27.7° C in December (Figure 2.4b).

The Awash region typically receives two periods of rainfall. The long rains occur between June and September, and the short rains fall intermittently between February and May (Swedell, 2006). During the main study period, I measured the precipitation at Filoha with a rain gauge. Total rainfall from March 2005 through February 2006 was 606.7 mm, almost half of which occurred during July and August (Figure 2.4a). Between June 30 and August 31, 324 mm of rain fell at Filoha; between October 2005 and February 2006, by contrast, rainfall totaled just 26.5 mm.

For analyses of seasonality, I consider June 30 through August 31, 2005 the wet season, and October 2005 through February 2006 the dry season. Data from March through June 29, 2005 were excluded from such analyses because of the intermediate amount of rainfall during this time period. While just 24.5 mm of rain fell in September, vegetation throughout the Filoha region was still lush from the previous two months' rain. September was also excluded from seasonality analyses, however, as very limited behavioral data exist for this month (see section 2.2.1).

Examination of long-term weather patterns in the Awash region indicates that 2005-2006 was a fairly typical year. Data collected from a weather station in Awash spanning the 50-year period of 1950-2000 show that the average annual temperature in Awash was 32.1° C; the average annual rainfall was 524 mm (European Commission, 2008). Averages for each month over this timespan show that the long-term seasonal patterns are consistent with those of 2005-2006 (Figure 2.4b). Namely, temperature peaks in June and is lowest in December. Furthermore, the majority of rainfall occurs in

July and August, with a period of moderate rainfall between March and June. Very little rain falls from October through February.

2.1.3 Fauna and Predation

In addition to hamadryas baboons, fauna at Filoha include warthog (*Phacochoerus aethiopicus*), lesser kudu (*Strepsiceros imberbis*), and Defassa waterbuck (*Kobus ellipsiprymnus defassa*). Smaller mammals include dik dik (*Madoqua saltiana*), Abyssinian hare (*Lepus capensis habessinicus*), black backed jackal (*Canis mesomelas*), rock hyrax (*Procapra habessinica*), bat-eared fox (*Otocyon megalotis canescens*), porcupine (*Hystrix cristata*), and caracal (*Caracal caracal nubica*). Leopard tortoise (*Testudo pardalis*) and crocodile (*Crocodylus niloticus*) also inhabit the Filoha region. The hamadryas baboons regularly encounter these species around sleeping cliffs and during daily travel. Nocturnal, terrestrial predators of baboons in the Filoha area include lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*). Both can sometimes be heard near the Filoha cliff at night. Historically, predators of baboons in this area also included leopard (*Panthera pardus*). Snakes also inhabit the Filoha region, and a snake bite was the presumed cause of death for at least one baboon (Swedell, 2006).

Despite the presence of predators, I did not witness any predation events. The baboons did alarm call in response to lion vocalizations at night and hyena encounters during daylight, but alarm calls were not systematically recorded so rates of alarm calling cannot be calculated. The baboons appeared to perceive lions to be a greater threat than hyenas. While the baboons only sometimes alarm called in response to hyena vocalizations or sightings, the baboons always alarm called in response to lion roars. While nocturnal predator presence away from the Filoha outpost was not systematically

assessed, my assistants and I sometimes heard lion vocalizations as we approached the Wasaro cliff before dawn and encountered their footprints several times in and around the Doho area, suggesting predation risk throughout Band 1's home range. I discuss the effect of predators on the baboons' ranging behavior in Chapter 5.

2.1.4 Afar Nomads

The Afar, nomadic pastoralists who depend largely on the milk and meat of their camels, cattle, and small hoof-stock, inhabit the lowlands of northeastern Ethiopia (Flood, 1975). As at other Ethiopian hamadryas sites, Afar nomads populate the Filoha region. A common presence around the outpost, Afar regularly bathe and water their cattle in the hot springs. While the Afar do not hunt baboons and do not appear to greatly impact their grouping and ranging patterns (Swedell, 2006; Chapter 5), they do often yell at, chase, and sometimes throw stones and sticks at the baboons. I discuss the Afar's influence on the baboons' travel patterns in Chapter 5.

2.2 Study Subjects

2.2.1 Filoha Population of Hamadryas Baboons

Several bands of hamadryas baboons populate the Filoha region, two of which, "Band 1" ("Group 1" in Swedell 2000, 2002a,b, 2006) and "Band 3" ("Group 3"), have been studied intermittently since 1996 (Swedell, 2000, 2002a, 2002b, 2006; Swedell and Tesfaye, 2003). In February 2006, Band 1 and Band 3 consisted of approximately 210 and 400 individuals, respectively. (Band sizes are inexact as it is difficult to obtain accurate counts of infants and small juveniles due to their small size and unknown identity.) A third band, "Band 2", was sometimes observed on and near the Wasaro cliff,

and numbered about 150 baboons. Another group of fewer than 100 baboons was also occasionally observed on the Wasaro cliff, but it was unclear whether this constituted a fourth band or was a fragment of Band 2. While Band 1 was the main focus of observations, Band 3 was also followed and observed on days when it had slept on a known and accessible sleeping cliff the previous night and Band 1 could not be located.

Because Band 1 has been studied on and off since 1996 and followed year-round by a local field assistant since 2003, the baboons were habituated to such an extent that I was able to follow them and collect travel routes and limited behavioral data immediately upon my arrival in March 2005. During March and April, Teklu Tesfaye, the Filoha Hamadryas Project field assistant, taught me the identities of known individuals. Previously unidentified individuals were recognized and distinguished based on fur color and patterns, facial coloring, scars, and other characteristic markings. By May 2005, I was able to consistently recognize all leader males and adolescent and adult females. The identities of most follower males, unaffiliated males, and juveniles were unknown, however, because of the prohibitively large number of individuals in the band.

From March 2005 through February 2006, I followed and observed Band 1 for 1,342 hours over 159 days. Observations were not distributed evenly over the study period, however, as there were periods of time that I could not locate the baboons (Table 2.1). I observed Band 1 on at least 10 days during each month except September 2005. During this month, I was able to find Band 1 on a known sleeping cliff on only four days. Because Band 1 fissioned in the middle of September (see section 6.3.3), I observed Band 1 in its entirety on only one of the observation days. Due to such limited observations, September data are excluded from analyses.

2.2.2 *Band 1*

At the start of the study period in March 2005, Band 1 consisted of about 190 individuals: 24 leader males, five follower males, about 15 adult and subadult males unaffiliated with an OMU, 54 adult females, nine adolescent females, and at least 80 juveniles and infants. At the end of the study period in February 2006, Band 1 consisted of approximately 210 individuals: 24 leader males, seven follower males, about 20 adult and subadult unaffiliated males, 53 adult females, 13 adolescent females, and at least 90 juveniles and infants (see Table 2.2 for descriptions of age classes used in this study).

From March 2005 through February 2006, a total of 32 adult and subadult males were leaders of a one-male unit (OMU). Table 2.3 shows the OMU composition of Band 1 over this time period. Females that belonged to different OMUs at different points in the study period are listed as members of each OMU to which they belonged. Due to their small size and indistinguishable features, it was difficult to both obtain accurate counts of juveniles and be certain which OMU they belonged to. The number of juveniles listed in each OMU, therefore, is approximate. Furthermore, it was sometimes difficult to ascertain whether OMUs had follower males, and if they consistently affiliated with the same OMU over the course of the study period, and so their numbers are also approximate.

2.3 Data Collection

2.3.1 *Ranging Behavior*

I collected data on ranging behavior (i.e., home range use and travel patterns) by conducting all-day follows of Band 1. Accompanied by a field assistant and/or an Ethiopian Wildlife Conservation Department scout, I located the baboons at their sleeping

cliff at 0600 hours and followed them until 1800, or for as long as possible until we had to leave them in order to arrive at camp before dark. I followed the band on days when the baboons slept on the Filoha cliff the previous night, as well as on some days when they slept on the Wasaro cliff the previous night. On days that the baboons returned to the Filoha cliff, I usually observed them until 1800. On most days that the baboons traveled to and slept on the Wasaro cliff, however, I terminated observations between 1600 and 1700 (depending on their location and distance from Filoha) so that my assistants and I could return to camp before dark. On these days, I confirmed that the band stayed and slept on the Wasaro cliff by locating them there the following morning.

During all-day follows, I mapped the geographic center of the band every 15 minutes (e.g., Sigg and Stolba, 1981) using a Garmin etrex Legend handheld Global Positioning System (GPS) unit. The GPS unit provided positional coordinate readings to the ten-thousandth of a minute, and was accurate to within 10 meters. GPS points were recorded in degrees-minutes (DM), which I then converted into decimal degrees by dividing the minutes by 60, and then adding the degrees. Sometimes I lost the baboons for periods ranging from 15 minutes to two hours during the course of the day when the baboons either traveled through habitat that I could not penetrate, such as dense *Acacia* scrubland, hot springs, or swamp vegetation, or traveled too fast to keep up with. On these occasions, I recorded the GPS coordinates where I relocated the baboons even if it did not fall on the 15-minute mark. On days that I had to leave the baboons to return to Filoha before they actually reached the Wasaro cliff, I used the GPS location of their usual Wasaro cliff sleeping site as the final point of their travel route, and confirmed this location the following morning.

I defined home range as the total area used by the band over the course of the study period. I calculated home range as the minimum convex polygon which includes all recorded locations (from full and partial observation days) using ArcView GIS 3.1 software (ESRI, 2001, Redlands, CA) (Ostro et al., 1999). I also calculated the baboons' home ranges for each month, as well as for both the dry and wet seasons.

Ranging patterns were determined based on observation days for which I recorded complete daily routes (i.e., from the morning to evening sleeping-site locations) (e.g., Altmann and Altmann, 1970; Sigg and Stolba, 1981). I computed daily path lengths by summing the distance between all mapped locations. I analyzed travel routes using ArcView GIS 3.1 software.

2.3.2 Activity Patterns, Habitat Use, and Feeding Behavior

Data on activity patterns, habitat use, and feeding behavior were collected using band scans at 15-minute intervals during all-day follows of Band 1. At each 15-minute interval starting at 0600, I recorded the activity or combination of activities that visible band members were engaged in. Four activities were recognized: rest, groom, travel, and feed. When members of the band were feeding, I recorded food items at the species level, as well as the plant parts being eaten.

During band scans, I also recorded the habitats in which the baboons were located. Five habitat types were recognized: *Acacia* scrublands, palm forests, open grasslands, swamp vegetation, and cliffs (Chapter 3). When the band was spread across more than one habitat, I recorded each habitat type once. When the band spread out too far for me to monitor them all at one time, my field assistant and I stayed on opposite ends of the band and communicated via hand-held radios regarding activity and habitat types.

Simultaneously with the band scans, I also conducted 30-minute focal samples of individual OMUs. At 2-minute intervals, I recorded the activity of the leader male and each adolescent and adult female (section 2.3.3). For grooming, I recorded whether each individual was grooming or being groomed, as well as the identity or age/sex class of the grooming partner. When individuals were feeding, I recorded the food item at the species level and the plant part being eaten whenever possible. These activity and feeding records were not used to compute activity budgets and diets, however, because preliminary analyses indicated that OMU focal samples were heavily skewed toward resting and grooming when all OMU members were more easily monitored, and toward food items eaten while in open areas (see section 4.2). Activity data from focal OMUs were used, however, in analyses of spatial cohesion in different activity states (Chapter 7).

2.3.3 Spatial Cohesion

At the start of each 30-minute OMU focal sample, I recorded the GPS location of the leader male, the identities of the leader male and each adolescent and adult female, and the habitat(s) in which each adolescent and adult OMU member was located. I recorded whether each adolescent and adult individual was on the ground or in a tree, and I noted the species when individuals were located in or underneath a tree.

To measure OMU cohesion, at each 2-minute interval I estimated the distance in meters between the two farthest individuals in the OMU, excluding juveniles and infants. I also estimated the distance in meters between the leader male and each adolescent and adult female, and noted and sketched the spatial relationships between them.

To measure the spread between OMUs and obtain an estimate of band and clan cohesion, I used a 10 m radius of the focal leader male as a spatial cohesion index (e.g., Chapman, 1990b). Within this radius, I recorded the number of OMUs and estimated the distance between the focal leader male and the leader males of the other OMUs. I recorded the identities of the other leader males whenever possible. To increase inter-sample independence, only focal scans separated by 10 minutes were used in analyses of spatial cohesion.

To measure band spread (the distance between the two farthest individuals in the band) more directly, my field assistant and I spread out on either end of the band. Communicating via hand-held radios, whenever possible we each located the baboon that was at the very edge of the band, and took GPS points. I computed the distance between two points via the great circle formula:

$$\text{Distance} = \text{acos}(\sin(\text{lat1}) * \sin(\text{lat2}) + \cos(\text{lat1}) * \cos(\text{lat2}) * \cos(\text{lon1} - \text{lon2})).$$

Spatial cohesion and grooming interactions were quantified for leader males and their females from the 31 OMUs for whom I had at least 50 2-minute instantaneous scan-samples. Table 2.4 shows the OMUs included in these analyses. As mentioned above, to increase independence of samples, I only used scans separated by 10 minutes; the number of scans shown in the table, therefore, represents the number of scans at 10-minute intervals. When the size and composition of an OMU varied over the study period, they were considered separate OMUs. For example, if a leader male had three females but then gained a fourth, data from the period of time in which he had three females were considered separately from when he led a four-female OMU. Thus, the 31 OMUs in the analyses represent just 24 different leader males. Five males – Peach, Shato, Yirdaw, Mac, and Len – had two OMUs each; one male – Teddy – had three OMUs, two with one

female and one with two females. The distinction between a leader male's different OMUs is indicated by the number following his name, which represents the number of females in the OMU. Teddy's two one-female OMUs are distinguished as Teddy1a for when Patch was his only female, and as Teddy1b for when Daisy was his only female.

2.3.4 *Ad Libitum Sampling*

I collected data on a number of other behaviors on an *ad libitum* basis, both within and outside band scans and focal OMU sampling. I recorded observations of extra-OMU interactions, including the participating individuals and a description of the interaction. I also recorded all interactions surrounding takeovers.

I recorded all encounters between baboons and Afar nomads. For each encounter I noted the time, GPS location, and habitat type, as well as the number, age, and sex of nomads and the presence of cattle, camels, goats, and/or donkeys. I recorded a description of the encounter (e.g., nomads walk by, yell at baboons, etc.) and noted whether the baboons altered their behavior and/or travel patterns in response to Afar (e.g., baboons change directions, increase travel speed, etc.).

I recorded Band 1's encounters with other bands during daily travel. I noted the identity of the other band, if known, as well as the time, location, and duration of the meeting. I described inter-band interactions, such as fighting (e.g., how many individuals involved, duration of fight, etc.) and traveling (e.g., bands traveled together, one band changed directions/alterd their travel route due to another band, etc.). When Band 1 shared a sleeping site with another band, I noted the interactions, or lack thereof, between the two bands in the morning and late afternoon, regardless of whether the bands traveled to or from the sleeping cliff together.

In addition, I recorded all interactions with potential predators. I noted the species of the potential predator, the location of the encounter, and the baboons' reactions. I also recorded when lion and hyena vocalizations were heard from the Filoha camp overnight. When footprints were encountered during daily travel, I noted the species they belonged to and the location where they were found. Whenever I observed the baboons hunting or eating freshly killed animals, I recorded the prey species, the location of the encounter, the identity of the hunter if known, and meat sharing behavior.

Band 1 separated for periods of three hours up to 31 days at a time from March 2005 through February 2006. I recorded the circumstances surrounding each of these fissions, including the OMU composition of each subgroup, the duration of the fission, and when and where the band separated and reunited.

2.4 Statistical Analyses

Data were analyzed using Statistica 6 Software (StatSoft, Inc, 2004, Tulsa, OK). I used parametric tests whenever possible (Sokal and Rohlf, 1995); when data did not meet the requirements for parametric statistics I used non-parametric tests (Siegal and Castellan, 1988). All tests were two-tailed with a level of significance set at $p < .05$, unless otherwise noted.

Table 2.1 Observations of Band 1 by month

<i>Month</i>	<i>Hours</i>	<i>Days</i>
March 05	129.0	19
April 05	185.0	19
May 05	140.0	15
June 05	129.5	13
July 05	73.8	10
August 05	78.5	10
September 05	24.3	4
October 05	153.3	18
November 05	85.7	11
December 05	167.2	17
January 06	107.1	13
February 06	68.6	10
Total	1,342.0	159

Table 2.2 Age-sex classes used in this study*

<i>Age-Sex Class</i>	<i>Description</i>	<i>Age Estimates (years)</i>
Black infant	Hair completely or partially black; face and perineal region pink; short snout	0-0.7
Yearling	Hair brown; short snout	0.7-1.3
Small juvenile	Longer snout; sitting height 25-30 cm; no differences between the sexes	1.3-2
Medium juvenile male	Sitting height 30-45 cm; no testicular bulges	2-5
Medium juvenile female	Sitting height 30-45 cm; first sexual swellings	2-4
Large juvenile male	Sitting height 45-55 cm; testes descending	5-6
Adolescent (or subadult) female	Sitting height 45-50 cm; reproductively cycling	4-5.5
Subadult male	Sitting height 55-60 cm; partial growth of mantle; no clear separation of testes	6-10
Adult female	Sitting height 50-55 cm; reproductively cycling regularly	5.5+
Adult male	Sitting height 60-65 cm; mantle fully developed; testes clearly separated	10+

* Based on Swedell, 2006 and Sigg et al., 1982

Table 2.3 Band 1 OMU composition March 2005 – February 2006

<i>Leader Male of OMU</i>	<i>Months as Leader Male</i>	<i>Adult Females</i>	<i>Adolescent Females</i>	<i>Names of Females</i>	<i>Infants</i>	<i>Juveniles</i>	<i>Solitary Males</i>
Andy	12	1	2	Rachel, Amina, Mimi	0	1	0-1?
Asheber	1	1	0	Hasna	1	1	0
Clodio	12	1	0	Clea	0-1	1	0-1
Cory	12	3	0	Sage, Lupy, Olive	0-3	3	0
Dinaw	3	1	0	Megan	0	0	0
DJ	12	0	1	Fugee	0	1	0
Ethan	4	0	1-2	Kate, Chewy	0	0	0
Evanga di	12	3-4	0-1	Yibeltal, Nuriya, Ashenafi, Lefty, Bontu	0-1	3	1
Ford	12	4	2-4	Mercedes, Toyota, Jeep, Porsche, Honda, Fiat, Mazda, Cherokee	0-2	4	1-2
Fruit	6	1-2	0	Mango, Papaya	0-1	2	0-1
Herb	12	4	1	Sony, Iris, Rose, Petunia, Kitten	0-2	4	1
Jack	3	2	0	Jill, Jen	0	2	1
Kalid	12	1	0	Marta	0-1	1	0-1
Len	10	0-1	1-4	Lila, Maxine, Mary, Maggie, Lee	0-2	0-1	0

Table 2.3 (cont.)

<i>Leader Male of OMU</i>	<i>Months as Leader Male</i>	<i>Adult Females</i>	<i>Adolescent Females</i>	<i>Names of Females</i>	<i>Infants</i>	<i>Juveniles</i>	<i>Solitary Males</i>
Mac	12	2-3	1	Hiwot, Nany, Abebech, Steffi	0-2	3	0-1
Mamush	3	0	1	Meko	0	1	0
Mercury	4	1	0	Daisy	1	1	0-1?
Mike	12	1	0	Julia	0-1	1	1
Morris	3	1	2	Maxine, Mary, Maggie	1	0	0
Nelson	9	0-1	0-1	Natalie, Lisa	0	1-2	0
Omo	3	1	0	Chaltu	0	0	0
Park	12	5-7	0-1	Betty, Marigold, Elsie, Darian, Candy, Cookie, Lydia, Dina, Eleni	0-3	3	0-1?
Peach	10	1-2	0	Papaya, Mango	0-1	0-1	0
Pete	12	1	0	Lizzy	0-1	2	0
Pope	3	2	0	Ruby, Rita	1	1	0
Redface	12	5	0	Tulip, Trish, Lola, Una, Sara	0-3	5	0
Sami	9	1	0	Hasna	1	1	0
Shato	8	0	0-2	Monica, Pat	0	0	1
Teddy	10	0-2	0	Patch, Daisy, Dolly	0-1	0-1	0

Table 2.3 (cont.)

<i>Leader Male of OMU</i>	<i>Months as Leader Male</i>	<i>Adult Females</i>	<i>Adole- scent Females</i>	<i>Names of Females</i>	<i>Infants</i>	<i>Juve- niles</i>	<i>Solitary Males</i>
Titi	12	3	0-3	Sue, Amy, Chachi, Handeri, Mignote, Jib	0-3	1	1
Tripp	12	3	0	Tory, Toni, Salata	1-3	4	0-1
Yirdaw	12	2-3	0	Mabel, Lily, Sophie	1-3	1	0-1

Table 2.4 OMUs included in spatial cohesion and social interaction analyses

<i>OMU</i>	<i>Number of Females in OMU</i>	<i>Names of Females</i>	<i>Number of Scan Samples</i>
Clodio	1	Clea	104
DJ	1	Fugee	37
Ethan	1	Kate	20
Fruit	1	Mango	23
Kalid	1	Marta	95
Mercury	1	Daisy	29
Mike	1	Julia	92
Nelson	1	Natalie	56
Peach1	1	Papaya	28
Pete	1	Lizzy	50
Sami	1	Hasna	33
Shato1	1	Monica	14
Teddy1a	1	Patch	19
Teddy1b	1	Daisy	26
Peach2	2	Papaya, Mango	45
Pope	2	Ruby, Rita	17
Shato2	2	Monica, Pat	32
Teddy2	2	Daisy, Patch	29
Yirdaw2	2	Mabel, Lily	37
Andy	3	Rachel, Amina, Mimi	106

Table 2.4 (cont.)

<i>OMU</i>	<i>Number of Females in OMU</i>	<i>Names of Females</i>	<i>Number of Scan Samples</i>
Cory	3	Sage, Lupy, Olive	69
Evangadi	3	Yibeltal, Nuriya, Ashenafi	40
Mac3	3	Hiwot, Nany, Abebech	35
Titi	3	Sue, Amy, Chachi	32
Tripp	3	Tory, Toni, Salata	104
Yirdaw3	3	Mabel, Lilly, Sophie	39
Len4	4	Lila, Maxine, Mary, Maggie	11
Mac4	4	Hiwot, Nany, Abebech, Steffi	22
Herb	5	Sony, Iris, Rose, Petunia, Kitten	16
Len5	5	Lila, Maxine, Mary, Maggie, Lee	11
Redface	5	Tulip, Trish, Lola, Una, Sara	52

Figure 2.1 Map of Ethiopia showing location of Awash National Park

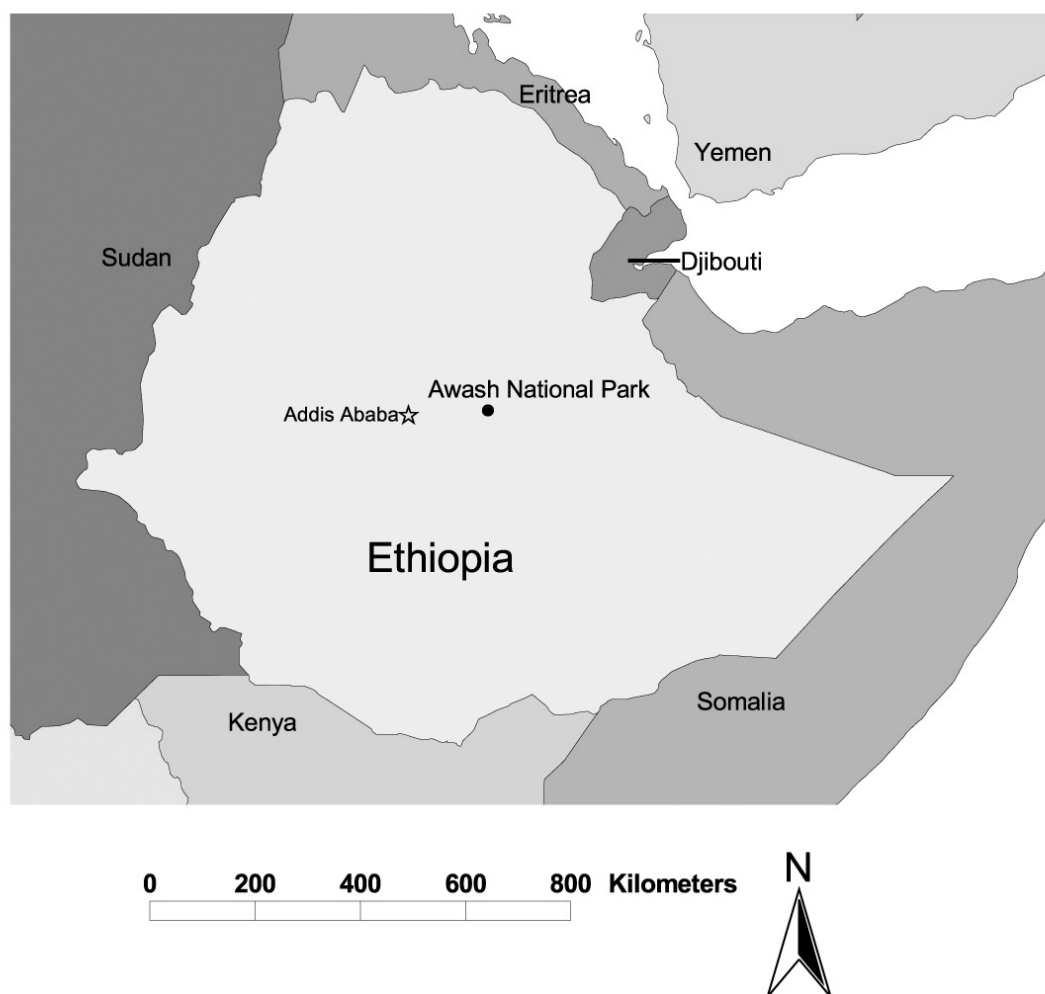
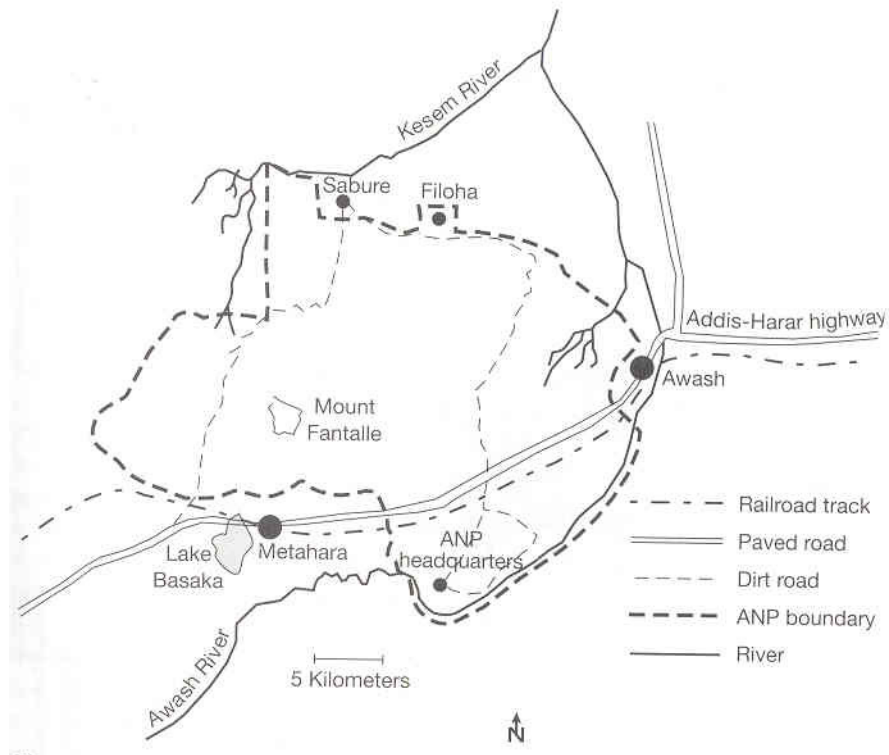


Figure 2.2 Map of Awash National Park



(From Swedell, 2006)

Figure 2.3 Map of Filoha Region

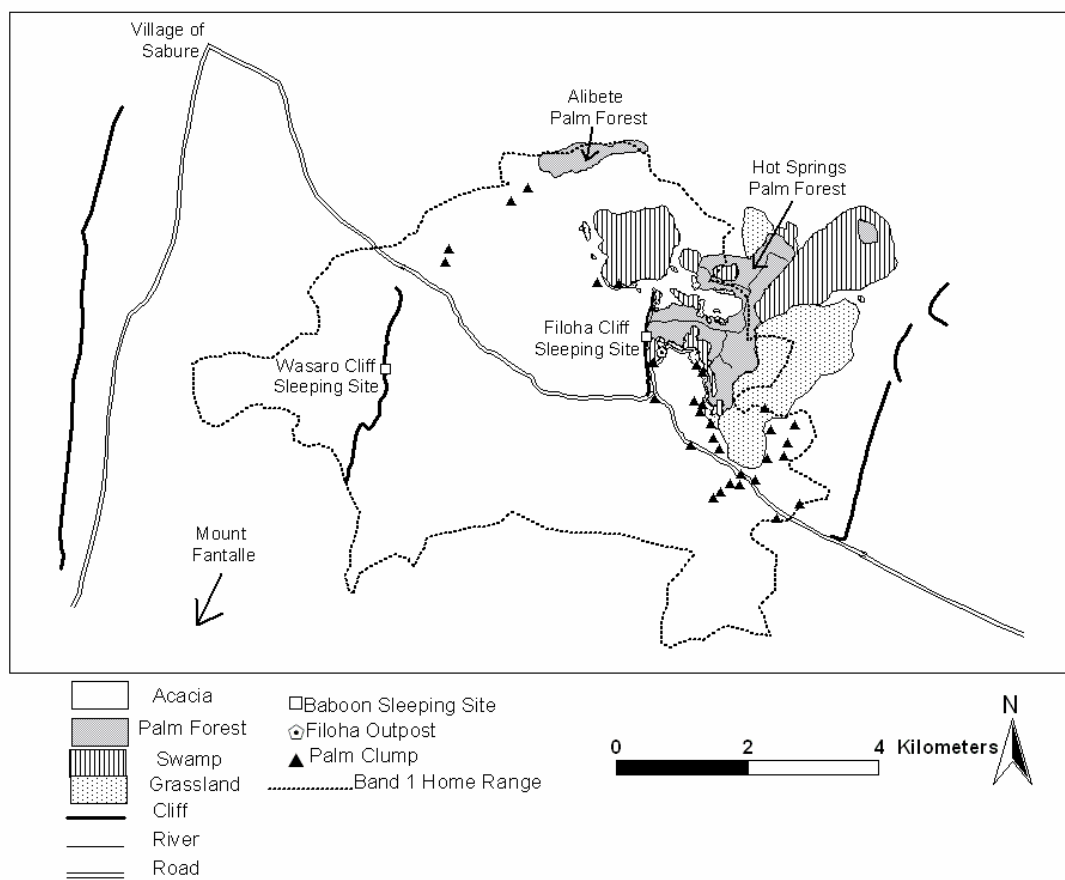
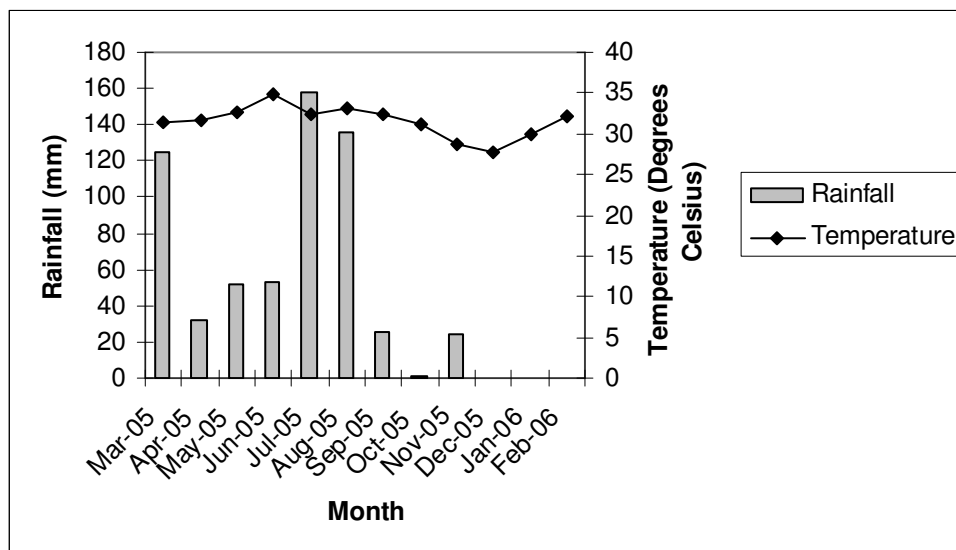
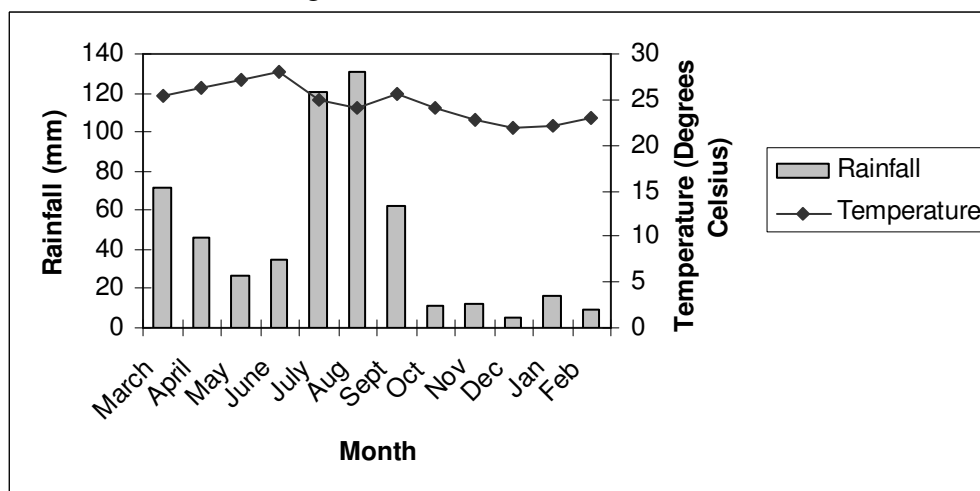


Figure 2.4 Monthly rainfall (mm) and mean daily temperature by month (°C)

a) Filoha outpost, March 2005 – February 2006



b) Awash Station, averages over 1950-2000



(Data from WorldClim, European Commission, 2008)

CHAPTER 3

VEGETATION STRUCTURE AND PHENOLOGY

In this chapter, I describe the vegetation structure of the Filoha region in detail, as well as the phenology of the two most frequently consumed food species by the baboons, *Acacia senegal* and *Hyphaene thebaica*.

3.1 Vegetation Structure

3.1.1 Ecological Sampling of Habitats

In January 2004, I visually characterized and mapped the Filoha region based on the dominant vegetation and topology, and described five habitat types: *Acacia* scrublands, palm forests, open grasslands, swamp vegetation, and cliffs. *Acacia* scrublands, open grasslands, and cliffs are all typical of hamadryas habitat in other parts of their geographic range (Kummer, 1968a; Sigg and Stolba, 1981; Biquand et al., 1992; Al-Safadi, 1994; Zinner et al., 2001a; Swedell, 2006). The presence of palm forests and swamp vegetation, however, is uncharacteristic of hamadryas habitats.

While there is some mixing of resource types across habitats (e.g., palm clumps exist in some areas of *Acacia* scrublands and open grasslands, and lone *Grewia* spp. bushes are located in several open grasslands), different habitat types are visually distinct from one another, with clear dominant species types (see below). *Acacia* scrublands at Filoha are dominated by *Acacia* spp. and/or *Grewia* spp. shrubs and trees (Swedell, 2002b; Abule et al., 2007). Palm forests are dominated by doum palm trees (*Hyphaene thebaica*). Open grasslands are characterized by various grass and/or herb species (i.e., non-woody seed-bearing plants which die annually after flowering or revert to storage

organs during non-growth seasons), and the absence of woody vegetation. Swamp vegetation is fed by permanent ground water and is dominated by continuous *Cyperus* spp. and/or *Typha latifolia*. Finally, I defined “cliff habitats” as consisting of a vertical rock face at least 4 m high (Larson et al., 2000) with a few horizontal meters of rock on one or both sides with no (or very little) vegetation.

I mapped the boundaries of each habitat using a handheld GPS unit as well as topographic maps of the region supplied by the Ethiopian Mapping Authority. I also mapped all permanent water sources including hot springs, rivers and streams, and ponds. All collected GPS points were downloaded into ArcView GIS 3.1 and overlaid onto the map of the Filoha region. I calculated the proportion of each habitat type in Band 1’s home range using ArcView GIS 3.1 software. Figure 2.3 shows the distribution of habitats in the Filoha region.

A patch is commonly defined as a single tree (e.g., Overdorff, 1996), but this is more applicable to tropical rain forest habitats than to the savannas more typical for baboons. Alternatively, a patch has been defined as an area of high food density (e.g., Chapman, 1990b). To distinguish among areas both within and between habitat types, I defined a “patch” as a distinct area of a particular habitat type that is surrounded by other habitat types or distinguished from other patches of the same habitat type by its species composition and density. Patches ranged in size from 0.01 to 0.59 km² (although only *Acacia* scrublands patches were larger than 0.20 km², see below). Open grasslands and swamp vegetation were always surrounded by other habitat types, and thus patches were clearly identifiable. Adjacent patches within large expanses of *Acacia* scrublands could be distinguished from one another based on the composition and density of woody species. Similarly, within the largest palm forest in the Filoha region, adjacent patches

could also be distinguished based on the size (in area) of continuous palm trees and the distances between them.

I conducted vegetative transects (e.g., Brower et al., 1990) for two main purposes: (1) to describe the baboons' home range, in terms of species composition, species density, and the distribution of food resources, and (2) to examine the relationship between spatial cohesion and resource distribution within habitat types. In July 2004, assisted by three colleagues, I conducted 37 vegetative transects. I conducted 28 additional transects during the main study period in 2005-2006 as the baboons occupied patches that were not sampled in 2004. Transects were 50 m x 4 m (50 m long x 2 m on each side) (e.g., Stoner, 1996; Ganzhorn, 2003) and transects were surveyed in patches of *Acacia* scrublands, open grasslands, palm forests, and swamp vegetation through which the baboons were observed traveling on multiple occasions. Transects were oriented at 0° along a N-S gradient, or as close to 0° that would allow for surveying a continuous length of 50 m within the patch. Because, by definition, cliffs have no (or very little) vegetation, no transects were carried out on cliff habitats. Transects were conducted, however, in *Acacia* scrublands on the top of cliffs, just west of the Filoha cliff sleeping site, and just east of the Wasaro cliff sleeping site.

In each transect, I recorded the presence of all woody species. Variables calculated for these species in *Acacia* scrublands and palm forests are described sections 3.1.2 and 3.1.3, respectively. To quantify the undergrowth in *Acacia* scrublands and palm forests and the percent cover in open grasslands and swamps, I estimated the percent cover of grasses, and other non-woody plants in five 2 m x 2 m quadrats evenly spaced throughout each transect (Brower et al., 1990). I then calculated the mean as an average sample of cover.

To test the possibility that larger patches are more heterogeneous than smaller ones, I conducted more than one transect in four *Acacia* scrublands patches, three palm forest patches, two open grasslands, and one swamp. These transects did not yield significant differences within habitat type in dominant species, species diversity, or resource density. Due to these results, coupled with the fact that each transect took between two and four hours and required the assistance of one to three other people, I conducted only one transect for each of the other patches sampled.

A total of 62 vegetation transects were conducted: 29 in *Acacia* scrublands, 16 in palm forests, 13 in open grasslands, and four in swamps. Because I originally intended to focus on Band 3, 15 of these transects are located outside Band 1's March 2005 – February 2006 home range. Because this dissertation is based only on Band 1, however, I present here the results of only those transects that fall within Band 1's home range. Furthermore, for the patches in which I conducted more than one transect (as described above), I include just that transect which is located most closely to the center of the patch. Therefore, transects from 41 patches represent Band 1's home range: 23 in *Acacia* scrublands, seven in palm patches, seven in open grasslands, and four in swamp vegetation. Due to its large size, I was unable to sample Band 1's home range in its entirety. Nevertheless, transects were conducted through most of its range, with an effort made to sample those patches that the baboons frequented so that data were available for spatial cohesion analyses.

3.1.2 *Acacia* scrublands

Acacia scrublands comprised 89.0% of Band 1's home range. I conducted twenty-three vegetation transects in *Acacia* scrublands, corresponding with patches that

the baboons regularly inhabited (Figure 3.1). These patches ranged in size from 0.06 km² to 0.59 km². In each transect, I recorded all woody vegetation at the species level (i.e., all woody perennial plants including shrubs and trees). I noted the number of stems on each tree and shrub, and measured the stem circumference (at the widest point before branching), shrub height, height below crown, and crown width (measured as the distance between the two widest points of the crown along the longest axis (Chapman et al., 1992).

I calculated the following variables for woody vegetation: dominant species = species with the highest abundance of individuals in the transect; species diversity = number of species in the transect; total abundance = number of individuals of all species in the transect; total density = number of individuals of all species per square meter; and relative density = number of individuals of each species per square meter (Brower et al., 1990; Kent and Coker, 1992).

Table 3.1 displays a summary of the *Acacia* scrublands transects. The number of woody species ranged from two to seven. The mean abundance of woody species (i.e., the number of individuals of all woody species averaged across transects) was 37.2, with a range of 11 to 102 woody species. The mean density of woody species (i.e., the number of individuals of all woody species per square meter averaged across transects) was 0.2/km², and ranged from 0.1/km² to 0.5/km². Table 3.2 shows a summary of each of the *Acacia* scrublands transects. *Acacia senegal* was the dominant species in 15 of the 23 transects, and was present in all but two of the transects. *Acacia nubica* was dominant in two transects, and *Acacia tortilis* was dominant in one. *Grewia erythraea* was the dominant species in four transects, and *Grewia tenax* was dominant in one. *Acacia* species were present in all five of the *Grewia*-dominated transects. Qualitative observations suggest that most of the *Acacia* scrublands areas that were not quantified

systematically were also dominated by *A. senegal*. Details of each transect and measurements of each woody vegetation species can be seen in Tables 3.3 and 3.4, respectively.

3.1.3 Palm Forests

Two palm forests occupy the Filoha region – one stretches east from the Filoha Cliff and encompasses 2 km² of natural hot springs and the other is located northwest of the Filoha cliff near the Afar village of Alibete and covers 0.4 km² (Figure 2.3). Both palm forests comprise several patches with sizes ranging from 0.04 km² to 0.20 km². (A third palm forest is located several kilometers northeast of the Filoha Cliff, but its size and composition were not quantified because it was not used by Band 1.) I defined palm patches as consisting of continuous palm trees with a total area estimate of at least 0.01 km². Clumps of two to ten palm trees are scattered throughout the Filoha region, and were considered part of a palm patch if they were within 100 m of any point of the closest patch. This criterion distinguishes palm clumps in the vicinity of palm forests from those located within other habitat types.

Palm forests comprised 4.2% of Band 1's home range. Vegetative transects were conducted in seven palm patches (Figure 3.2). I recorded the abundance of palm trees and the number of crowns on each tree (trunks usually split at ~4 m or higher, separating into two or more crowns), which corresponds to the amount of available fruit. I measured the trunk circumference and calculated the diameter at breast height (DBH), and calculated density as the number of palm trees per square meter.

Table 3.5 shows a summary of the palm patch vegetation transects. The mean density of palm trees was 0.05 trees per square meter, and ranged from 0.03 to 0.07 trees

per square meter. Summaries of each transect and details of each transect's undergrowth can be seen in Tables 3.6 and 3.7, respectively.

3.1.4 Open Grasslands

I defined open grasslands as areas that are dominated by grass species and lack woody vegetation. While open areas exist within *Acacia* scrublands, they tend to lack vegetation. Furthermore, while all open grasslands are at least 0.01 km², open areas within *Acacia* scrublands generally cover smaller areas (around .05 km² or less). There are several open grasslands in the Filoha region. The largest is 2.7 km² and is located several kilometers east of the Filoha cliff (Figure 2.3). Only a small portion of this grassland (0.5 km²), however, falls within Band 1's home range. The rest of the grasslands are much smaller, ranging in size from 0.01 km² to 0.06 km² and each comprise a single patch.

Overall, open grasslands comprised 3.2% of Band 1's home range, within which seven vegetation transects were conducted. More than one transect was conducted in both of the grasslands that are larger than 0.03 km² (as described in section 3.1.1 above). There were no differences in percent cover or species diversity, indicating general homogeneity within grassland patches.

Table 3.8 displays a summary of the seven open grasslands transects (see Figure 3.3 for locations of transects). The mean percent cover was 35.5%, and ranged from 21.5% to 60.5%. Areas that were not covered by vegetation consisted of bare soil and/or rock. *Sporobolus* species dominated the open grasslands. Details of each transect can be seen in Table 3.9.

3.1.5 Swamp Vegetation

Swamp vegetation is fed by permanent ground water and dominated by either *Cyperus* spp. or *Typha latifolia*. There are two large swamps in the Filoha region: the first covers 1.2 km² and is located just north of the Filoha cliff, and the second covers 1.9 km² and is located several kilometers east of the Filoha cliff (Figure 2.3). It should be noted that various interior sections of these two swamps appear to lack vegetation and consist solely of standing water. These areas may be more accurately described as ponds, and the size of these swamps may therefore be overestimated. Like open grasslands, the rest of the swamps ranged in size from 0.01 km² to 0.09 km² and each comprised a single patch.

Swamps cover 4.3% of Band 1's home range. Due to prohibitively deep water and patches of quicksand in *Typha latifolia* swamps (including the two large swamps described above), I was only able to conduct transects in swamp vegetation that was dominated by *Cyperus* spp.

Summaries of the four swamp vegetation transects can be seen in Table 3.10 (see Figure 3.4 for map of locations). The mean percent cover of *Cyperus* spp. was 76.3%, with a range of 70.6% to 81.6%. Details of each transect can be seen in Table 3.11. In addition to the dominant species type, swamp vegetation differs from open grasslands in its greater vegetation cover and higher soil moisture.

3.1.6 Cliff Habitats

I defined cliffs as consisting of a vertical rock face at least 4 m high (Larson et al., 2000) with up to several horizontal meters on one or both sides that lack (or have very

little) vegetation. There are at least four cliffs in the Filoha vicinity (Figure 2.3). The Filoha cliff is located about 200 m from camp. It is 1.5 km long and its height ranges from 9 m to 18 m; it is 12 m high at the baboons' sleeping site. It is situated adjacent to hot springs and palm trees grow along its base. The Wasaro cliff is located about 4 km west of Filoha. It is at least 2.5 km long, its height ranges from 21 m to 42 m, and it is 32 m high at the baboons' sleeping site. A third cliff is located about 4 km further west of Wasaro near the village of Sabure, and the fourth is situated about 3 km east of Filoha; the baboons only rarely sleep on these cliffs (Swedell, 2006; Hailemeskel, pers. comm.). The baboons likely sleep on additional cliffs as they have disappeared from the Filoha and Wasaro regions for periods of up to a month – during which Afar nomads reported that the baboons slept on cliffs near Mount Fantalle, southwest of Wasaro as well as southeast of Filoha near the Gabaro Afar village – but these sleeping sites have not yet been identified.

3.2 Phenology

While I had originally intended to sample the abundance of plant parts of the most frequently eaten species (based on a previous study by G. Hailemeskel of the Ethiopian Wildlife Conservation Department; Swedell et al., 2008) bi-monthly in each vegetative transect, this was not possible due to the prohibitively large size of Band 1's home range and the limited personnel available to help for this purpose. Furthermore, the baboons expanded their home range over the study period and while I was able to complete additional vegetative transects as the baboons exploited new areas, these regions were not monitored consistently over the study period. In light of these circumstances, I monitored the phenology of the two most frequently consumed food species by the baboons – A.

senegal and *H. thebaica* (section 4.3.1) – in patches in which Band 1 regularly foraged and which were easy to reach, either because they were a short walk from Filoha or were on one of two regular paths taken between the Filoha and Wasaro sleeping sites.

3.2.1 *Acacia senegal*

I sampled the abundance of fresh leaves, seed-pods, and flowers for *A. senegal* (the most frequently consumed species; section 4.3.1) monthly in six transects spread throughout Band 1's home range corresponding with high use by the baboons: Transect 1, just west of the Filoha cliff sleeping site; Transect 5, south of the Filoha camp, and just north of the car road; Transect 13, about 2 km northwest of the Filoha cliff sleeping site; Transect 17, about 2 km southwest of the Filoha cliff; Transect 18, just east of the Wasaro cliff sleeping site; and Transect 19, west of the Wasaro cliff (Figure 3.1). I did not begin systematically monitoring *A. senegal* until April 2005, and therefore I do not have data for the first month of the study.

I estimated the presence of fresh leaves, seed-pods, and flowers on each tree on a scale of 1 to 4 (1=0-25% coverage; 2=26-50% coverage; 3=51-75% coverage; 4=76-100% coverage) (e.g., Chapman et al., 1994b; Peres, 1994; Cunningham, 2003). Within transects, the scores for each tree were almost always the same, and when they differed, they varied only between scores of 3 and 4, or 1 and 2, suggesting that abundance was clearly high or low within a transect. Therefore, for each transect, I averaged the abundance scores of each to provide one score for each plant part per month. The average scores across transects were also almost always the same, and when they varied, they did so only by one point on the abundance scale.

Due to this similarity across transects, results are presented as an average of all six transects (Figure 3.5). Leaves were the most abundant *A. senegal* plant part over the study period. *A. senegal* trees were completely covered with fresh leaves during and just after the wet season in July, August, and September. Seed-pods never received an abundance score over 2. During June and October, however, the baboons ate *A. senegal* seeds almost exclusively from the ground. During these months trees were essentially devoid of seed-pods, but dry seeds covered much of the area beneath the trees. Unfortunately, I did not quantify the abundance of plant parts underneath trees, and the abundance scores for seed-pods are therefore misleading for these periods. Finally, *A. senegal* flowers were available only in April and August, following large amounts of rainfall.

The phenology of *Tribulus cistoides* – the third most frequently consumed species (section 4.3.1) – was not systematically quantified over the course of the study period. However, qualitative observations suggest a high correspondence between its flowering patterns and that of *Acacia* spp. Namely, the flowers of *T. cistoides* were available throughout Band 1's home range during August. During other months of the year, leaves and/or seeds were available, but not flowers. The flowering patterns of *A. senegal* and *T. cistoides* and the availability of surface water correspond with rainfall. Namely, surface water was readily available throughout July, August, and most of September, as well as in the day(s) just following rain during other times of the year.

3.2.2 Doum Palm Fruit

I sampled the abundance of ripe doum palm fruit (*H. thebaica*) – the second most frequently consumed food species (section 4.3.1) – in four palm patches: Transect 1,

about 1 km east of the Filoha cliff sleeping site; Transect 3, about 2 km southeast of the Filoha cliff sleeping site; Transect 5, about 1.5 km northeast of the sleeping site in the Hot Springs palm forest; and Transect 7 in the Alibete palm forest (Figure 3.6). Band 1 first traveled to and ate from the palm clumps in *Acacia* scrublands southeast of Filoha in June 2005, and I monitored the abundance of fruit there for the remainder of the study period.

Doum palm fruit occurs in bunches and I estimated the abundance of ripe fruit on a scale of 1 to 4 based on the percentage of bunches that bore ripe fruit (1=bunches 0-25% full; 2=bunches 26-50% full; 3=bunches 51-75% full; 4=bunches 76-100% full). Ripe fruit is orange in color and has a softer exterior than unripe fruit, which is more purple in color. As with *A. senegal*, the amount of fruit on the ground underneath trees was not quantified. I monitored the abundance of palm fruit from the onset of the study period in March 2005 for Transects 1, 5, and 7, but I did not score abundance in Transect 3 until April.

Within palm patches, the abundance of palm fruit across trees did not differ by more than one point during any month. Results, therefore, are presented as an average abundance score for each transect per month. While the same general pattern of fruiting over the course of the study period was consistent across transects, average abundance scores did differ by more than one point during four months. Therefore, average abundance scores are presented separately for each of the four transects (Figure 3.2).

Figure 3.2 shows that, overall, the abundance of ripe palm fruit in palm forests was highest at the beginning of the study period, and then declined to very low levels by July. The abundance of ripe fruit then increased in the last few months of the study period. It should be noted that the palm clumps in *Acacia* scrublands southeast of Filoha

had average abundance scores of between 2.8 and 3.5 from June through December when the abundance of ripe palm fruit in the Hot Springs and Alibete palm forests was low.

Table 3.1 Summary of *Acacia* Scrublands vegetative transects (N=23)

<i>Woody Vegetation</i>			<i>Undergrowth</i>	
<i>Species Diversity</i> ¹ (# woody species)	<i>Total Abundance</i> ² (# individuals)	<i>Total Density</i> ³ (individuals per square meter)	<i>Percent Cover</i> ⁴	<i># Grass/Herb Species</i>
4.5 (1.7) 2-7	37.2 (22.5) 11-102	0.2 (0.11) 0.0-0.5	23.9 (20.4) 0.0-81.0	7.3 (1.1) 3-12

mean (standard deviation)

range

¹Species Diversity = Number of woody species in transect²Total Abundance = Number of individuals of all woody species in transect³Total Density = Number of individuals of all woody species per square meter⁴Percent Cover = Mean percent cover of grass/herbs/non-woody plant species over five 2 m x 2 m quadrats

Table 3.2 Summary of each *Acacia* Scrublands vegetative transect

Transect	Size (sq km)	Woody Vegetation				Undergrowth		
		Dominant Species ¹	Species Diversity ² (# woody species)	Total Abundance ³ (# individuals)	Total Density ⁴ (individuals per square meter)	Percent Cover ⁵	# Grass Species	# Herb Species
1	0.15	<i>Acacia senegal</i>	2	10	0.05	39.0	2	4
2	0.34	<i>Grewia erythraea</i>	4	102	0.51	10.0	8	7
3	0.06	<i>Grewia tenax</i>	6	11	0.06	13.6	9	7
4	0.10	<i>Grewia erythraea</i>	6	61	0.31	no data	6	5
5	0.13	<i>Acacia senegal</i>	5	69	0.35	30.2	12	8
6	0.30	<i>Acacia senegal</i>	7	70	0.35	57.0	7	7
7	0.19	<i>Acacia senegal</i>	4	62	0.31	22.4	7	5
8	0.21	<i>Acacia nubica</i>	2	29	0.15	19.2	1	3
9	0.10	<i>Acacia senegal</i>	4	34	0.17	8.6	0	6
10	0.35	<i>Acacia senegal</i>	2	28	0.14	8.0	1	5
11	0.17	<i>Acacia senegal</i>	3	34	0.17	9.0	1	9
12	0.11	<i>Acacia senegal</i>	5	30	0.15	25.2	1	9

Table 3.2 (cont.)

Transect	Size (sq km)	Woody Vegetation				Undergrowth		
		Dominant Species	Species Diversity (# woody species)	Total Abundance (# individuals)	Total Density (individuals per square meter)	Percent Cover	# Grass Species	# Herb Species
13	0.21	<i>Acacia senegal</i>	6	33	0.17	21.2	0	4
14	0.16	<i>Acacia senegal</i>	6	30	0.15	7.6	0	7
15	0.17	<i>Grewia erythraea</i>	7	33	0.17	15.4	0	10
16	0.35	<i>Acacia senegal</i>	3	18	0.09	31.0	3	7
17	0.59	<i>Acacia senegal</i>	5	34	0.17	15.0	1	6
18	0.14	<i>Acacia senegal</i>	5	42	0.22	19.0	1	5
19	0.32	<i>Grewia erythraea</i>	6	23	0.12	64.0	0	6
20	0.17	<i>Acacia tortilis</i>	4	19	0.10	81.0	0	4
21	0.24	<i>Acacia senegal</i>	6	24	0.12	12.0	3	7
22	0.52	<i>Acacia senegal</i>	2	11	0.06	39.0	2	7
23	0.27	<i>Acacia rubica</i>	3	47	0.24	2.2	2	1

¹Dominant Species = Species with highest abundance in transect ⁵Percent Cover = Mean percent cover of non-woody

²Species Diversity = Number of woody species in transect species in transect

³Total Abundance = Number of individuals of all woody

⁴Total Density = Number of individuals of all woody species per square meter

Table 3.3 Abundance, density, and mean tree measurements of woody species in each *Acacia* scrublands vegetative transect

Transect	Species	Abundance ¹ (# individuals)	Density ³ (individuals per square meter)	Mean Height (m)	Mean Height to Canopy (m)	Mean Crown Width ⁴ (m)	Mean Stem Circumference ⁵ (cm)	Mean # Stems
1	<i>Acacia senegal</i> <i>Grewia erythraea</i>	8 2	0.04 0.01	2.6 0.9	0.7 *	3.6 1.4	31.6 4.5	1.9 26.0
2	<i>Grewia erythraea</i> <i>Acacia senegal</i> <i>Grewia villosa</i> <i>Acacia mellifera</i>	53 28 19 2	0.27 0.14 0.10 0.01	1.2 3.6 1.5 2.0	* 1.2 * 0.6	0.2 3.3 1.3 1.7	3.6 23.3 3.8 13.0	10.5 1.7 16.5 2.0
3	<i>Grewia tenax</i> <i>Acacia senegal</i> <i>Acacia rubica</i> <i>Grewia erythraea</i> <i>Grewia villosa</i> <i>Grewia schweinfurthii</i>	3 2 2 2 1 1	0.02 0.01 0.01 0.01 0.01 0.01	1.7 4.0 1.3 1.3 0.5 0.6	* 1.2 0.3 * * *	2.4 5.9 1.8 2.6 0.6 0.8	5.0 31.5 4.5 8.0 3.0 3.0	17.0 1.5 5.0 10.0 6.0 7.0
4	<i>Grewia erythraea</i> <i>Acacia senegal</i> <i>Acacia mellifera</i> <i>Acacia tortilis</i> <i>Grewia villosa</i>	30 23 5 2 1	0.15 0.12 0.03 0.01 0.01	2.0 3.4 3.3 1.8 3.4	* 1.8 2.0 0.5 *	1.8 2.6 2.6 1.9 3.2	7.4 12.9 10.3 8.3 5.0	9.1 1.3 1.8 2.5 10.0
5	<i>Acacia senegal</i> <i>Grewia erythraea</i> <i>Acacia rubica</i> <i>Acacia tortilis</i> <i>Grewia villosa</i>	37 26 2 2 2	0.19 0.13 0.01 0.01 0.01	3.2 1.4 0.6 5.5 1.0	1.1 * 0.4 1.3 *	2.3 1.2 1.8 4.7 0.7	17.4 3.5 2.5 39.5 2.3	1.7 5.3 3.5 2.0 7.5

Table 3.3 (cont.)

Transect	Species	Abundance (# individuals)	Density (individuals per square meter)	Mean Height (m)	Mean Height to Canopy (m)	Mean Crown Width (m)	Mean Stem Circumference (cm)	Mean # Stems
6	<i>Acacia senegal</i>	43	0.22	3.4	1.4	2.8	14.5	1.4
	<i>Grewia tenax</i>	12	0.06	1.7	*	1.2	4.8	7.3
	<i>Grewia villosa</i>	5	0.03	1.3	*	1.2	4.2	7.4
	<i>Grewia egyptiaca</i>	4	0.02	1.7	*	1.5	9.4	8.0
	<i>Grewia</i> <i>schweinfurthii</i>	3	0.04	1.5	*	2.5	11.7	6.3
	<i>Acacia nubica</i>	2	0.01	2.6	0.7	2.6	9.2	4.0
	<i>Acacia mellifera</i>	1	0.01	4.5	1.0	5.0	30.0	1.0
7	<i>Acacia senegal</i>	38	0.19	2.8	0.8	2.7	19.2	1.8
	<i>Grewia egyptiaca</i>	12	0.06	1.1	*	1.2	4.0	14.0
	<i>Acacia nubica</i>	11	0.01	1.7	0.4	1.5	18.8	5.3
	<i>Acacia tortilis</i>	1	0.01	1.8	0.7	2.6	8.0	1.0
8	<i>Acacia nubica</i>	20	0.10	2.1	0.6	2.2	21.9	5.0
	<i>Acacia senegal</i>	9	0.05	2.4	0.5	2.7	21.3	1.7
9	<i>Acacia senegal</i>	20	0.10	2.3	0.8	2.9	20.9	1.6
	<i>Grewia egyptiaca</i>	10	0.05	1.4	*	1.8	5.8	13.7
	<i>Grewia villosa</i>	3	0.02	0.7	*	1.1	4.0	15.0
	<i>Acacia tortilis</i>	1	0.01	6.3	0.5	4.0	51.0	1.0
10	<i>Acacia senegal</i>	23	0.12	1.9	0.5	2.6	19.2	1.6
	<i>Grewia egyptiaca</i>	5	0.03	0.8	*	0.8	3.8	11.4
11	<i>Acacia senegal</i>	27	0.14	3.5	1.4	3.7	21.2	1.4
	<i>Grewia egyptiaca</i>	6	0.03	1.6	*	2.0	5.0	23.8
	<i>Grewia villosa</i>	1	0.01	1.3	*	0.6	4.0	11.0

Table 3.3 (cont.)

Transect	Species	Abundance (# individuals)	Density (individuals per square meter)	Mean Height (m)	Mean Height to Canopy (m)	Mean Crown Width (m)	Mean Stem Circumference (cm)	Mean # Stems
12	<i>Acacia senegal</i>	15	0.08	3.5	1.4	4.1	21.67	1.5
	<i>Grewia erythraea</i>	8	0.04	1.4	*	1.2	5.63	12.4
	<i>Grewia villosa</i>	5	0.03	1.1	*	1.0	3.80	11.0
	<i>Acacia mellifera</i>	1	0.01	3.5	1.1	5.5	24.00	5.0
	<i>Grewia</i> <i>schweinfurthii</i>	1	0.01	1.4	*	2.2	12.00	4.0
13	<i>Acacia senegal</i>	11	0.06	3.7	1.6	4.9	nd	1.7
	<i>Grewia erythraea</i>	8	0.04	1.7	*	1.7	nd	11.4
	<i>Grewia</i> <i>schweinfurthii</i>	5	0.03	1.1	*	1.3	nd	14.3
	<i>Acacia mellifera</i>	4	0.02	3.6	1.4	4.0	nd	3.3
	<i>Godoba</i> <i>rotundifolia</i>	3	0.02	1.2	*	1.2	nd	3.0
14	<i>Grewia villosa</i>	2	0.01	0.8	*	1.5	nd	17.5
	<i>Acacia senegal</i>	17	0.09	2.9	1.0	3.4	nd	1.8
	<i>Grewia erythraea</i>	6	0.03	0.4	*	1.0	nd	12.7
	<i>Acacia tortilis</i>	3	0.02	3.4	0.8	4.1	nd	1.3
	<i>Grewia villosa</i>	2	0.01	0.6	*	0.5	nd	8.0
	<i>Grewia tenax</i>	1	0.05	0.5	*	0.4	nd	8.0
	<i>Grewia</i> <i>schweinfurthii</i>	1	0.05	1.3	*	1.5	nd	5.0

Table 3.3 (cont.)

Transect	Species	Abundance (# individuals)	Density (individuals per square meter)	Mean Height (m)	Mean Height to Canopy (m)	Mean Crown Width (m)	Mean Stem Circumference (cm)	Mean # Stems
15	<i>Grewia erythraea</i>	14	0.07	1.6	*	1.4	nd	20.0
	<i>Acacia senegal</i>	10	0.05	2.8	1.1	3.2	nd	1.4
	<i>Grewia villosa</i>	4	0.02	1.1		0.8	nd	8.5
	<i>Grewia</i>	2	0.01	0.9	*	1.2	nd	6.0
	<i>schweinfurthii</i>							
	<i>Grewia tenax</i>	1	0.01	1.1	*	0.8	nd	8.5
	<i>Goodea</i>	1	0.01	1.8	*	2.0	nd	7.0
	<i>rotundifolia</i>							
	<i>Doberea persica</i>	1	0.01	2.9	*	2.6	nd	2.0
16	<i>Acacia senegal</i>	11	0.06	2.5	0.6	3.1	27.4	1.4
	<i>Acacia tortilis</i>	5	0.03	2.5	0.6	3.8	21.3	1.5
	<i>Grewia erythraea</i>	2	0.01	1.8	*	1.5	7.5	18.5
17	<i>Acacia senegal</i>	18	0.09	2.7	0.6	2.4	20.8	2.1
	<i>Acacia nubica</i>	10	0.05	1.3	0.5	1.5	14.1	3.9
	<i>Acacia tortilis</i>	4	0.02	2.4	0.6	2.7	13.3	1.3
	<i>Grewia erythraea</i>	1	0.01	1.0	*	0.6	3.0	8.0
	<i>Grewia villosa</i>	1	0.01	0.7	*	0.4	4.0	6.0
18	<i>Acacia senegal</i>	15	0.08	2.1	0.6	2.3	22.1	2.0
	<i>Grewia erythraea</i>	14	0.07	1.7	*	1.7	4.8	22.6
	<i>Grewia villosa</i>	10	0.05	1.3	*	1.5	4.2	18.6
	<i>Acacia mellifera</i>	2	0.01	1.5	0.2	1.0	10.0	3.0
	<i>Acacia nubica</i>	1	0.01	2.3	0.2	2.4	40.0	13.0

Table 3.3 (cont.)

Transect	Species	Abundance (# individuals)	Density (individuals per square meter)	Mean Height (m)	Mean Height to Canopy (m)	Mean Crown Width (m)	Mean Stem Circumference (cm)	Mean # Stems
19	<i>Grewia erythraea</i>	11	0.06	2.2	*	2.4	9.5	21.1
	<i>Godoba rotundifolia</i>	7	0.04	2.5	0.8	2.8	22.1	5.1
	<i>Acacia rubica</i>	2	0.01	1.3	0.2	1.7	10.0	1.5
	<i>Acacia mellifera</i>	1	0.06	3.9	0.9	5.6	18.0	4.0
	<i>Acacia tortilis</i>	1	0.06	5.5	2.0	4.8	32.0	1.0
20	<i>Grewia villosa</i>	1	0.06	2.1	*	1.3	5.0	12.0
	<i>Acacia tortilis</i>	12	0.06	5.9	2.7	6.2	44.1	1.3
	<i>Grewia erythraea</i>	4	0.02	1.5	*	1.4	5.1	7.5
	<i>Godoba rotundifolia</i>	2	0.01	2.3	0.7	3.1	13.3	9.5
	<i>Acacia senegal</i>	1	0.01	2.6	0.5	2.0	14.0	3.0
21	<i>Acacia senegal</i>	8	0.04	2.7	0.6	3.2	13.4	2.6
	<i>Grewia erythraea</i>	7	0.04	1.1	*	1.3	5.0	20.6
	<i>Grewia</i>	5	0.03	0.6	*	0.7	5.2	10.8
	<i>schweinfurthii</i>							
	<i>Godoba rotundifolia</i>	2	0.01	1.7	0.3	2.5	15.5	4.0
	<i>Acacia mellifera</i>	1	0.01	4.0	1.0	6.0	22.0	11.0
	<i>Grewia villosa</i>	1	0.01	0.2	*	0.5	3.0	10.0
	<i>Acacia senegal</i>	10	0.05	2.8	0.9	4.0	19.4	1.9
22	<i>Grewia erythraea</i>	1	0.01	1.3	*	1.0	4.0	4.0

Table 3.3 (cont.)

Transect	Species	Abundance (# individuals)	Density (individuals per square meter)	Mean Height (m)	Mean Height to Canopy (m)	Mean Crown Width (m)	Mean Stem Circumference (cm)	Mean # Stems
23	<i>Acacia rubrica</i>	44	0.22	2.0	0.3	2.0	34.6	8.5
	<i>Grewia erythraea</i>	2	0.01	0.1	*	0.4	2.0	17.0
	<i>Acacia tortilis</i>	1	0.01	2.1	0.5	2.9	11.0	1.0

¹Abundance = Number of individuals of each species

²Density = Number of individuals of each species per square meter

³Crown width = distance between the two widest points of the crown along the longest axis

⁴Stem circumference measured at highest point before branching

⁵nd=no data

**Grewia* species do not have a canopy

Table 3.4 Woody vegetative measurements (mean, standard deviation, range) by species

Species	Height (m)	Height to Canopy (m)	Crown Width¹ (m)	Stem Circumference² (cm)	# Stems
<i>Acacia senegal</i> (N=* ¹)	3.0 (1.2) 0.2-5.9	1.0 (0.6) 0.0-3.5	3.0 (1.5) 0.0-7.0	19.3 (14.0) 0.5-7.8	1.7 (0.8) 1-5
<i>Acacia nubica</i> (N=* ²)	1.9 (0.9) 2.0-4.4	0.4 (0.2) 0.0-1.1	2.0 (0.8) 0.6-5.7	26.0 (20.9) 1.0-96.0	6.7 (4.8) 1-21
<i>Acacia tortilis</i> (N=* ³)	4.3 (2.2) 0.6-7.0	1.5 (1.3) 0.3-4.0	4.6 (2.4) 0.8-10.0	31.5 (21.6) 4.0-73.0	1.4 (0.6) 1-3
<i>Acacia mellifera</i> (N=* ⁴)	3.3 (1.0) 1.5-4.5	1.3 (0.7) 0.2-2.7	3.6 (1.8) 1.0-6.0	16.1 (7.8) 5.0-30.0	3.2 (2.5) 1-11
<i>Grewia erythraea</i> (N=* ⁵)	1.5 (0.7) 0.1-4.0	no canopy	1.4 (0.8) 0.2-4.3	5.1 (4.1) 1.0-43.0	12.8 (10.6) 1-61
<i>Grewia villosa</i> (N=* ⁶)	1.3 (0.6) 0.2-3.4	no canopy	1.2 (0.7) 0.1-3.2	3.9 (1.2) 1.0-7.0	13.6 (8.9) 1-49
<i>Grewia tenax</i> (N=* ⁷)	1.5 (0.7) 0.5-3.0	no canopy	1.4 (1.0) 0.4-4.2	4.8 (2.6) 3.0-11.0	9.2 (6.8) 3.0-33.0
<i>Grewia schweinfurthii</i> (N=* ⁸)	1.0 (0.5) 0.3-2.1	no canopy	1.4 (1.0) 0.6-5.0	7.6 (6.0) 3.0-23.0	9.3 (5.0) 2.0-19.0
<i>Godoba rotundifolia</i> (N=* ⁹)	2.1 (0.7) 0.9-3.0	0.7 (0.2) 0.1-0.9	2.5 (1.3) 0.7-4.6	19.3 (9.0) 9.5-37.0	5.4 (3.3) 2-11

¹Crown width = distance between the two widest points of the crown along the longest axis

²Stem circumference measured at highest point before branching

N*¹ = 359, 349, 352, 314, 355 respectively

N*² = 89, 86, 87, 88, 88 respectively

N*³ = 30, 30, 30, 27, 30 respectively

N*⁴ = 15, 15, 14, 10, 15 respectively

N*⁵ = 226, no canopy, 225, 196, 224 respectively

N*⁶ = 58, no canopy, 58, 50, 58 respectively

N*⁷ = 17, no canopy, 17, 15, 17 respectively

N*⁸ = 17, no canopy, 17, 10, 17 respectively

N*⁹ = 14, 11, 14, 11, 14 respectively

Table 3.5 Summary of palm patch vegetative transects in Band 1's home range (N=7)

<i>Palm Trees</i>				<i>Undergrowth</i>
<i>Abundance</i> ¹ (# trees)	<i>Density</i> ² (# trees per square meter)	<i>DBH</i> ³ (cm)	<i># Crowns</i> ⁴	<i>Total % Cover</i> ⁵
9.9 (2.6) 5-13	0.05 (0.03) 0.03-0.07	28.2 (3.0) 22.6-30.9	2.4 (0.5) 1-5	58.0 (36.2) 14.8-95.9

mean (standard deviation)
range

¹Abundance = Number of palm trees in transect

²Density = Number of palm trees per square meter

³DBH = Trunk diameter at breast height

⁴# Crowns = Number of crowns on each palm tree

⁵Total % Cover = Total % cover of all undergrowth species

Table 3.6 Summaries of each palm patch vegetative transect in Band 1's home range

Transect	Size (sq km)	Abundance ¹ (# trees)	Palm Trees		Undergrowth		
			Density ² (# trees per square meter)	Mean DBH ³ (cm)	Mean # Crowns ⁴	Total % Cover ⁵	# Grass Species # Herb Species
1	0.11	9	0.05	22.6	2.1	95.9	5 2
2	0.10	9	0.05	26.3	2.8	81.2	2 0
3	0.09	13	0.07	29.3	2.4	79.9	3 1
4	0.04	11	0.06	30.9	3.0	14.8	6 4
5	0.09	12	0.06	29.8	2.7	16.7	2 0
6	0.10	10	0.05	28.0	1.9	89.1	3 1
7	0.20	5	0.03	30.6	1.8	28.7	2 0

¹Abundance = Number of palm trees in transect²Density = Number of palm trees per square meter³DBH = Trunk diameter at breast height⁴# Crowns = Number of crowns on each palm tree⁵Total % Cover = Total % cover of all undergrowth species

Table 3.7 Composition of undergrowth in palm patch vegetative transects

<i>Transect</i>	<i>Total % Cover</i> ¹	<i>Species</i>	<i>% Cover</i> ²
1	95.9	<i>Hyphaene thebaica</i>	49.2
		<i>Sporobolus consimilis</i>	34.2
		Unidentified <i>Sporobolus</i> spp. ³	8.6
		Unidentified herb	2.2
		Unidentified vine	1.0
		<i>Coelachyrum poiflorum</i>	0.8
2	81.2	Unidentified <i>Sporobolus</i> spp.	34.6
		<i>Hyphaene thebaica</i>	28.6
		<i>Sporobolus spicatus</i>	17.2
		<i>Sporobolus consimilis</i>	0.9
3	79.9	<i>Cyperus</i> spp.	40.4
		<i>Hyphaene thebaica</i>	31.2
		<i>Sporobolus consimilis</i>	3.7
		Unidentified <i>Sporobolus</i> spp.	2.7
		<i>Sporobolus spicatus</i>	1.9
4	14.8	<i>Hyphaene thebaica</i>	4.3
		<i>Cyperus</i> spp.	2.0
		Unidentified grass	1.8
		Unidentified herb	1.7
		Unidentified vine	0.8
		<i>Sporobolus spicatus</i>	0.4
		<i>Godoba rotundifolia</i>	0.2
		<i>Pentarrhinum insipidum</i>	0.1
5	16.7	<i>Hyphaene thebaica</i>	14.0
		<i>Sporobolus consimilis</i>	1.6
		<i>Sporobolus spicatus</i>	1.1
6	89.1	<i>Cyperus</i> spp.	42.0
		<i>Hyphaene thebaica</i>	25.7
		<i>Sporobolus consimilis</i>	15.9
		<i>Sporobolus spicatus</i>	5.4
7	28.9	<i>Hyphaene thebaica</i>	16.1
		<i>Sporobolus consimilis</i>	11.2
		<i>Sporobolus spicatus</i>	1.5

¹Total % Cover = Total % cover of all undergrowth species

²% Cover = % cover of each species

³when no flowers were present, *Sporobolus* species could not be distinguished

Table 3.8 Summary of open grasslands transects in Band 1's home range (N=7)

<i>Total % Cover¹</i>	<i>Species Diversity² (# species)</i>	<i># Grass/Herb Species</i>
35.5 (15.23) 21.5-60.5	4.0 (3.0) 2-10	3.6 (2.5) 2-9

mean (standard deviation)
range

¹Total % Cover = Percent cover of all grass species combined

²Species Diversity = Number of all species within transect

Table 3.9 Species composition of open grasslands vegetative transects

Transect	Size (sq km)	Total % Cover ¹	# Grass/Herb Species	Species	% Cover ²	Abundance ³ (# herb or woody species)
1	0.06	60.5	4	<i>Sporobolus consimilis</i> <i>Sporobolus spicatus</i> <i>Cyperus</i> spp. <i>Tephrosia uniflora</i> <i>Grewia erythraea</i>	40.5 13.6 6.3	3 1 1
				<i>Hyphaene thebaica</i>		11
2	0.29	36.8	2	<i>Sporobolus spicatus</i>	36.8	
3	0.01	51.8	2	<i>Sporobolus spicatus</i> <i>Cyperus</i> spp.	40.5 11.5	
4	0.02	21.8	3	<i>Sporobolus spicatus</i> <i>Sporobolus consimilis</i> <i>Sporobolus ioclades</i>	12.8 7.5 1.6	
5	0.01	27.6	9	<i>Sporobolus spicatus</i> <i>Sporobolus ioclades</i> <i>Sporobolus</i> spp. <i>Sporobolus consimilis</i> <i>Tribulus cistoides</i> <i>Psilotrichum gnaphalobryum</i> <i>Hibiscus macranthus</i> <i>Cactus</i> spp. herb "235" herb "275" <i>Grewia tenax</i>	19.2 4.0 2.9 1.4	4 9 5 2 20 12 1
6	0.03	21.5	2	<i>Sporobolus spicatus</i> <i>Cyperus</i> spp.	13.7 8.3	

Table 3.9 (cont.)

Transect	Size (sq km)	Total % Cover¹	# Grass/Herb Species	Species	% Cover²	Abundance³ (# herb or woody species)
7	0.02	28.2	3	Sporobolus spicatus Cyperus spp. Sporobolus ioclades	18.1 0.1 3.2	

¹Total Percent Cover = Percent cover of all grass species combined

²% Cover = % cover of each grass species in transect

³Abundance = number of each herb or woody species in transect

Table 3.10 Summary of swamp vegetative transects in Band 1's home range (N=4)

<i>Total % Cover</i>	<i>Species Diversity¹ (# species)</i>	<i># Grass/Herb Species²</i>
76.3 (5.35)	2.0 (0.8)	2.0 (0.8)
70.6-81.6	1-3	0-2

mean (standard deviation)

range

¹Total % Cover = Percent cover of all grass species combined

²Species Diversity = Number of all species within transect

Table 3.11 Species composition of swamp vegetative transects

Transect	Size (sq km)	Total % Cover¹	# Grass/Herb Species	Species	% Cover²
1	0.05	81.6	3	<i>Cyperus</i> spp.	81.6
2	0.05	80.1	3	<i>Cyperus</i> spp.	66.8
				<i>Sporobolus spicatus</i>	11.5
				<i>Sporobolus consimilis</i>	1.8
3	0.06	73.0	2	<i>Cyperus</i> spp.	63.4
				<i>Sporobolus spicatus</i>	9.5
4	0.01	70.6	2	<i>Cyperus</i> spp.	66.3
				<i>Sporobolus spicatus</i>	4.2

¹Total Percent Cover = Percent cover of all grass species combined

²% Cover = % cover of each grass species in transect

Figure 3.1 Map of *Acacia* scrublands transects

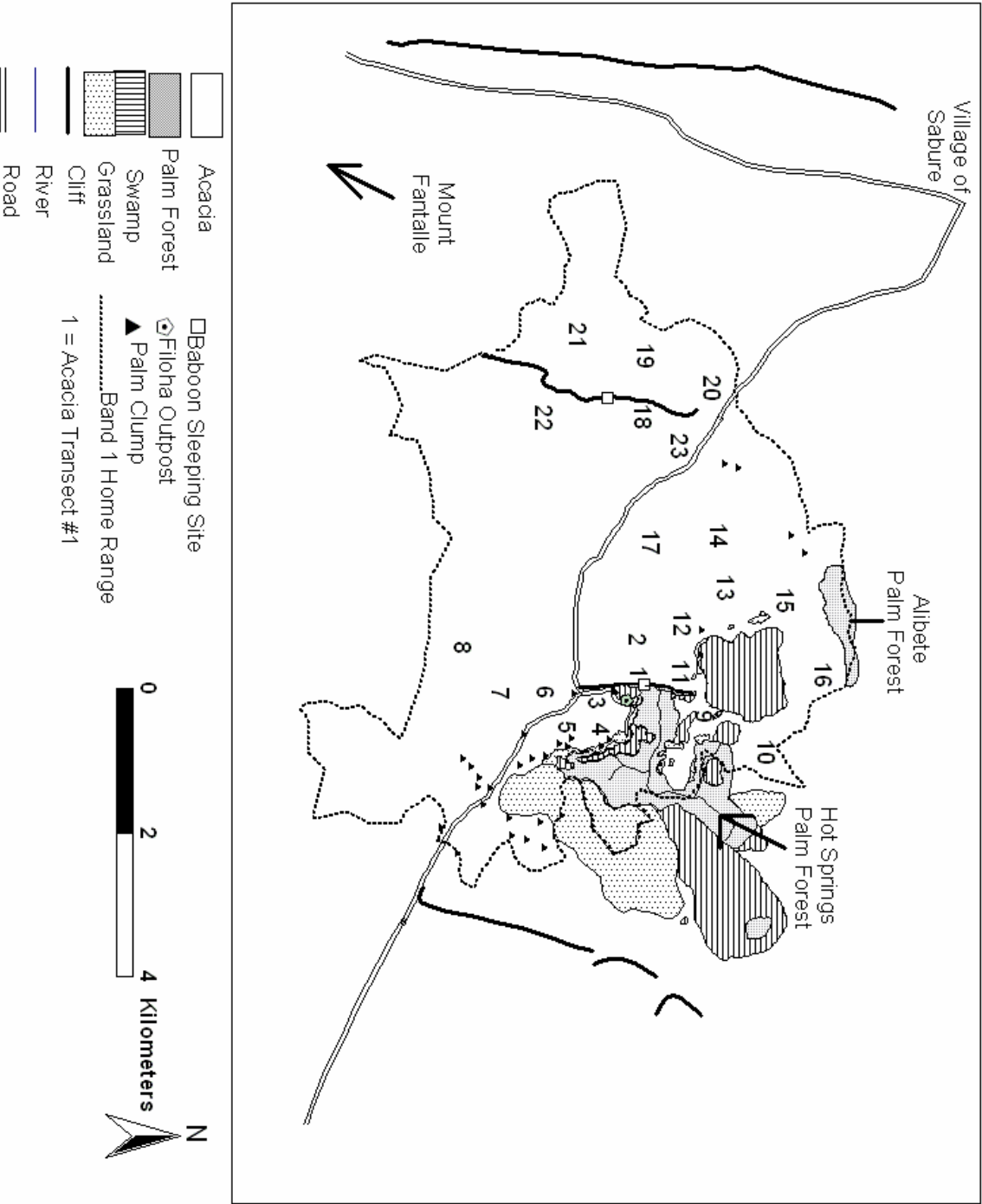


Figure 3.2 Map of palm forest transects

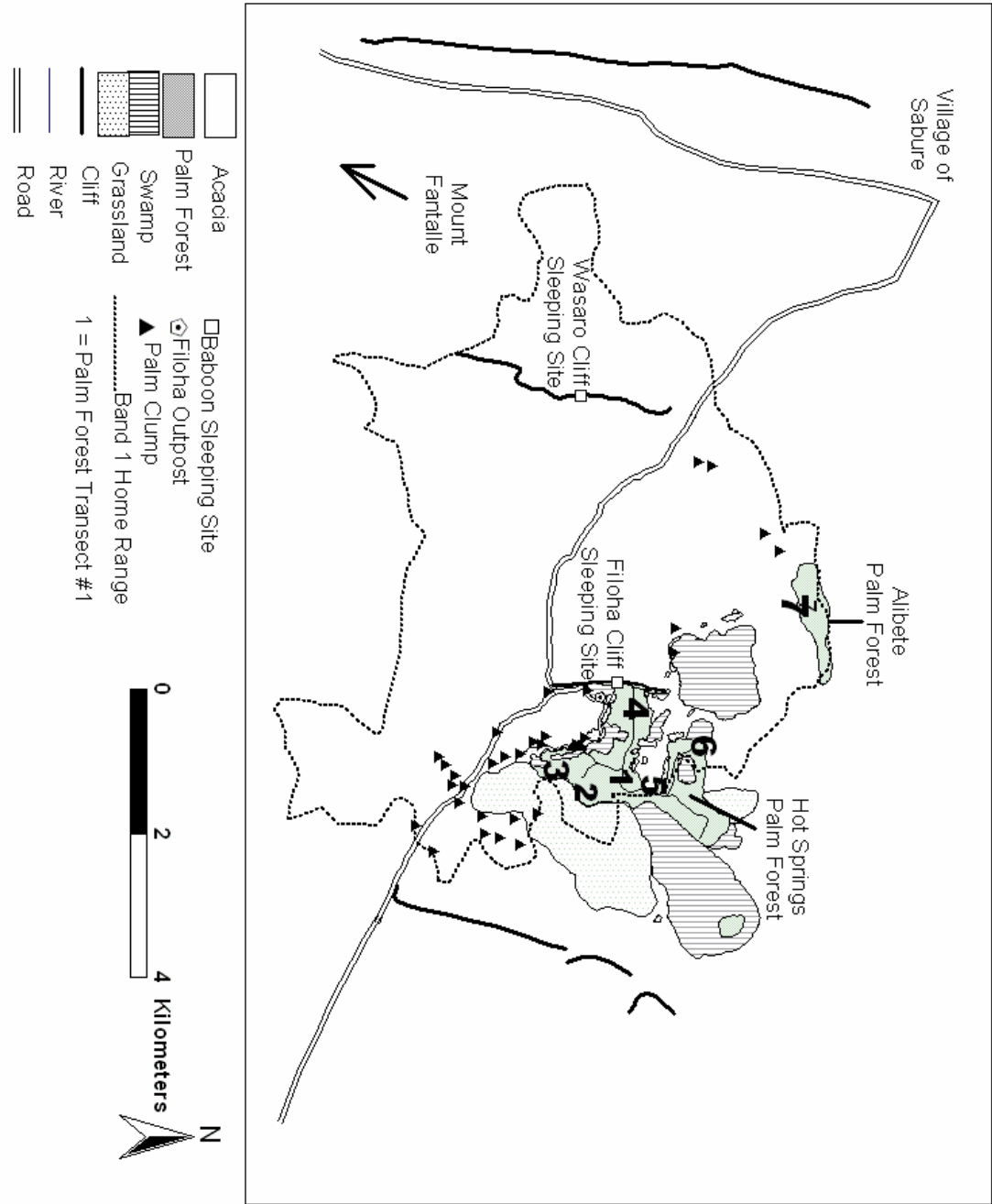


Figure 3.3 Map of open grasslands transects

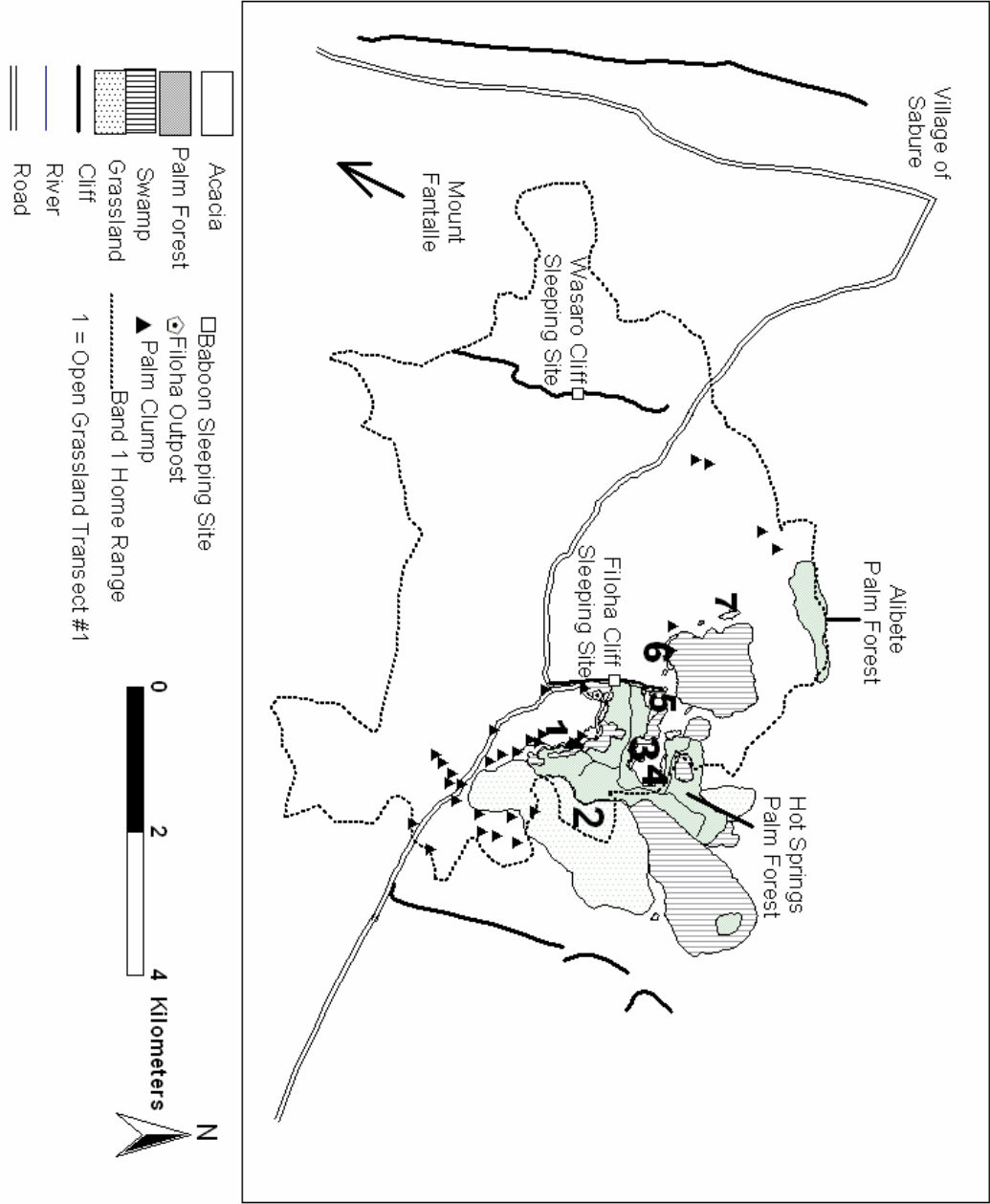


Figure 3.4 Map of swamp transects

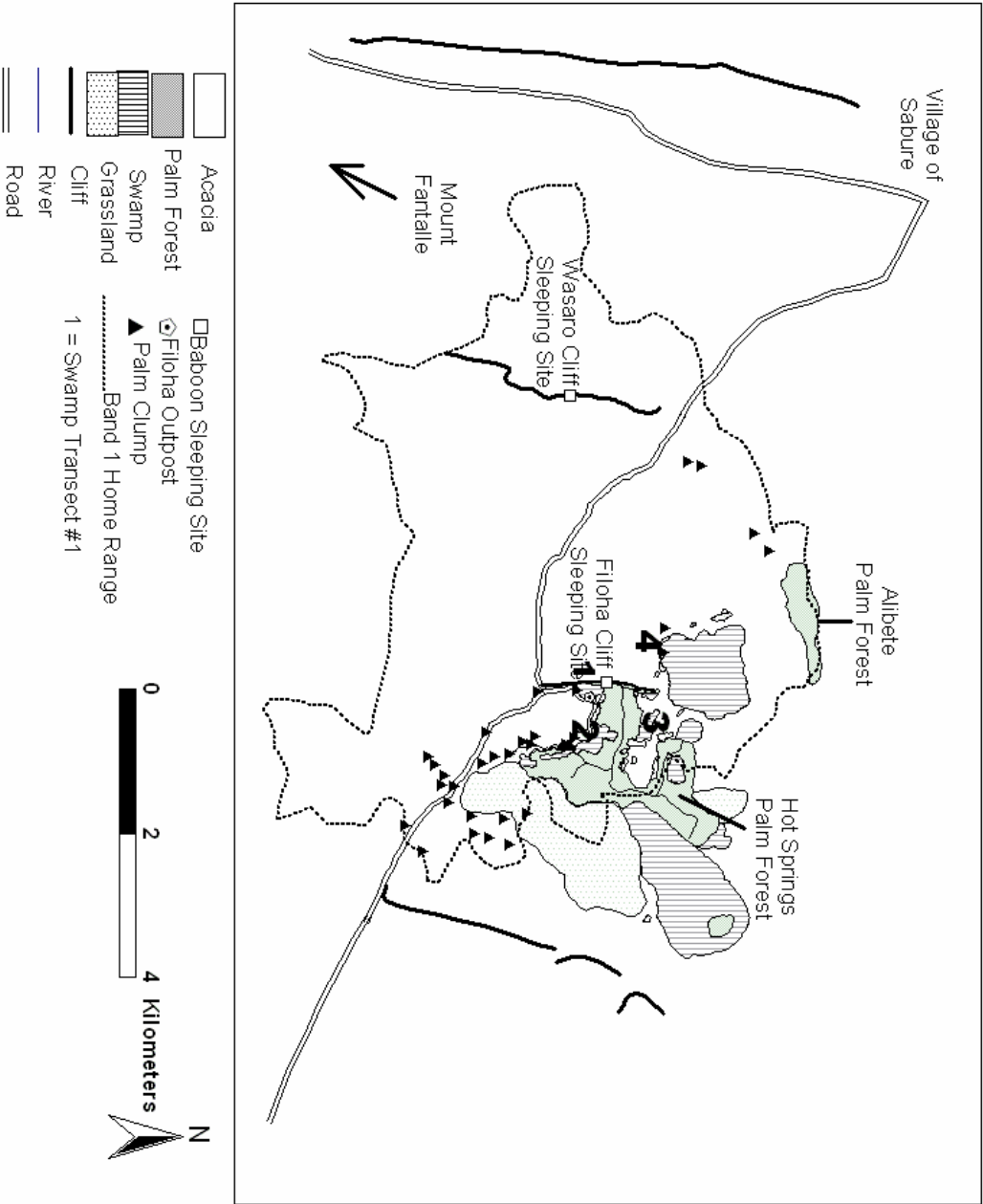


Figure 3.5 Average abundance of *Acacia senegal* plant parts

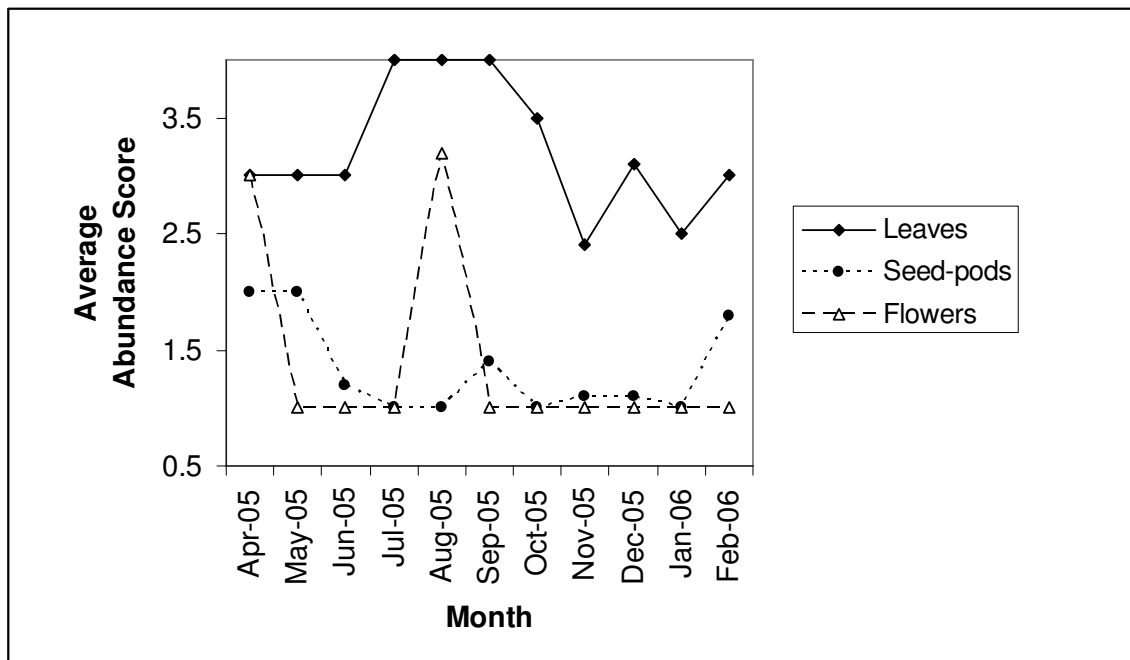
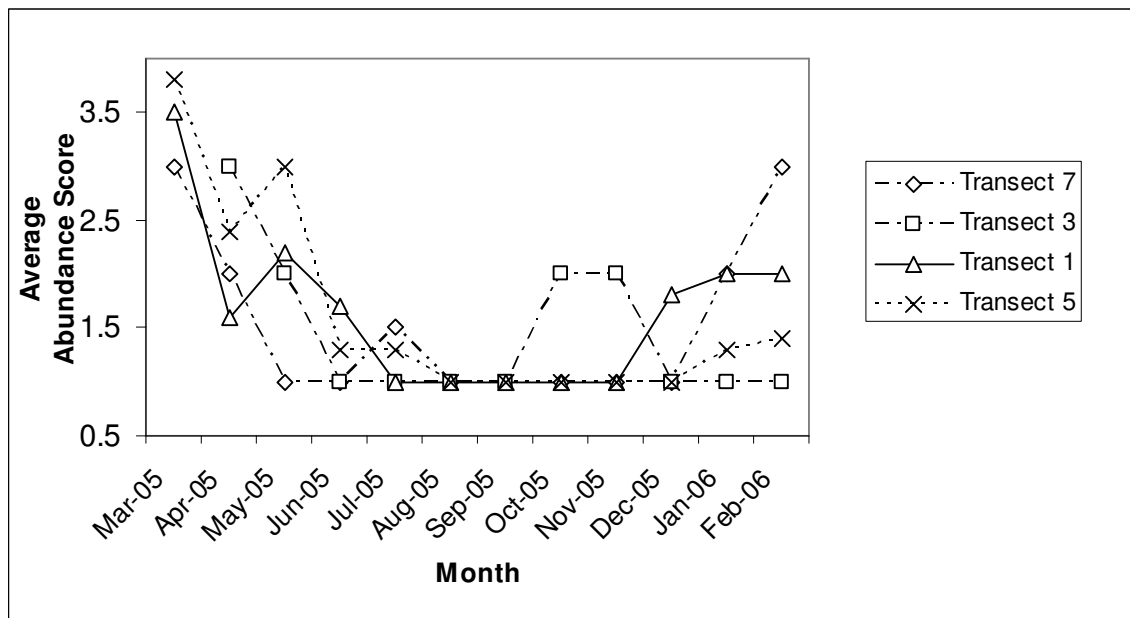


Figure 3.6 Average abundance of ripe doum palm fruit in palm forests



CHAPTER 4

FEEDING BEHAVIOR AND ACTIVITY PATTERNS

4.1 Introduction

Animals must obtain enough food to sustain basic metabolic processes and reproduce successfully; therefore, an efficient foraging strategy is critical for their survival. Feeding patterns vary among primates according to the spatial and temporal availability of food resources, as well as factors such as body size, group size, and reproductive state (Oates, 1987).

While many primate taxa specialize on particular food types, baboons are known for their diverse diets (Altmann and Altmann, 1970; Hamilton et al., 1978; Post, 1982; Norton et al., 1987; Whiten et al., 1987). Baboons exploit a wide array of food sources from a variety of vegetation levels, and it has been suggested that this is an adaptation to the range of habitats in which baboons live (Whiten et al., 1991). This flexibility in diet is especially important for hamadryas baboons, which live in semi-desert habitats with limited and sparsely distributed food resources (Kummer, 1968a; Sigg and Stolba, 1981; Biquand et al., 1992; Al-Safadi, 1994; Swedell, 2006).

Generalist diets notwithstanding, baboons are highly selective feeders (Norton et al., 1987; Whiten et al., 1987). Baboons choose foods based on their nutrient composition as well as their availability (Whiten et al., 1991; Barton et al., 1993; Barton and Whiten, 1994). Various food constituents such as protein, fiber, alkaloids, and phenolics have been shown to influence baboon diets, and a high protein-to-fiber ratio has been reported to be the most important factor in baboons' choice of foods (Hamilton et al., 1978; Whiten et al., 1990, 1991; Barton and Whiten, 1994). Altmann (1998) showed

that energy was the crucial factor in food choice for yellow baboons in Amboseli, Kenya, suggesting that baboons should also choose food based on carbohydrate levels. Because seeds and fruits contain high levels of protein and carbohydrates, respectively (Altmann et al., 1987; Whiten et al., 1991; Barton and Whiten, 1994), baboons are expected to concentrate their feeding on seeds and fruits, and rely on less nutritious food items such as leaves only when their preferred foods are not available. The feeding patterns of a wide range of baboon populations have been quantified, and several studies have examined the relationships between dietary composition, ecological variables, and activity patterns (e.g., Dunbar 1992, 1996; Hill, 1999; Hill and Dunbar, 2002). To date, however, there are few quantitative data on the feeding behavior of hamadryas baboons.

In this chapter, I describe the feeding behavior and activity patterns of Band 1 at Filoha from March 2005 through February 2006. The home ranges of the bands at Filoha consist of *Acacia* scrublands, open grasslands, and cliffs, all of which are typical of hamadryas habitat in other parts of their geographic range (Chapter 3). Unlike many other areas inhabited by hamadryas baboons, however, the Filoha area also contains palm forests, hot springs, and swamp vegetation (Figure 2.3). These habitat types provide the baboons with food and water resources typically unavailable elsewhere in their range. Previous studies at Filoha have shown that doum palm fruit, *Hyphaene thebaica*, is a major component of the baboons' diet (Swedell, 2002b, 2006; Swedell et al., 2008). While I did not conduct nutritional analyses of plant species at Filoha, analyses of two closely related species, *H. coriacea* and *H. compressa*, indicate that this palm fruit is high in carbohydrates and rich in a variety of important minerals including calcium, iron, and zinc (Hoebekke, 1989; Lokuruka, 2007). This finding supports the argument that baboon feeding preferences are based on the nutritional quality of food types.

Due to the presence of *H. thebaica* at Filoha, I expected the baboons' feeding behavior to differ markedly from that of other baboons. If the baboons at Filoha spend much of their feeding time on doum palm fruit, they would not need to rely as heavily on other food sources. A previous study by G. Hailemeskel, which focused on adult males in Band 3 at Filoha, found a low dietary diversity relative to other baboon populations (Swedell et al., 2008), and I predicted that my data on all age-sex classes would show this pattern as well. Secondly, I expected the baboons at Filoha to consume a greater proportion of fruit than other baboon populations due to the relatively high abundance and availability of fruit at Filoha, compared to other baboon sites. Third, because doum palm fruit is a high-energy food resource, the Filoha population of hamadryas should spend less time feeding overall than other baboons. Finally, the contribution of *H. thebaica* to the baboons' feeding at Filoha should be related to the abundance of its fruit throughout Band 1's home range. When palm fruit is not available, the baboons should eat other high quality foods such as seeds. Only when both doum palms and other fruit and seeds are not available are the baboons expected to rely on lower quality food items such as leaves.

In this chapter, I describe Band 1's feeding behavior by food species. I also describe the temporal variation in food consumption and its relation to the abundance of food items in the baboons' home range. In addition, I describe the overall characteristics and temporal variation of the baboons' activity patterns. These data will allow me to examine the role that *H. thebaica* plays in the feeding ecology and activity budgets of Band 1 at Filoha, and how these foraging patterns compare with those of other baboon populations.

4.2 Methods

4.2.1 Feeding Behavior

In January and July 2004, I learned to recognize and identify the food species that contributed to Band 3's diet in 2001-2002 (Swedell et al., 2008), as well as other plants in their home range, from G. Hailemeskel of the Ethiopian Wildlife Conservation Department. Because of the extensive overlap between the feeding behavior and home ranges of Band 1 and Band 3, I was able to identify almost every species consumed by Band 1 from March 2005 through February 2006. Band 1, however, did consume five plant species that I could not identify. These five species combined contributed only 0.6% (N=39) of Band 1's annual feeding and were not consumed in more than two months of the year (section 4.3.1).

During band scans conducted every 15 minutes during all-day follows, I recorded food items at the species level, as well as the plant parts being eaten, when members of Band 1 were feeding. Because my original intention in conducting band scans was to document the habitat use and activity patterns of Band 1 as a whole, and not to quantify feeding behavior, a food species was recorded just once regardless of how many individuals were eating it, as opposed to recording the foods being eaten by every visible baboon. These data, therefore, do not take into account how many individuals were eating a particular food species at a given time. As a result an element of bias exists in these data, as it is possible that commonly eaten foods are underrepresented in this dataset, and rarely eaten foods are overrepresented, as a frequently consumed food counted as much as an uncommon food even if, say, fifty baboons were feeding on the former and only one on the latter. When members of the band were eating different plant parts of a particular species during a scan I noted each plant part, but counted it as just

one feeding record. The plant part data therefore contain the same potential bias as the food species dataset.

There are substantially fewer feeding records in March than in any other month (Table 4.1) because during this time I focused on learning the identities of the baboons and following them for a complete day. Furthermore, during the last two weeks of March, Band 1 fissioned for six days (as described in Chapter 6), during which I observed only one half of the band. Data that I collected during this time period did not contribute to these analyses because I am focused here on patterns regarding the band as a whole, not when the band split into independent subgroups. I also spent three days during the last week of March following Band 3 because Band 1 could not be located. The existing feeding records, therefore, almost certainly do not accurately reflect Band 1's March feeding habits. In addition, as described in Chapter 2, data from September are absent from these analyses because I observed Band 1 in its entirety for only one full observation day during that month.

The contributions of different food species and plant parts to Band 1's annual feeding habits were calculated as a proportion of the total number of all feeding records. Monthly feeding habits were calculated as proportions of the feeding records for each month. Feeding breadth refers to the number of different plant species contributing to the total feeding records each month (Swedell et al., 2008). Data on predation were collected on an ad libitum basis.

4.2.2 Activity Budgets

I collected data on activity patterns for the band as a whole during band scans. Four activities were recognized: rest, groom, travel, and feed (Table 4.2). Due to the

large band size and visibility restrictions, I could not sample all adult members of the band during each scan. During band scans, each activity was recorded only once, so the number of individuals engaged in each activity was not taken into account. As with the feeding records, potential bias exists in that activities that the baboons engaged in more commonly may be underrepresented in the dataset while less common activities may be overrepresented.

I calculated the activity budgets for each individual activity as a proportion of the total activity records. There was not an equal number of scans for each of the 48 15-minute time slots between 0600 and 1800 because I sometimes lost the baboons for periods of time ranging from 15 minutes to two hours. Additionally, when the baboons slept on the Wasaro cliff I had to leave the baboons before 1800 to return to Filoha before dark. To calculate activity budgets, therefore, following Bronikowski and Altmann (1996) I first computed the average proportions of each of the four activities overall, for each of the 12 hours of the day (0600-1800). These hourly values were then averaged to calculate monthly activity budgets. The annual activity budgets represent the average of the monthly activity budgets.

4.3 Results: Feeding Behavior

I collected a total of 3669 feeding records over 2429 band scans (Table 4.1). The baboons were observed eating just one food species in over half (55.8%) of these scans, and two different food species in 31.0% of the scans. Band members were observed eating three different food species at the same time in 10.6% of these band scans, four food species in 2.4%, and five species in 0.2% of the scans in which I collected feeding records. I recorded the plant part that the baboons consumed in 86.4% (N=3170) of the

total feeding records. The baboons were observed eating just one plant part of a food species 91.5% of the time. In 8.2% of the feeding records in which plant part was recorded the baboons were observed feeding on two different plant parts of a single food species at a given time, and they fed on three different plant parts of a food species in the remaining 0.3% of the records.

4.3.1 Annual Feeding Habits

The baboons were observed feeding from 41 species of plants belonging to at least 28 genera and 21 families (Table 4.3). Although the baboons ate a variety of species, only 17 plant species each contributed at least 1% of the annual feeding records (Table 4.4). These species together constituted at least 90.7% of the total feeding records, and thus 24 plant species comprised the remaining 9.3% of Band 1's feeding records.

The top three plant species, from three different families, comprised over half (52.9%) of Band 1's annual feeding records, and the ten most frequently-consumed species together made up at least 80.4% of the feeding records. The baboons fed most frequently on the seeds, leaves, flowers and sap of *Acacia senegal* (23.0%), followed by doum palm fruit (*Hyphaene thebaica*) (20.4%). The baboons ate these foods while situated in *A. senegal* shrubs and palm trees, respectively, as well as underneath them. They most commonly sat in the shrubs and trees or on the ground with an upright posture while using both hands to manipulate the food items. The baboons also sometimes stood bipedally on the ground underneath *Acacia* shrubs, using both hands to reach and manipulate food items. The flowers, leaves, and seeds of *Tribulus cistoides* comprised at least 9.5% of Band 1's feeding records, and no other plant species contributed more than 8% of the total feeding records. The baboons always ate *T. cistoides* while sitting on the

ground with upright torso, using both hands to pick the seeds, leaves, and flowers off of the stems and insert them into their mouths. The baboons ate all five *Acacia* species that were present in their home range. *A. senegal*, *A. nubica*, *A. tortilis*, and *A. mellifera* were four of the top seven species consumed. Only *A. nilotica* did not contribute at least 1% to Band 1's annual feeding records.

The general plant types in the baboons' diet included woody vegetation (i.e., woody perennial plants including shrubs and trees), and grass and/or herb species (i.e., non-woody seed-bearing plants which die annually after flowering or revert to storage organs during non-growth seasons). The baboons fed on the following plant parts: blades, flowers, fruit, gum, leaves, roots, seeds, and stems. I recorded the plant part as 'fruit' as opposed to 'seed' when the baboons ate the fleshy part surrounding the seed, but not the seed itself. The baboons also occasionally consumed animal matter, including invertebrates, birds, and small mammals.

Species from the shrub layer of vegetation (i.e., woody plants between 10 m and 15 cm tall) comprised at least two-thirds (66.1%) of Band 1's feeding records. The baboons fed from the herb layer of vegetation (i.e., all herbaceous species regardless of height and woody plants less than 15 cm high) at least 32.4% of the time. The remaining 1.5% of the feeding records were composed of subterranean items (which were counted as a separate category from the herb layer) (0.9%) and animal matter (0.6%).

Data on plant part consumed were available for 86.4% of the total feeding records. The baboons relied most heavily on seeds (36.0%) and fruits (23.1%) (Figure 4.1). The five *Acacia* species were the most important sources of seeds, although the baboons also fed on the seeds of several herb species. The majority of the fruit that the baboons consumed was that of *H. thebaica*; the baboons ate the fleshy part surrounding the seed,

and discarded the seed. Following seeds and fruit, the next most prevalent plant part in the baboons' feeding was leaves (21.2%). While the maturity of leaves was not regularly quantified during scans, observations indicated that the baboons most frequently consumed young leaves. Flowers comprised at least 12.0% of Band 1's annual feeding records. The remaining 7.6% of the feeding records consisted of stems, gum, roots, and blades.

As mentioned above, the baboons also occasionally consumed animal matter, both vertebrates and insects. I observed baboons eating vertebrate meat on 28 occasions (Table 4.5). The baboons most commonly consumed dikdik (*Madoqua kirki*) (N=9), Guinea fowl (*Numida meleagris*) (N=6), and Abyssinian hare (*Lepus capensis habessinicus*) (N=5). They were also observed eating lesser kudu (*Tragelaphus imberbis*) and lizards (unknown spp.) three times each, as well as francolin (*Francolinus spp.*) and an unknown bird species once each. The baboons also caught and ate dragonflies, locusts, and grasshoppers. While I usually observed vertebrate-eating on an *ad libitum* basis, observations of insect-eating were made during band scans, and comprised 0.6% of the annual feeding records.

4.3.2 Predation by Baboons

While the prey animal had already been killed in most of the occasions that I observed the baboons eating vertebrates, I did witness the predation event ten times. Twice solitary male baboons grabbed a lizard and bit into it, eating the lizards while still alive. On another occasion a juvenile male snatched a lizard, and then rolled it in his hands and on the ground until it died, before eating it. Once I observed a large juvenile male baboon run after a small (presumably juvenile) dikdik, grab it, bite into its thigh and

begin to eat while it was still alive. Similarly, when a Guinea fowl was on the ground, a solitary male baboon grabbed it, bit into its neck, and began eating it. In the case of the unknown bird species, a hawk was flying above an *A. tortilis* tree, seemingly trying to hunt the bird, but it was unsuccessful. The leader male Sami was sitting on a branch and shook the tree, which led to the hawk flying away; Sami then grabbed and bit into the bird, before coming down to the ground and eating it.

I also witnessed two of the lesser kudu predatory events. The first time, a 2-3 month old kudu and its mother were standing next to an *A. senegal* tree about 15 m from the leader male Park. Park ran toward the kudus and the mother fled, but he bit the young kudu on the lower back. Park began to eat from the kudu's back and ribs while it screamed and struggled to escape. When Park finished eating and left the kudu about ten minutes later, the kudu was still alive and screaming.

In each of the observations described thus far, baboons hunted animal prey individually. Some elements of cooperation such as coordination (i.e., several hunters focus on the same prey) and collaboration (i.e., hunters carry out different actions toward the same prey) (Boesch and Boesch, 1989) seemed evident, however, in the second kudu hunt. In this case, a 2-3 month old lesser kudu walked through an area of *Acacia* scrubland that was inhabited by at least 20 baboons. About 10 baboons – both males and females – slowly approached it, surrounding the kudu on three sides. Two adult male baboons then ran toward the kudu, which responded by backing up to the trunk of an *A. senegal* shrub and crouching to the ground. One of the baboons then bit into the kudu's stomach area and began to eat while the kudu was still alive. The other baboons screamed and barked, the baboon that hunted the kudu picked it up and ran into dense

bush, and the rest of the baboons followed. I could not ascertain whether the meat was then shared due to the prohibitively obstructive vegetation.

Adult males were the first individuals observed eating vertebrate meat on 22 of the 27 occasions, split evenly between leader males and those unaffiliated with an OMU. Adult females, by contrast, were observed eating fresh meat only four times. Twice, females ate the meat alongside their leader male, and the other two times the females ate alone. On one of these occasions an adult female from Park's OMU was eating fresh meat from Abyssinian hare, and Park tried to obtain some, first by grunting at her, and then chasing her around a tree. The female ran away with the hare in her mouth without Park eating any of it. Juvenile males hunted animals twice, as described above. As far as known individuals, the leader males Park and Titi were both observed consuming meat three times, and the leader males Redface and Cory were both observed eating meat twice.

Overall, it appeared that the baboons did not share meat. Twice, females and their leader males consumed meat together, but in all other cases only one individual ate the meat. Other baboons (both males and females from different age-classes) often sat nearby, sometimes in contact with the (presumed) hunter, but they generally did not attempt to eat any meat. At least nine times other baboons ate animal remains after the original baboon traveled away. Often these other baboons appeared to wait their turn, maintaining a distance of several meters but not approaching or attempting to eat any meat until the original baboon departed. Six of these times it was Pluto, an old male unaffiliated with an OMU, who was observed eating animal remains. Three times Pluto waited within several meters of the other baboon for at least 40 minutes before he had the opportunity to eat any meat. Once, he followed another unaffiliated male baboon who

was eating dikdik for 44 minutes, traveling several hundred meters, but never approached closer than 4 m before he finally managed to eat a few scraps of meat. On another occasion, Pluto was chased off by another unaffiliated male after he waited 45 minutes to eat lesser kudu.

4.3.3 Temporal Patterning of Feeding Behavior

Although the top 17 plant species together comprised at least 90.7% of Band 1's annual feeding records, their inclusion was quite variable on a monthly basis (Table 4.6). Five of the seven most frequently consumed species – *A. senegal*, *T. cistoides*, *A. tortilis*, *Pentarrhinum insipidum*, and *A. mellifera* – were consumed in all 11 months included in these analyses. The baboons consumed the other two top-seven species – *H. thebaica* and *A. nubica* – during 10 months. No other species was eaten in more than nine months.

Of the three most frequently consumed plant species, *A. senegal* contributed at least 16% to the feeding records each month. *H. thebaica* made up at least 20% of the feeding records during seven months, and was the most frequently eaten species during six of them. It did not, however, contribute more than 8% of the feeding records in the remaining four months, and the baboons were not observed eating doum palm fruit during August, the peak of the wet season. *T. cistoides* contributed less than 6% of the feeding records in eight months, but made up more than 10% of the records in the remaining three months. It comprised at least 59.4% of the feeding in August, a substantially higher percentage than any other plant species' contribution to any month's feeding records.

Clear seasonal patterns existed in the baboons' consumption of *H. thebaica* and *T. cistoides*, but not *A. senegal* (Figure 4.2). While the baboons' use of *A. senegal* remained consistent across seasons, they fed on *H. thebaica* with much greater frequency during the

dry season than the wet season. The baboons' consumption of *T. cistoides* displayed the greatest seasonal disparity, contributing 36% of the wet season feeding records, but only 5% during the dry season. The fourth through sixth most prevalent food species – *A. nubica*, *A. tortilis*, and *P. insipidum* – each contributed 10% of the feeding records during two months of the year (Table 4.6). Seasonal patterns were not clear, however, and these peaks likely reflect the availability of preferred plant parts in the baboons' home range (see below).

Seeds and fruits comprised over half of Band 1's annual feeding records. Variation existed across months, however, in the contribution of different plant parts to the feeding records (Figure 4.3). Feeding on seeds peaked at 60.4% in October, and reached its lowest at 7.7% of the feeding records in August. The proportion of fruit consumed by Band 1 reached its peak at 45.5% in March, while the baboons did not eat any fruit in August. Leaf consumption varied from a high of 50.0% of feeding records in July to a low of 6.3% of feeding records in June. The baboons' consumption of flowers varied the most extensively, peaking at 78.3% in August but not contributing to the feeding records in February. The temporal variation of the consumption of different plant parts, therefore, reflects seasonality, with seeds and fruits together comprising more than 60% of the feeding records in the dry season, and flowers constituting almost 50% of the feeding records in the wet season (Figure 4.4).

The consumption of less frequently used plant parts also displayed seasonal patterns. The baboons' consumption of roots and other subterranean items comprised at least 7.0% and 4.1% of the feeding records in October and November, respectively, but did not make up more than 2.1% of the feeding records in any other month. Similarly, gum contributed 5.7% and 4.9% of the feeding records in October and November but not

more than 2% of any other monthly diet. The consumption of both subterranean items and gum, therefore, peaked at the beginning of the dry season.

The baboons appeared to prefer flowers, when available, to other plant parts. In August, when the abundance of fresh leaves, seeds, and flowers was at its peak throughout Band 1's home range, flowers contributed 78.3% of the feeding records. No other plant part ever contributed more than 60.4% of any month's feeding records. Despite the fact that the abundance of leaves was most consistent across months, the baboons appeared to rely on leaves only when they were fresh and other preferred plant parts were not available. Leaves made up the greatest portion of the feeding records in July – when young leaves were fresh, and there was a low abundance of both doum palm fruit and *Acacia* spp. seeds and flowers (and the baboons appeared to have depleted most of the dry seeds on the ground) – and in November, when flowers and seeds were not abundant and palm fruit was not yet ripe in most areas of Band 1's home range.

The temporal consumption of different plant parts was also tied to the proportion of Band 1's most frequently consumed food species. Across months, there were significantly positive relationships between the consumption of fruit and the proportion of *H. thebaica* in the diet ($r_s = 0.907$, $p = 0.000$, $N = 10$), and the consumption of flowers and the proportion of *T. cistoides* in the diet ($r_s = 0.974$, $p = 0.000$, $N = 10$). There was a positive relationship between the consumption of seeds and the proportion of *A. senegal* in the diet, but this relationship was not significant.

The consumption of *H. thebaica* was coupled somewhat with the abundance of its fruit. The proportion of *H. thebaica* in the feeding records was positively related to the overall abundance of doum palm fruit in Band 1's home range, but this relationship was not significant. The abundance of palm fruit was quantified in four palm forest patches

(section 3.2.2; Figure 3.2). Positive relationships existed between *H. thebaica*'s contribution to feeding records in each of these patches, but only that of Transect 1 was significant ($r_s = 0.919$, $p = 0.000$, $N = 10$).

While fruit was the only part of *H. thebaica* that the baboons consumed, they ate several different plant parts of both *A. senegal* and *T. cistoides*, and this consumption varied seasonally (Figure 4.5). The proportion of *A. senegal* leaves consumed did not vary across seasons, but the baboons ate the seeds almost twice as frequently in the dry season (60.5%) than in the wet season (37.8%). Similarly, the baboons consumed the gum 12.7% of the time they fed on *A. senegal* in the dry season, but only 2.1% of the time during the wet season. Conversely, 34.0% of the time that the baboons ate *A. senegal* in the wet season was devoted to flowers which were not available during the dry season.

The baboons' consumption of *A. senegal* flowers corresponded to their abundance in band 1's home range (Figure 4.6a). These flowers made up over 60% of the baboons' consumption of *A. senegal* in August when their average abundance peaked at over 3 (see section 3.2.1 for abundance scale); during the rest of the year – with the exception of April – the abundance of flowers was low and consequently the baboons relied on other plant parts. While the abundance of *A. senegal* leaves was relatively high throughout the study period (Figure 4.6b), the baboons appeared to feed on them only when other plant parts were not available. The baboons' preference for young (vs. mature) leaves was indicated by the fact that *A. senegal* leaves were eaten most frequently in November, when during the last week of the month after two days of rain (the only rain in two months), *A. senegal* young leaves were abundant, and the flowers not available, as well as in July when leaves were fresh (and flowers not yet abundant). There is no clear relationship between the consumption of *A. senegal* seeds and their abundance (Figure

4.6c); this can be attributed to the fact that in June and October the baboons fed predominantly on dry seeds from the ground underneath shrubs which were not taken into account during phenological monitoring (section 3.2.1).

The seasonal patterns of the consumption of the different parts of *T. cistoides* were more extreme than those of *A. senegal* (Figure 4.5). The baboons fed on the seeds 98.9% of the time that they consumed *T. cistoides* during the dry season and only 2.4% of the time during the wet season. Conversely, the baboons ate the flowers 81.7% of the time during the wet season, but only 1.1% of the time during the dry season. The phenological patterns of *T. cistoides* were not quantified, but qualitative observations indicated that it flowered throughout Band 1's home range by the last week of July, peaked through August, and had mostly died by 5 September, indicating a high correspondence between the consumption of the flowers and their availability.

The number of plant species that the baboons consumed also varied across months, although these patterns did not appear to reflect seasonality (Figure 4.7). Feeding breadth was lowest in March and February, with 15 plant species contributing to the feeding records, and peaked with 28 species contributing to the feeding records in July and November. Feeding breadth was high, therefore, during the wet season month of July, but low in August when the baboons consumed only 16 plant species. The large numbers of plant species eaten in July and November may reflect the baboons' focus on leaves during these months. While the abundance of leaves was high in July due to the onset of the long rains, flowers were not available until August. The baboons, therefore, ate a wider variety of food species when leaves were the most abundant food item in their range, but narrowed the number of food species that they consumed when their preferred plant part was available. The presence of leaves explains the July peaks in the

consumption of *P. insipidum* and *A. mellifera* (Table 4.6), species whose leaves were eaten exclusively. The abundance of fresh leaves at the end of November may also explain the peak in breadth at this time. There was a negative correlation between feeding breadth and the contribution of *H. thebaica* to the baboons' feeding records, although this relationship did not reach significance. When the baboons spend more time eating doum palm fruit, therefore, they do not rely as heavily on other food sources.

Despite considerable monthly variance in Band 1's feeding breadth, the baboons were selective feeders. The baboons fed predominantly on *H. thebaica* when its fruit was available, and preferred the dry seeds and flowers of *Acacia* spp. The baboons consumed leaves, by contrast, only when young fresh leaves were abundant and preferred food items were unavailable.

Although meat-eating comprised a small portion of the baboons' overall feeding records, some temporal patterns were evident (Figure 4.8). Members of Band 1 were observed eating vertebrates during seven months during the study period, with a peak in October. The nine times that the baboons were observed eating vertebrate meat during October occurred in the last two weeks of the month, when the band reunited after a month-long fission (Chapter 6). The percentage of insects of the monthly feeding records was never greater than two. The months with the most insect-eating corresponded with periods of two to five days in which swarms of locusts were moving through the Filoha region.

4.3.4 Comparisons with Other Baboons

The composition of Band 1's feeding records in 2005-2006 was similar to that of both Band 1 and Band 3 during previous periods. Swedell (2006) reported that the main

food items consumed by Band 1 in 1996-1998 were doum palm fruit and the leaves, seeds, and flowers of *A. senegal*, *A. nubica*, and *A. mellifera*.

The diet of Band 3 at Filoha was quantified in 2001-2002 (Swedell et al., 2008). Similar to the 41 plant species that Band 1 consumed in 2005-2006, 44 plant species contributed to Band 3's diet. As with Band 1, the top two species in Band 3's diet were *H. thebaica* and *A. senegal*, and all 12 plant species that contributed at least 1% to Band 3's diet also contributed at least 1% to Band 1's feeding records. Band 3 spent almost half their feeding time (47.4%) eating *H. thebaica*, however, and 11.6% feeding time on *A. senegal*, compared to 20.4% and 23.0% respectively for Band 1 in 2005-2006. Band 3 also relied more heavily on *T. latifolia* and *Cyperus* spp. than did Band 1. These disparities in diet may reflect differences in the home ranges of Band 1 and Band 3 (Schreier and Swedell, 2008).

Seasonal patterns of Band 3's diet were similar to those of Band 1's. As in 2005-2006, consumption of *A. senegal* did not vary seasonally, whereas the baboons relied more heavily on *H. thebaica* during the dry season. Band 1's spike in use of *T. cistoides* in August 2005 mirrors that of Band 3, which spent 56.2% of feeding time in August 2001 eating *T. cistoides* (Swedell et al., 2008). This suggests that the baboons at Filoha take advantage of *T. cistoides*' seasonal flowering in August. While Band 3 relied on fewer plant species during the dry season than the wet season, seasonal patterns in feeding breadth were not clear for Band 1 in 2005-2006.

Hamadryas baboons rely on *Acacia* species throughout their range (Nagel, 1973; Kummer 1968a; Kummer et al., 1981; Al-Safadi, 1994). In Ethiopia, Nagel (1973) reported that hamadryas baboons at the Awash River most commonly fed on the flowers, seeds, and fresh shoots of *A. senegal*, *A. nubica*, *A. tortilis*, and *A. clavigera*, and

appeared to prefer the flowers when they were available. At Erer Gota, *Acacia* species comprised the majority of the diet across seasons, and the baboons preferred *Acacia* flowers and grass seeds when they were available (Kummer, 1968a). Saudi Arabian hamadryas populations also fed primarily on *Acacia* trees and other semi-desert plants such as *Grewia* spp. and *Dobera glabra* (Kummer et al., 1981; Al-Safadi, 1994).

Differences between Band 1 at Filoha and other hamadryas populations emerged, however, in the composition of feeding records by plant part. Overall, baboons at Erer Gota spent 45% of feeding time consuming fruits and seeds, 28% of time eating leaves, 22% eating flowers, and 2% eating subterranean items (Kummer, 1968a), and Band 1 at Filoha spent 59.1%, 21.2%, 12.0%, and 1.7% of feeding time on fruits and seeds combined, leaves, flowers, and subterranean items, respectively. The increased consumption of fruits and seeds and decreased consumption of flowers at Filoha compared to Erer Gota likely reflects Band 1's reliance on the fruit of *H. thebaica*, which is not available at Erer Gota.

Like *H. thebaica* at Filoha, plant species specific to particular localities also play an important role in the diet of other hamadryas populations. At Erer Gota and in Eritrea, hamadryas baboons ate the fruits and young shoots of prickly pear (*Opuntia* spp.) and the baboons' use of this species appeared to be responsible in part for the determination of home ranges (Kummer, 1968a; Zinner et al., 2001). This species is not present at Filoha. While baboons at Filoha have little access to human food sources, hamadryas populations in both Eritrea and Saudi Arabia have been reported to feed from garbage dumps and raid crops (Biquand et al., 1992; Zinner, et al., 2001).

A comparison across baboon species suggests that *Acacia* species and grasses dominate baboons' diets virtually everywhere they exist (DeVore and Hall, 1965;

Altmann and Altmann, 1970; Hamilton et al., 1978; Ransom, 1981; Norton et al., 1987; Barton et al., 1993). It appears, however, that hamadryas baboons rely on fewer plant species than do other baboons. The total of 41 species consumed by Band 1 at Filoha during this study, and the 44 species consumed by Band 3 in 2001-2002 is comparable to the 45 species that contributed to the diet of anubis baboons from Chololo, on the Laikipia Plateau, Kenya (Barton et al., 1993). Anubis baboons at Gombe, however, consumed 75 plant species (Ransom, 1981) and chacma baboons in the Cape Peninsula consumed 94 plant species (Hall, 1963). In Mikumi National Park, Tanzania, yellow baboons consumed 185 plant species over five years (Norton et al., 1987).

Despite considerable variation across taxa and habitats, fruits, seeds, and leaves dominate baboon diets (Whiten et al., 1991). Overall, Band 1 at Filoha consumed more fruits and seeds, however, than did other baboon populations. While fruits and seeds together comprised at least 59.1% of Band 1's feeding records, anubis baboons in Chololo spent 23% of their time feeding on fruits and seeds (Barton, 1989), and yellow baboons in both Amboseli, Kenya and Mikumi spent 27% and 43% of their feeding time on fruits and seeds (Post, 1982; Bronikowski and Altmann, 1996; Norton et al., 1987). Chacma baboons in the Drakensburg Mountains devoted only 3% of their feeding time to fruits and seeds (Whiten et al., 1987, 1991). Although no distinction was made between fruits and seeds in most of these studies, the higher proportion of fruits and seeds in Band 1's diet almost certainly reflects the presence of *H. thebaica* at Filoha.

Despite the increase in fruits and seeds consumed by Band 1, the proportion of leaves and flowers in their feeding records is comparable to that of other baboon populations (Davidge, 1978; Barton, 1989; Bronikowski and Altmann, 1996; Norton et al., 1987; Whiten et al., 1987). Hamadryas baboons, however, consume subterranean

food items less frequently than do other baboons. Roots and other underground plant parts contributed to just 1.7% of Band 1's feeding records at Filoha, and 2% of the diet at Erer Gota (Kummer, 1968a). Underground food items in other baboon species, by contrast, contributed up to 52% of the diet in yellow baboons and 53% of the diet in chacma baboons (Rasmussen, 1978; Whiten et al., 1987). Analyses of dietary composition and feeding time of 15 baboon populations suggest that subterranean items are consumed when higher quality foods are not available (Hill and Dunbar, 2002). Band 1 did eat roots most frequently at the beginning of the dry season when doum palm fruit was not ripe and seed abundance was low, but rates of consumption were still low. When doum palm fruit and *Acacia* seeds were not available, leaves and flowers, in turn, were abundant. The presence of *H. thebaica* at Filoha, therefore, may limit Band 1's need to rely more heavily on underground food items.

Seasonal dietary patterns are common across species with baboons feeding on items such as flowers, young leaves, and grass seeds when they are available and switching to less preferred items during the dry season (Kummer, 1968a; Altmann and Altmann, 1970; Whiten et al., 1987; Norton et al., 1987). Band 3 at Filoha as well as yellow baboons at Mikumi and Amboseli, Kenya consumed fewer food species during the dry season months and a greater number of species in the wet season (Swedell et al., 2008; Norton et al., 1987; Post, 1982). The feeding breadth of Band 1 at Filoha, however, had both peaks and low points during July and August, the wettest months.

Overall, the feeding patterns of Band 1 at Filoha are similar to those of other baboons in that they fed predominantly on *Acacia* species and preferred their flowers when available. Band 1, however, consumed fewer plant species compared with other baboons. Furthermore, a greater proportion of its diet was devoted to fruits and seeds,

and a lower proportion to subterranean items compared with other baboons. These differences can be attributed the presence of *H. thebaica* at Filoha and its substantial contribution to the baboons' feeding records.

4.4 Results: Activity Patterns

I collected a total of 10,335 activity records over 4163 band scans. In 9.4% of these scans, the entire band was engaged in the same activity. The baboons engaged in two different activities in over half of these band scans (52.6%), while they engaged in three of the activities at once in 20.8% of the scans. Finally, in 17.2% of the band scans, the baboons were engaged in all four activities at once.

4.4.1 Activity Budgets

Figure 4.9 shows Band 1's overall activity budget. The baboons spread their time fairly evenly among resting, grooming, traveling, and feeding. They spent 29.0% of their time feeding, 27.6% traveling, 23.5% resting, and 19.9% grooming.

The proportion of time spent in each activity varied over the course of the day (Figure 4.10). The baboons devoted the first two hours of the day, 0600-0800, mostly to resting and grooming. By the third hour, the proportion of time spent resting and grooming declined as the baboons spent a greater proportion of time both traveling and feeding. The proportion of the hourly activity budget spent traveling was relatively consistent between 0800 and 1559. Feeding followed a similar pattern, and it peaked during the hour 1000-1059. Between 1600 and 1659 the baboons spent roughly equal proportions of time resting, grooming, traveling, and feeding. During the last hour of the day, however, the baboons mostly rested and groomed.

These patterns in activity budget mirror Band 1's habitat use over the course of the day (section 5.3.2). The baboons spent the early and late parts of the day on sleeping cliffs, and the majority of the time between 0900 and 1600 in *Acacia* scrublands, palm forests, open grasslands, or swamp vegetation.

Activity patterns also varied across months (Figure 4.11). The proportion of time the baboons spent resting remained relatively constant across months, ranging from 21.8% in July to 25.8% in October. The proportion of time spent grooming varied more widely, accounting for just 16.6% of the baboons' activity budget in April and reaching a high of 24.5% of the time in October. The baboons spent the lowest proportion of time traveling (22.8%) in October, and traveled the most in July (30.8%). Furthermore, the baboons spent the lowest proportion of time feeding (26.0%) in June, and fed the most in August (32.9%).

Some of this variation in activity patterns across months was related to seasonality in rainfall. The baboons traveled the most during the first month of the wet season (July) and spent the greatest proportion of time feeding during the second month of the wet season (August). The differences between the two wet season months were likely related to food abundance. The baboons may have traveled more during July to take advantage of the abundance of fresh leaves throughout their home range when flowers were not yet available (section 5.4.4). It is also possible, however, that they spent a greater proportion of time traveling in July simply because drinking water was available throughout their range at this time and so they were not restricted by access to water (Swedell, 2002b).

The baboons spent the largest proportion of time feeding in August when their diet consisted mostly of flowers. It is possible that *T. cistoides* flowers require more handling and processing time than do other plant parts. Although the nutritional qualities

of foods were not examined the increase in feeding time may reflect nutritional content – the baboons may have needed to spend a greater proportion of time eating flowers in order to obtain sufficient nutrients and energy.

4.4.2 Comparisons with Other Baboons

Similar to the proportion of time that Band 1 spent feeding (29.0%), Band 3 at Filoha spent 25.6% of their time feeding in 2001-2002 (Swedell et al., 2008). The amount of time devoted to feeding varied more widely across months, however, for Band 3 than Band 1. While Band 1 devoted between 26% and 33% of their monthly activity budgets to feeding, the proportion of time Band 3 spent feeding varied from 18% to 34%. The activity patterns of other hamadryas populations have been reported only at one other study site. Nagel (1973) reported that the hamadryas baboons at Awash River, like Band 1 at Filoha, spent a greater proportion of time resting and a lower proportion of time feeding during the first and last two hours of the day than they did in the hours between 0800 and 1600. Unlike at Filoha, however, the Awash River baboons spent roughly equal proportions of time moving over the course of the day. Nagel's data derive from just 14 days in October and November, however, and may not reflect the baboons' activity patterns over a longer period of time.

Results from the Filoha population in both 2001-2002 and 2005-2006 indicate that hamadryas baboons spend a lower proportion of time feeding than do other baboons. Hall (1962) reported that South African chacma baboons spent 80% of their time feeding and chacmas in the Drakensburg Mountains spent more than half of their time (56.6%) feeding (Whiten et al., 1987). Two groups of yellow baboons in Amboseli, Kenya spent an average of 45% and 48% of their time feeding, yellow baboons at Mikumi, Tanzania

spent 36.5% of their time feeding, and anubis baboons in Chololo, Kenya spent 40% of their time feeding (Bronikowski and Altmann, 1996; Norton et al., 1987; Barton, 1989).

Although hamadryas baboons spend a lower proportion of time feeding than other baboons, patterns across species in time spent traveling are less clear. Comparable to the 27.6% of time that Band 1 spent traveling over the study period, yellow baboons in both Amboseli and Mikumi spent 26.1% of their time moving (Bronikowski and Altmann, 1996; Norton et al., 1987). Anubis baboons at Chololo spent more time traveling than Band 1 (35.8%) (Barton, 1989), while chacma baboons in the Drakensburg Mountains spent less time moving (17.7%) (Whiten et al., 1987). Because hamadryas baboons have longer daily path lengths than other baboons (Chapman and Chapman, 2000; Swedell, 2006) but spend comparable or less time moving, hamadryas must travel faster than other baboons (Chapter 5).

4.5 Chapter Summary and Conclusions

Over the study period, Band 1 at Filoha fed most frequently on the fruit of *H. thebaica*, and the seeds, leaves, and flowers of *Acacia* species. The top three plant species – *A. senegal*, *H. thebaica*, and *T. cistoides* – comprised more than half of the baboons' annual feeding records. Their consumption, however, varied seasonally. The baboons fed on *H. thebaica* predominantly during the dry season, and they consumed *T. cistoides* with much greater frequency during the wet season. The contribution of different plant parts to the baboons' feeding records also varied over the study period.

As predicted, the proportion of *H. thebaica* contributing to Band 1's feeding records was positively related to the overall abundance of doum palm fruit in Band 1's home range. Despite considerable variety in Band 1's annual feeding behavior, the

baboons were still selective feeders. The baboons fed predominantly from *H. thebaica* when its fruit was available, and preferred the dry seeds and flowers of *Acacia* spp. The baboons consumed leaves, by contrast, only when young fresh leaves were abundant and preferred food items were unavailable. These preferences correspond to their abundance in the baboons' home range.

Overall, the feeding patterns of Band 1 at Filoha are similar to those of other baboons in that they fed predominantly on *Acacia* species and preferred their flowers when they were available. By contrast, Band 1 consumed fewer plant species compared with other baboons, as predicted based on the availability of doum palm fruit at Filoha. Also confirming expectations, a greater proportion of their feeding records consisted of fruit compared with other baboons. Furthermore, hamadryas baboons at Filoha spent less time feeding than other baboons. These differences can be attributed to the presence of *H. thebaica* at Filoha, and its considerable contribution to the baboons' feeding records.

In addition to the major role *H. thebaica* plays at Filoha in determining the baboons' feeding behavior and activity patterns, its presence also impacts Band 1's use of its home range. The relationship between travel patterns and the distribution of resources in the baboons' home range is explored in the following chapter.

Table 4.1 Feeding records by month (band scans)

<i>Month</i>	<i>Feeding Records</i>	<i>Observation Days</i>
March 05	95	19
April 05	357	19
May 05	447	15
June 05	347	13
July 05	294	10
August 05	315	10
October 05	299	18
November 05	352	11
December 05	626	17
January 06	364	13
February 06	213	10
Total	3,669	155

Table 4.2 Activities recorded during band scans

<i>Activity</i>	<i>Description</i>
Rest	Individual sitting or lying, and not engaged in any other activity except for self-grooming
Groom	Individual grooms another individual, or is recipient of grooming by another individual
Travel	All locomotion
Feed	All food handling and processing, drinking

Table 4.3 Composition of Band 1's annual feeding records by species

Family	Species	Parts Eaten¹	Contribution to Diet (%)	Months Consumed²
Acanthaceae	<i>Barleria spinisepala</i>	L, Se	1.1	6
Acanthaceae	<i>Justicia odora</i>	L	0.0	1
Aloeaceae	<i>Aloe spp.</i>	Rs	0.1	2
Amaranthaceae	<i>Psilotrichum gnaphalobryum</i>	L, Se	1.6	5
Amaranthaceae	<i>Pupalia lappacea</i>	Fl, L	0.2	5
Apparidaceae	<i>Godoba rotundifolia</i>	L, Se	0.6	9
Arecaceae	<i>Hyphaene thebaica</i>	Fr	20.4	10
Asclepiadaceae	<i>Pentarrhinum insipidum</i>	Fl, L	4.5	11
Asclepiadaceae	<i>Sarcostemma viminalis</i>	La	0.3	3
Balanitaceae	<i>Balanites aegyptiaca</i>	Fr, L, Se	1.9	8
Boraginaceae	<i>Heliotropium strigosum</i>	Fl, L	0.2	1
Cactaceae	<i>Cactus spp.</i>	R	0.0	1
Caesalpinioideae	<i>Delonix elata</i>	Se	0.0	1
Convolvulaceae	<i>Seddera bagshawei</i>	L, Se	1.8	9
Convolvulaceae	<i>Seddera latifolia</i>	L	0.1	2
Cyperaceae	<i>Cyperus rotundus</i>	Bl, Fl, R, St	1.6	9
Lamiaceae	<i>Ocimum americanum</i>	L, R, Se, St	0.2	3
Mimosoideae	<i>Acacia mellifera</i>	L, Fl, Se	2.8	11
Mimosoideae	<i>Acacia nilotica</i>	Se	0.8	10
Mimosoideae	<i>Acacia nubica</i>	L, Fl, Se	7.6	10
Mimosoideae	<i>Acacia senegal</i>	G, L, Fl, Se	23.0	11
Mimosoideae	<i>Acacia tortilis</i>	G, L, Fl, Se	5.5	11
Poaceae	<i>Coelachyrum poiflorum</i>	Bl	0.0	1
Poaceae	<i>Chrysopgon plumulosus</i>	R	0.1	1
Poaceae	<i>Sporobolus consimilis</i>	Bl, Fl, R, St	1.1	8
Poaceae	<i>Sporobolus ioclados</i>	Bl, Fl, R, St	0.5	7

Table 4.3 (cont.)

Family	Species	Parts Eaten¹	Contribution to Diet (%)	Months Consumed²
Poaceae	<i>Sporobolus spicatus</i>	Bl, Fl, R, St	2.4	9
Salvadoraceae	<i>Salvadora persica</i>	Fl, Fr, L	2.3	8
Solanaceae	<i>Solanum dubium</i>	Se	0.0	1
Tiliaceae	<i>Grewia erythraea</i>	Fr, L, Se	1.1	7
Tiliaceae	<i>Grewia tenax</i>	Se	0.1	2
Tiliaceae	<i>Grewia villosa</i>	Fr, L	0.1	4
Typhaceae	<i>Typha latifolia</i>	RS, St	2.4	9
Verbenaceae	<i>Chaseanum laetum</i>	L	0.1	1
Zygophyllaceae	<i>Tribulus cistoides</i>	Fl, L, Se	9.5	11
Unidentified	"171" ³	Bl, R	0.4	4
Unidentified	"255" ³	L, Se	0.1	2
Unidentified	"275" ³	L, Fl	0.4	2
Unidentified	"235" ³	L	0.1	2
Unidentified	"225" ³	L, Fl	0.1	1

¹B=blades, Fr=fruit., Fl=flowers, G=gum, L=leaves, La=latex, R=roots, RS=root sheath, Se=seeds, St=stems

²Out of a total of 11 months (September not included in annual diet because only 1 full observation day exists)

³number assigned to unidentified plant species

Table 4.4 Species contributing at least 1% of annual feeding records, ranked in order of percent contribution

Rank	Family	Species	Percent Annual Feeding Records	Cumulative Percent	Months Consumed¹
1	Mimosoideae	<i>Acacia senegal</i>	23.0	23.0	11
2	Arecaceae	<i>Hyphaene thebaica</i>	20.4	43.4	10
3	Zygophyllaceae	<i>Tribulus cistoides</i>	9.5	52.9	11
4	Mimosoideae	<i>Acacia nubica</i>	7.6	60.5	10
5	Mimosoideae	<i>Acacia tortilis</i>	5.5	66.1	11
6	Asclepiadaceae	<i>Pentarrhinum insipidum</i>	4.5	70.6	11
7	Mimosoideae	<i>Acacia mellifera</i>	2.8	73.3	11
8	Typhaceae	<i>Sporobolus spicatus</i>	2.4	75.8	9
9	Gramineae	<i>Typha latifolia</i>	2.4	78.1	9
10	Salvadoraceae	<i>Salvadora persica</i>	2.3	80.4	8
11	Balanitaceae	<i>Balanites aegyptiaca</i>	1.9	82.3	8
12	Convolvulaceae	<i>Seddera bagshawei</i>	1.8	84.1	9
13	Amaranthaceae	<i>Psilotrichum gnaphalobryum</i>	1.7	85.8	5
14	Cyperaceae	<i>Cyperus rotundus</i>	1.6	87.4	9
15	Tiliaceae	<i>Grewia erythraea</i>	1.1	88.5	7
16	Gramineae	<i>Sporobolus consimilis</i>	1.1	89.6	8
17	Acantaceae	<i>Barleria spinisepala</i>	1.1	90.7	6

¹Out of a total of 11 months (September not included in annual diet because only 1 full observation day of Band 1 exists)

Table 4.5 Vertebrate species consumed by Band 1

<i>Common name</i>	<i>Species name</i>	<i>Instances</i>
Dikdik	<i>Madoqua kirki</i>	9
Guinea fowl	<i>Numida meleagris</i>	6
Abyssinian hare	<i>Lepus capensis habessinicus</i>	5
Lesser kudu	<i>Tragelaphus imberbis</i>	3
Lizards	species unknown	3
Francolin	<i>Francolinus spp.</i>	1
Bird	Unidentified species	1

Table 4.6 Top 17 plant species' contribution (%) to monthly feeding records

	Mar 05	Apr 05	May 05	Jun 05	Jul 05	Aug 05	Oct 05	Nov 05	Dec 05	Jan 06	Feb 06
<i>Acacia senegal</i>	16.8	19.9	22.6	40.6	24.8	21.0	21.7	25.0	16.8	15.9	32.4
<i>Hyphaene thebaica</i>	46.3	24.7	25.3	19.6	8.2	0.0	5.4	4.3	32.9	31.9	31.5
<i>Tribulus cistoides</i>	5.2	3.4	5.6	0.3	10.9	59.4	16.7	5.1	2.7	1.1	0.9
<i>Acacia nubica</i>	0.0	4.2	9.0	6.1	6.1	7.9	17.7	13.6	3.7	7.7	5.2
<i>Acacia tortilis</i>	2.1	3.1	2.5	2.6	2.4	1.6	0.3	8.0	11.8	12.9	4.7
<i>Pentarrhnum insipidum</i>	1.1	0.8	0.5	1.7	15.3	1.3	2.0	6.8	3.2	10.4	4.7
<i>Acacia mellifera</i>	3.2	1.1	3.4	0.6	7.1	0.3	4.7	4.6	2.6	1.9	1.4
<i>Typha latifolia</i>	2.1	3.6	0.9	3.2	0.0	0.0	1.0	1.7	4.2	4.4	2.8
<i>Sporobolus spicatus</i>	0.0	3.9	5.2	7.5	1.4	0.3	3.0	0.9	1.4	0.3	0.0
<i>Salvadora persica</i>	0.0	1.1	1.1	0.3	0.7	0.0	0.0	4.5	5.1	2.5	7.5
<i>Balanites aegyptiaca</i>	0.0	1.4	0.0	0.9	1.0	0.0	2.3	3.4	3.7	3.0	2.8
<i>Seddera bagshewi</i>	0.0	8.4	1.6	0.9	0.3	2.2	3.0	1.7	0.0	0.6	0.5
<i>Psilotrichum gnaphalobryum</i>	2.1	6.7	0.0	0.0	0.0	0.0	0.0	7.4	1.4	0.3	0.0
<i>Cyperus rotundus</i>	1.1	3.9	2.9	1.2	0.3	0.0	1.7	0.9	3.0	0.0	0.5
<i>Grewia erythraeae</i>	1.1	1.1	1.3	4.6	4.4	0.0	0.3	0.0	0.2	0.0	0.0
<i>Sporobolus consimilis</i>	0.0	0.0	0.5	1.4	0.3	0.0	2.0	0.3	1.6	4.1	0.5
<i>Barleria spinisepala</i>	0.0	0.0	2.5	1.2	1.4	0.0	4.4	2.0	0.0	0.2	0.0

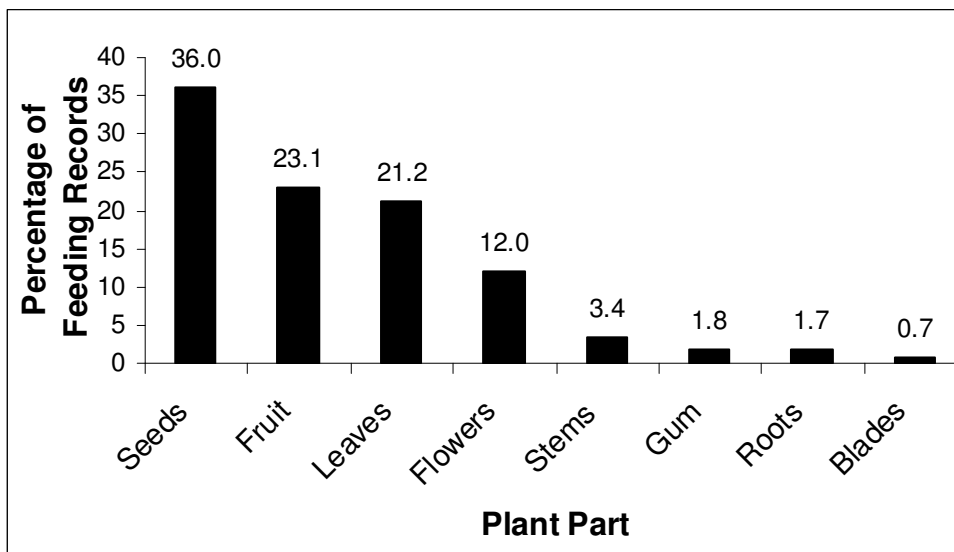
Figure 4.1 Annual feeding records by plant part

Figure 4.2 Seasonal consumption of the three most important food species

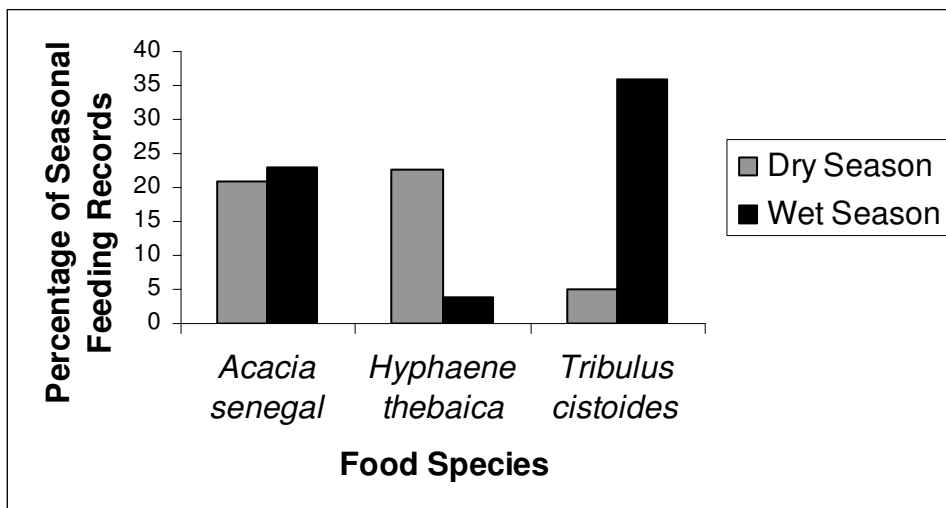
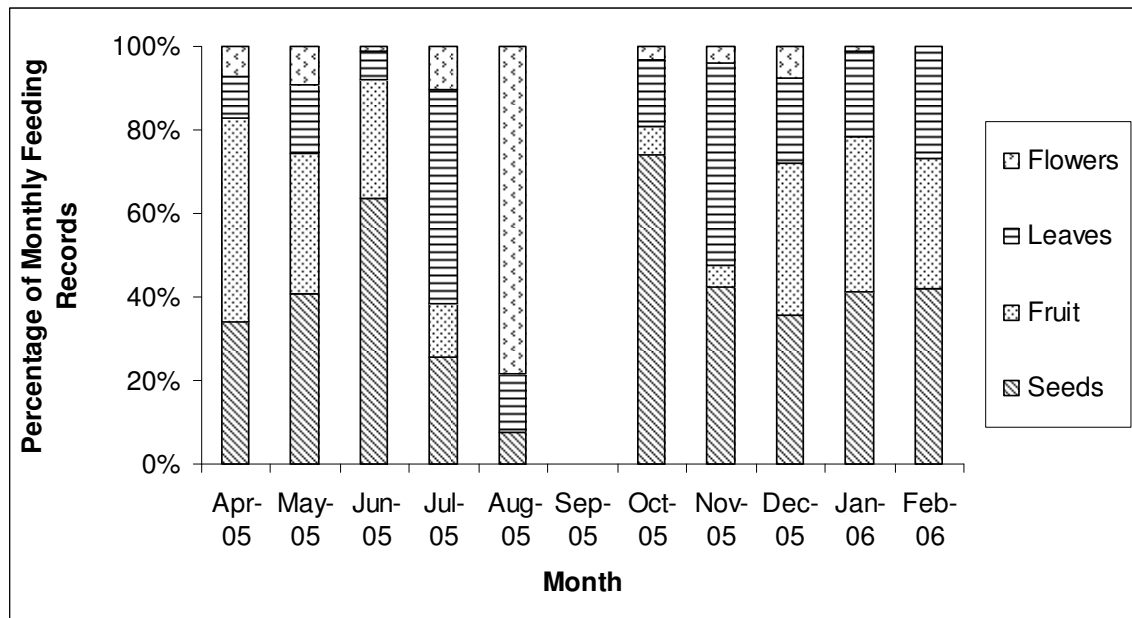


Figure 4.3 Temporal variation in consumption of plant parts



Dry Season = October, November, and December 2005; January and February 2006

Wet Season = July and August 2005

Figure 4.4 Seasonal consumption of seeds, fruits, leaves, and flowers

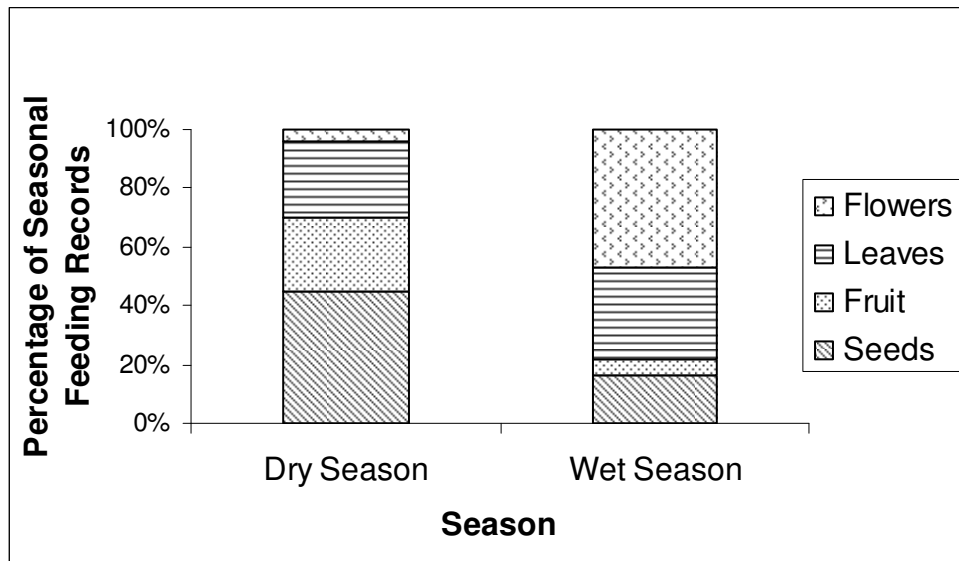
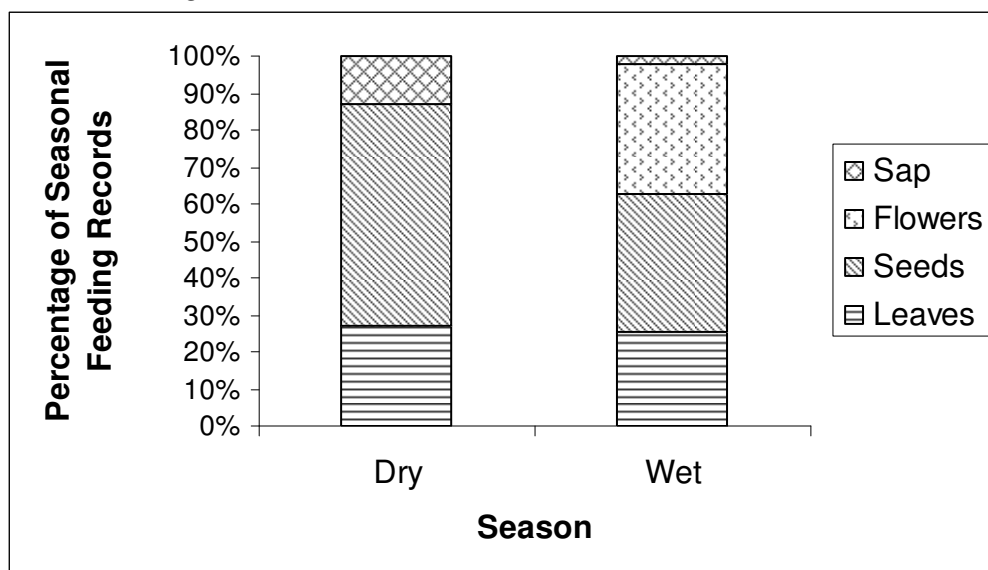


Figure 4.5 Seasonal consumption of the plant parts of *Acacia senegal* and *Tribulus cistoides*

a) *Acacia senegal*



b) *Tribulus cistoides*

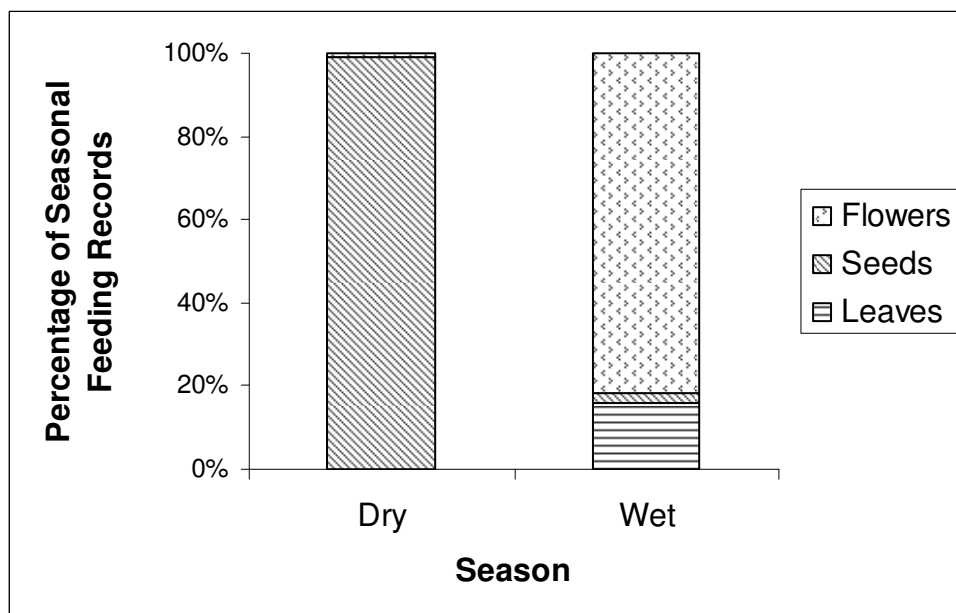
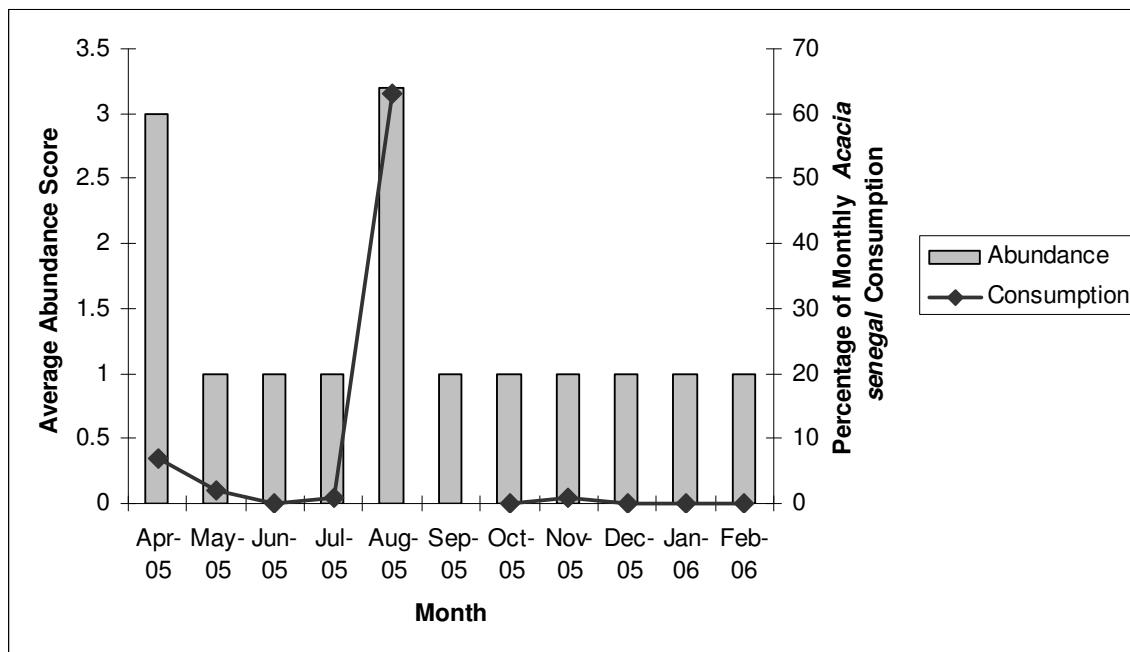
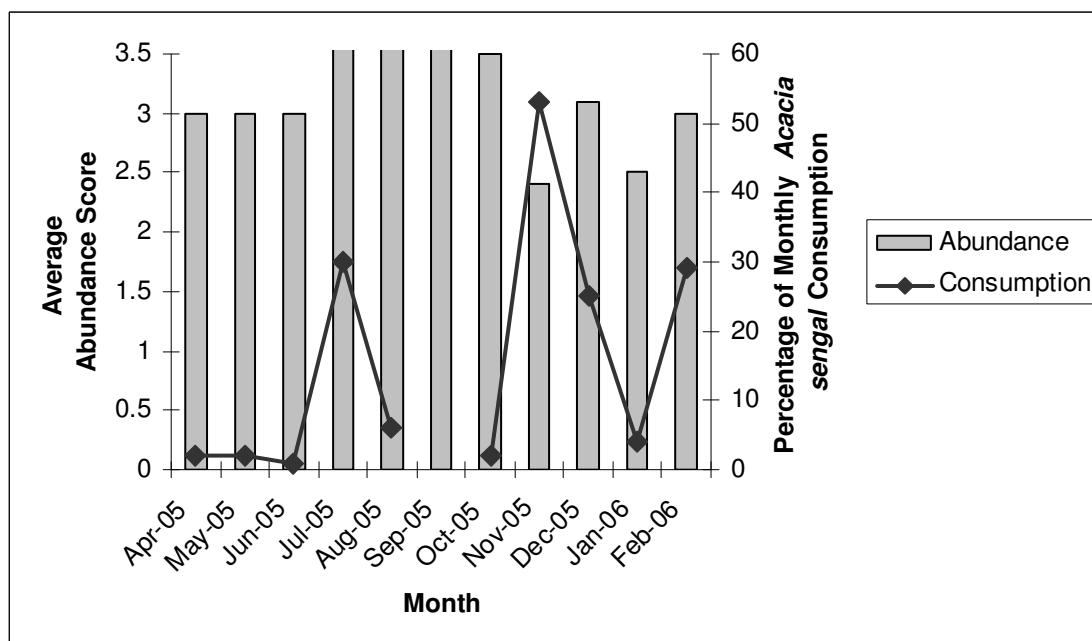
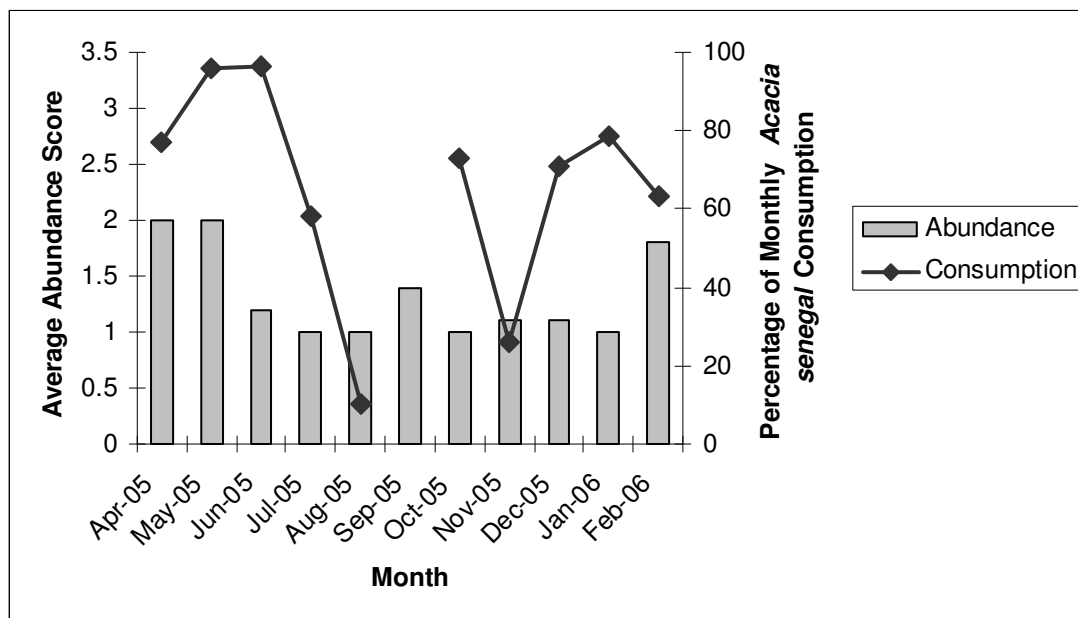


Figure 4.6 Monthly consumption and abundance of *Acacia senegal* plant parts**a) Flowers****b) Leaves**

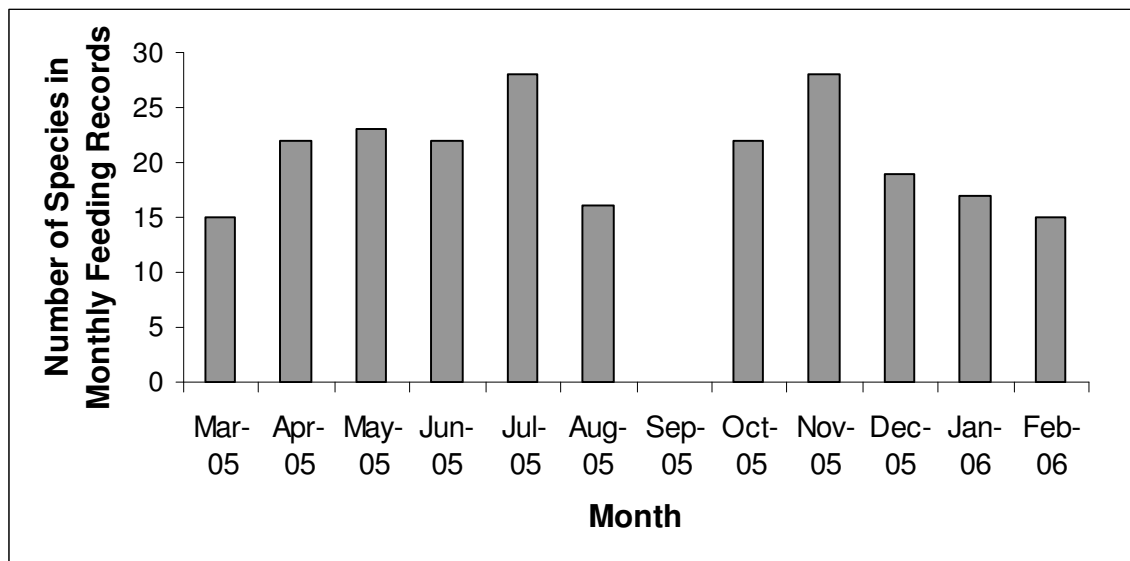
Dry Season = October, November, and December 2005; January and February 2006
 Wet Season = July and August 2005

Figure 4.6 (cont.)

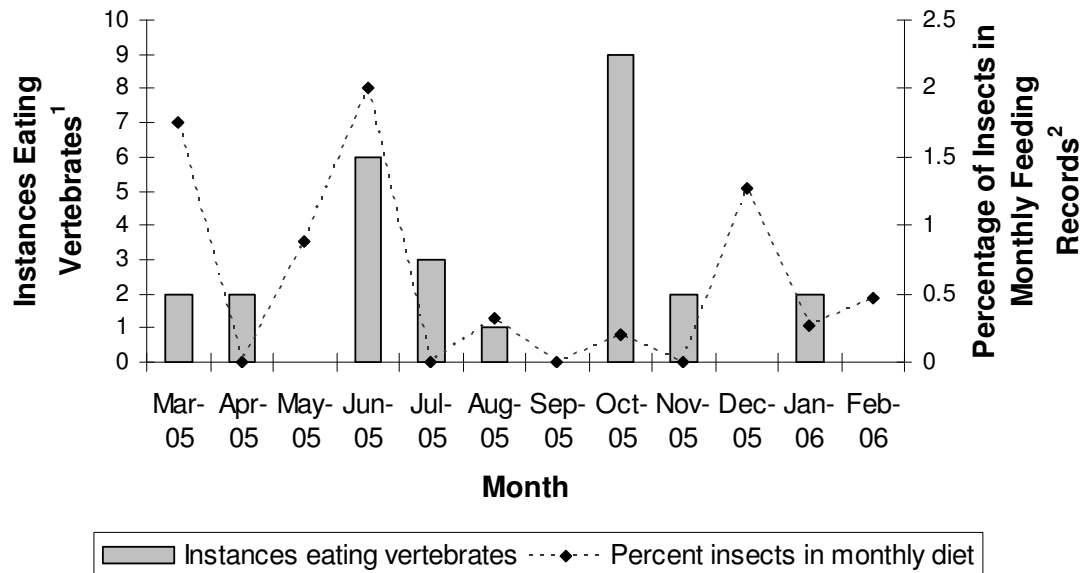
c) Seeds



Dry Season = October, November, and December 2005; January and February 2006
 Wet Season = July and August 2005

Figure 4.7 Feeding breadth

Dry Season = October, November, and December 2005; January and February 2006
Wet Season = July and August 2005

Figure 4.8 Temporal variation in consumption of animal matter

¹Vertebrates include Dik dik, Guinea fowl, Abyssinian hare, Lizards, Lesser kudu, Francolin, unknown bird species

²Insects include dragonflies, locusts, grasshoppers

Dry Season = October, November, and December 2005; January and February 2006

Wet Season = July and August 2005

Figure 4.9 Band 1's annual activity budget

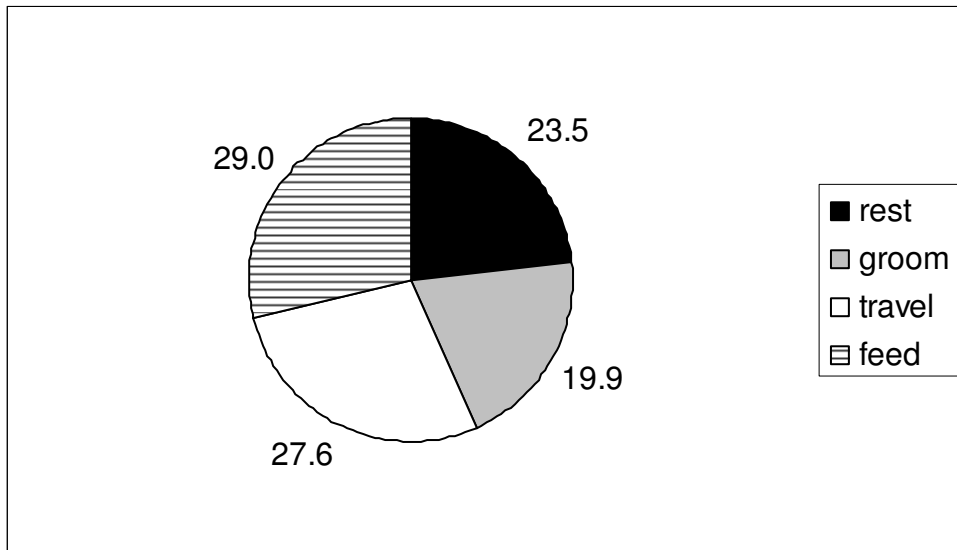


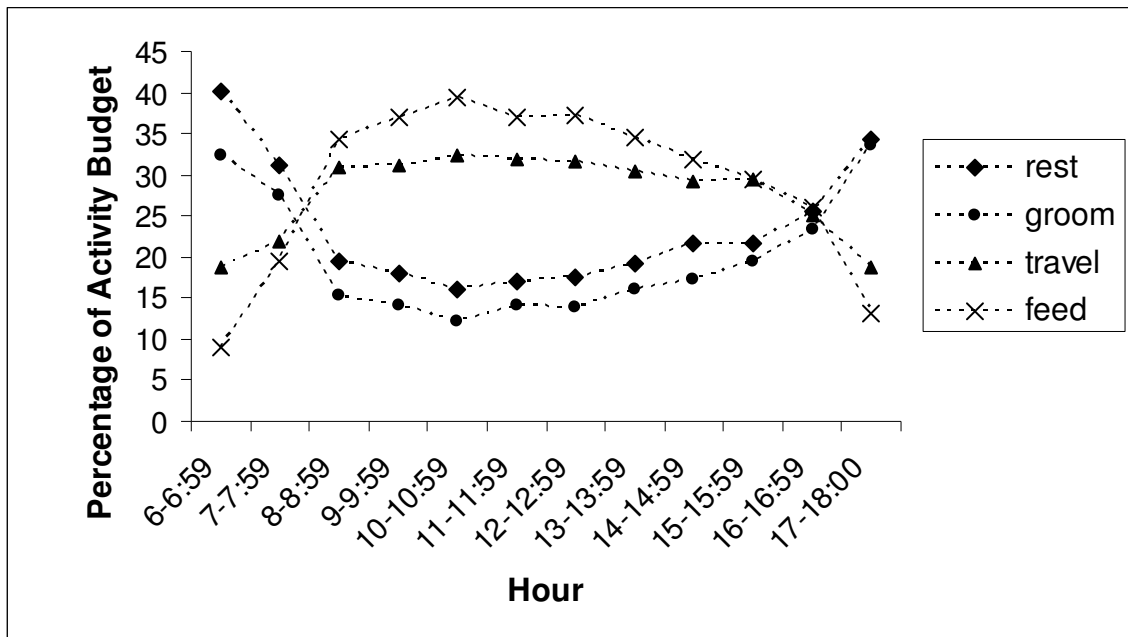
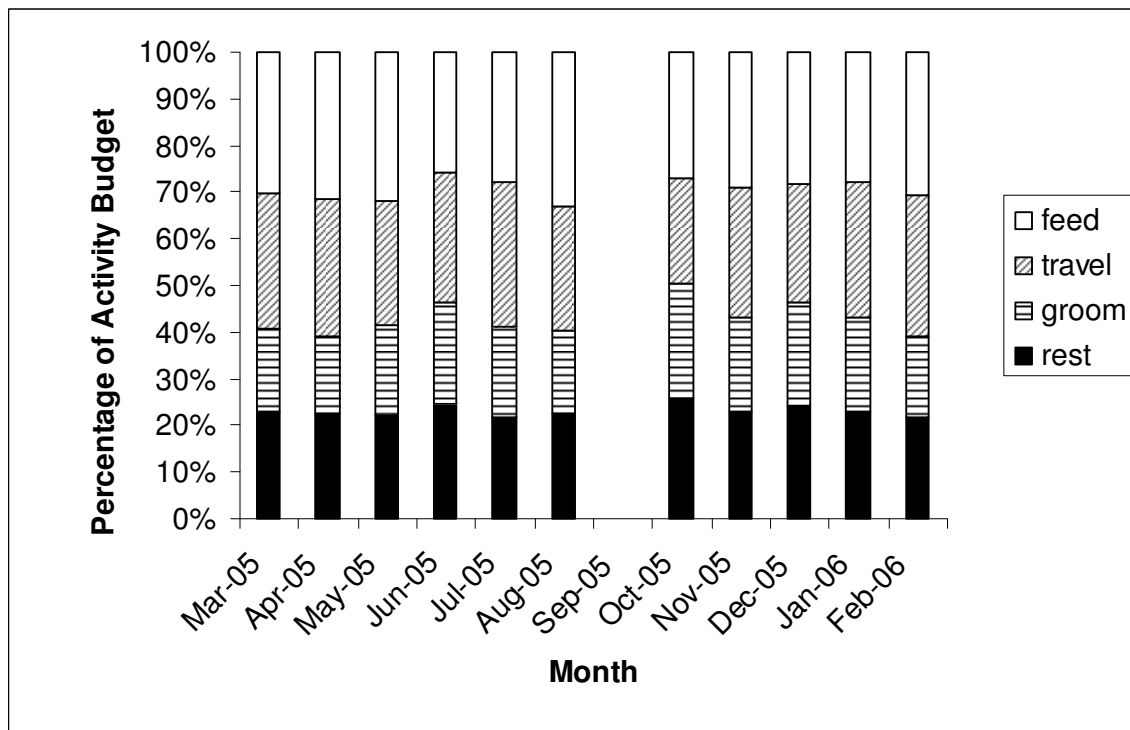
Figure 4.10 Activity budget by hour of the day

Figure 4.11 Monthly activity budgets

Dry Season = October, November, and December 2005; January and February 2006

Wet Season = July and August 2005

CHAPTER 5

HOME RANGE USE AND TRAVEL PATTERNS

5.1 Introduction

Previous research has shown that the spatial distribution of important resources determines how baboons use their home ranges (Barton et al., 1992). Furthermore, seasonal variation in the availability of these resources strongly influences baboon travel patterns (e.g., Kummer, 1968a; Altmann and Altmann, 1970; Whiten et al., 1987; Barton et al., 1992). In baboons, the three resources cited to play the largest roles in shaping home range use and travel patterns are (1) *food* (e.g., Devore and Hall, 1965; Altmann and Altmann, 1970; Barton et al., 1992; Henzi et al., 1992; Altmann, 1998), (2) *water* (e.g., Altmann and Altmann, 1970; Barton et al., 1992; Altmann, 1974, 1998), and (3) *sleeping sites* (e.g., Devore and Hall, 1965; Altmann and Altmann, 1970; Anderson, 1984, 1998, 2000). In addition, predation risk has been shown to influence which habitats baboons forage in and how much time they spend on or near refuges (Cowlshaw, 1997; Hill, 1999), and it is likely that encounters with both conspecifics and local human populations also affect baboon home range use and travel patterns.

Hamadryas baboons are known to have among the largest home ranges and longest daily path lengths of all primate species, both of which have been ascribed to the sparse distribution of food and water in their habitats (Kummer, 1968a; Sigg and Stolba, 1981; Swedell, 2002b, 2006). At Erer Gota, Ethiopia, baboons used areas of their home range containing sleeping cliffs, water holes, and acacia trees more frequently than areas without these resources (Kummer, 1968a, 1971). Similarly, Sigg and Stolba (1981) reported several lines of evidence showing that hamadryas baboons at this site are

familiar with the spatial arrangement of important resources in their home range. First, the departure direction (from the sleeping cliff) and the location (relative to the sleeping cliff) of the midday water hole were highly correlated. Although band members often split up after leaving the sleeping cliff in the morning, they reunited at midday water holes, reaching them from a variety of directions and morning travel routes (Sigg, 1986). Second, the baboons arrived at commonly visited resources from a wider assortment of departure directions than sites that they traveled to less regularly. Furthermore, the baboons habitually increased their travel speed when traveling directly to such resources, even when those resources were not in sight.

In this chapter, I describe the home range use and travel patterns of Band 1 at Filoha from March 2005 through February 2006. Unlike other hamadryas sites, the natural hot springs at Filoha provide the baboons with a permanent water source. The Filoha outpost is also surrounded by about 2 km² of doum palm trees (*Hyphaene thebaica*) (Chapter 3; Figure 2.3). As discussed in the previous chapter, doum palm fruit is a preferred food resource of Band 1, comprising 20.4% of its annual diet, second only to *Acacia senegal*.

I expected the baboons to use their home range unevenly, corresponding with the availability of resources such as food, water, and sleeping sites. Due to the accessibility of both water and a preferred food resource in proximity to the Filoha cliff sleeping site, I predicted that home range size would be smaller and daily path lengths shorter than those at other hamadryas sites. I also expected an inverse relationship between daily path length and the proportion of palm fruit in the baboons' diet because the baboons at Filoha do not need to travel far distances to obtain important food resources. Furthermore, I predicted that the baboons would spend more time away from Filoha in the wet season

than the dry season, and that daily path lengths would be shorter during the dry season so as to remain closer to permanent water sources. As at other Ethiopian hamadryas sites, both Afar nomads and potential predators of baboons are present at Filoha (Swedell, 2006; Chapter 2). I predicted that the baboons would change directions and increase their travel speed when they were approached by Afar. I also expected the baboons to alter their ranging patterns so as to avoid predators. Namely, I predicted that the baboons would leave the sleeping cliff later on mornings after lion or hyena vocalizations were heard from the Filoha camp overnight than on mornings when no predators were heard overnight.

5.2 Methods

As described in section 2.3.1, I collected data on ranging patterns by conducting all-day follows of Band 1. I defined home range as the total area used by the band over the course of the study period. I calculated home range as the minimum convex polygon which includes all recorded locations (from full and partial observation days) using ArcView GIS 3.1 software (Ostro et al., 1999). In this method, all points are connected by the smallest-area polygon with internal angles less than or equal to 180°. I also calculated home ranges for each month, as well as for both the dry and wet seasons.

Data on habitat use derive from band scans conducted during all-day follows of Band 1. At 15-minute intervals, starting at 0600, I recorded the habitats in which the baboons were located. Five habitat types were recognized: *Acacia* scrublands, palm forests, open grasslands, swamp vegetation, and cliffs (Chapter 3). When the band was spread across more than one habitat, I recorded each habitat type. When the band spread out too widely for me to monitor them all at one time, my field assistant and I stayed on

opposite ends of the band and communicated via hand-held radios regarding which habitat types the baboons were occupying.

I calculated the baboons' use of each habitat type over the study period as a proportion of the total habitat records. I used a chi-square test to determine whether the baboons used certain habitat types more frequently than expected based on the habitat composition of their home range. I also calculated habitat use for each of the 12 hours of the day (0600-1800), each month, and for the wet and dry seasons. Nightly sleeping sites were noted whenever a known band was observed on a cliff at dusk or at dawn the next morning.

To quantify how the baboons spent their time in each of the five habitat types, I used activity records only from when the entire band was in the same habitat at the same time because when the band was spread across more than one habitat type I did not distinguish which activities the baboons were engaged in each habitat. All band members were in the same habitat 78.0% of the time and I calculated activity budgets for each habitat, therefore, as a proportion of these scans.

In analyses of activity patterns in Chapter 4, I included scans in which the baboons were drinking in the category 'feed'. Because previous research has shown that access to water is a determining factor of baboons' home range use (Altmann and Altmann, 1970; Barton et al., 1992; Altmann, 1998), I examine drinking behavior more explicitly in this chapter. Out of the complete observation days (see below), I counted how many days the baboons were observed drinking and calculated the average number of times that the baboons were observed drinking per day. I calculated the number of drinking scans in each habitat type as a proportion of total drinking scans.

Travel patterns were determined based on observation days for which I recorded complete travel routes (i.e., from the morning sleeping site to the evening sleeping-site, N=105) (e.g., Altmann and Altmann, 1970; Sigg and Stolba, 1981). I computed daily path lengths by summing the distance between all mapped locations of the band's geographic center. On days when I had to leave the baboons before they arrived at the Wasaro cliff, I calculated the straight distance from where I left the baboons to their usual Wasaro cliff sleeping site (confirming this location the following morning). As the baboons most likely did not travel directly to their sleeping site, these daily path lengths represent the minimum distances traveled. I analyzed travel routes using ArcView GIS 3.1 software. Specifically, I overlaid each travel route onto the map of the Filoha region and examined its patterns (i.e., geometric form, locations visited, start and end points, etc.) as well as patterns of travel routes over time (i.e., seasonal, monthly).

I calculated travel speeds by computing the distance traveled between the four consecutive 15-minute scans taken per hour to provide one distance measure per hour (e.g., Henzi et al., 1992). To obtain an average travel speed per hour of the day (0600-1800) over the study period, I averaged the distances traveled for each hour of the day across all complete observation days.

I recorded all interactions with potential predators. I noted the species of the potential predator, the location of the encounter, and the baboons' reactions. I also recorded when lion and hyena vocalizations were heard from the Filoha camp overnight.

I recorded Band 1's encounters with other bands during daily travel. I noted the identity of the other band, if known, as well as the time, location, and duration of the meeting. I described inter-band interactions, such as fighting (e.g., how many individuals involved, duration of fight, etc.) and traveling (e.g., bands traveled together, one band

changed directions/alterd their travel route upon encountering another band, etc.). When Band 1 shared a sleeping site with another band, I noted the interactions, or lack thereof, between the two bands in the morning and late afternoon, regardless of whether the bands traveled to or from the sleeping cliff together. When Band 1 began daily travel with another band, I calculated the distance that the two bands traveled together and noted the time that they separated.

I recorded all encounters with Afar nomads. For each encounter I noted the time, GPS location, and habitat type, as well as the number, age, and sex of nomads and the presence of cows, camels, goats, and/or donkeys. I recorded a description of the encounter (e.g., nomads walk by, yell at baboons, etc.) and noted whether the baboons altered their behavior and/or travel patterns in response to the encounters (e.g., baboons change directions, increase travel speed, etc.).

5.3 Results: Home Range and Habitat Use

5.3.1 Home Range Size

Band 1's home range from March 2005 through February 2006 was calculated to be at least 38.6 km² (Figure 2.3). It should be noted that the baboons likely ranged over a substantially larger area as I could not locate the baboons for most of September. During this time, the baboons did not sleep on either the Filoha or Wasaro sleeping cliffs, and it is thought that they were sleeping and ranging southwest of Wasaro near Mount Fantalle. Afar nomads reported that they observed hamadryas baboons sleeping at Fantalle, but I was unable to confirm if they were members of Band 1.

A plot of the cumulative area used by the band reached an asymptote by August (Figure 5.1), suggesting that the study period was sufficiently long to provide a reliable

estimate of the baboons' home range. Figure 5.1 shows that the cumulative area used doubled from 17.0 km² in May to 34.0 km² in June. This increase corresponds with a shift in use of the northern portion of the home range to that of the southern portion, reflecting where the baboons foraged on palm fruit (see below).

There was virtually no difference between the size of the ranging areas in the dry season (22.4 km²) and wet season (21.9 km²). Differences did emerge, however, in the size of the area that the baboons used across months (Table 5.1). While the mean monthly home range was 12.8 km², the sizes of monthly home ranges were largest in June and July at 22.1 km² and 19.1 km², respectively. Conversely, the baboons ranged over the smallest areas in August (5.0 km²) and October (4.8 km²). The relationship between home range size and rainfall, therefore, was inconsistent. The two largest monthly home ranges were those of June, a dry month just prior to the onset of the long rains, and July, the wettest month of the year. Similarly, the smallest home ranges were those of August, the second wettest month of the year, and October, a month with virtually no rain at all.

The large home range in June reflects a shift in home range use from the northern portion of the annual home range to the southern portion, reflecting where the baboons fed on palm fruit. While in March, April, and May the baboons ate palm fruit almost exclusively from the Hot Springs and Alibete palm forests, by mid-April no fruit was available in the Alibete palm forest and by June very little fruit remained throughout the Hot Springs palm forest east of Filoha. In June, therefore, the baboons began to range throughout the southern portion of their home range, where they ate the majority of palm fruit from palm clumps southeast of the Filoha cliff (section 5.4.5; Figure 5.15).

In July, the first month of the wet season, water was available throughout Band 1's home range, as were fresh *Acacia* spp. leaves. The wide availability of both food and

water may have provided the baboons the flexibility to range more widely (Swedell, 2002b, 2006) (Figure 5.14). In August, by contrast, when standing water as well as both fresh leaves and flowers were available throughout their home range, the baboons mostly ranged in a small area just west of the Wasaro Cliff (Figure 5.14). The disparity in ranging patterns between the two wet season months is discussed in greater detail in section 5.4.4.

The small home range in October likely reflects the baboons' need to stay close to the Filoha cliff because by this time water was no longer available throughout their range. October also marked the band's reunion after a month-long fission (Chapter 6). As described in Chapter 2, only data from the entire band are included in this dissertation, and the home range size reported here for October, therefore, derives only from data collected during the last 12 days of the month when the baboons traveled as a cohesive band. It should be noted that in 12 days before the band reunited, the half of Band 1 that I followed ranged over 14.4 km². The substantial difference between the home range size of half the band in the first part of the month versus that of the entire band in the latter part of the month (4.8 km²) may reflect the fact that in the beginning of the month some fresh leaves and water were still available in areas of their home range away from Filoha. By the second half of October, by contrast, the Filoha hot springs and swamps were once again the only available water sources.

5.3.2 *Habitat Use*

Band 1's home range comprised 88.0% *Acacia* scrublands, 4.3% swamp vegetation, 4.2% palm forests, 3.2% open grassland, and 0.4% cliffs (Figure 5.1; Chapter 3). While the baboons did use each of the five habitat types over the study period, they

did not do so evenly (Figure 5.2). Band 1 spent almost half of its time (47.2%) in *Acacia* scrublands, and a quarter of its time (23.6%) on cliffs. The baboons spent 15.9% of their time over the year in palm forests, and the remaining time was split between swamp vegetation (7.4%) and open grasslands (5.9%). Chi-square tests comparing the percentage of time spent in each habitat type with the expected percentage based on the habitat composition of their home range revealed significant differences between observed and expected values for each habitat ($X^2=1437.7$, $df=4$, $p=0.00$). The baboons spent less time than expected in *Acacia* scrublands, and more time than expected on cliffs and in palm forests, swamp vegetation, and open grasslands (Figure 5.3). This uneven use of their home range corresponds with the large proportion of time that the baboons spent resting and grooming on sleeping cliffs (Chapter 4), and the clumped availability of doum palm fruit, a frequently consumed food resource.

The baboons engaged in certain activities more frequently in some habitat types than others (Figure 5.4). When on cliffs, the baboons spent 85% of their time resting and grooming. By contrast, in *Acacia* scrublands, open grasslands, swamp vegetation, and palm forests the band spent at least 60% of its time traveling and feeding. The baboons split their time fairly evenly between traveling and feeding in the former three habitats, but they spent twice as much time feeding in palm forests (40.4%) as they did traveling (20.0%). When the baboons were in palm forests, they split their time more evenly across activity states than when they were in any of the other habitat types. While they spent most of their time in palm forests feeding, they also spent almost 40% of their time either resting or grooming. Commonly, after the baboons spent time eating palm fruit, they rested and groomed while sitting under palm trees (in the shade) before traveling out of the palms.

All band members were in the same habitat type at the same time 78.0% of the time over the course of the study period. The entire band was in *Acacia* scrublands in 75.9% of the total scans in this habitat. Similarly, the entire band was on a cliff together during 71.2% of the total number of scans in which any band members were on a cliff. The entire band was in palm forests, however, just under half (44.5%) of the total number of palm scans. Many of the cases in which the baboons were spread over palms and adjacent habitats occurred when the band was on the Filoha cliff and some band members foraged in palm trees along the base of the cliff, or when most of the band was in a palm forest but some baboons were in *Acacia* scrubland. This generally occurred when most of the band had finished foraging on palm fruit and were resting and grooming; some band members often rested and groomed on the edge of *Acacia* scrubland or grasslands bordering palm forests.

The entire band spent very little time exclusively in either swamps or open grasslands. All band members were in grasslands in only 15.9% of the total grassland scans. While the entire band did occasionally stop to rest and groom in grasslands, it was much more common for the baboons to travel through open grasslands from one *Acacia* area to another, or between *Acacia* scrublands and palm forests; the baboons often foraged as they traveled, but it was rare for the whole band to stop and feed in grasslands all together. Areas of open grassland are also adjacent to swamps in several places, and at times some baboons traveled around the edge of a swamp on grassland, while others fed or drank in the swamp.

All band members were in swamps in only 3.5% of total swamp vegetation scans. It was common for some baboons to drink or eat in the swamp right at the bottom of the Filoha cliff while the rest of the band remained on the cliff. When the band traveled

through swamps, it was common for some baboons to make their way through the swamp vegetation, while the rest of the band remained in adjacent habitats, usually *Acacia* scrublands and open grasslands.

The proportion of time spent in each habitat type varied over the course of the day (Figure 5.5). The baboons spent the first two hours of the day, 0600-0800, mostly on cliffs. By the third hour, the amount of time spent on cliffs declined as the baboons spent almost half of their time in *Acacia* scrublands. The baboons spent the majority of their time in *Acacia* scrublands until 1600, when the pattern reversed and the baboons once again spent most of their time during the last two hours of the day, 1600-1800, on cliffs. The percentage of time spent in palms peaked at 23.0% between 0800 and 0859 and remained relatively constant until it declined between 1400-1459. The baboons did not spend more than 11.1% of their time in either open grasslands or swamp vegetation during any hour of the day.

The baboons' habitat use over the course of the day mirrors that of their activity budget (see section 4.4.1, Figure 4.11). The baboons spent the majority of their time during both the first and last two hours of the day resting and grooming on cliffs. Conversely, the baboons devoted the majority of their time between 0800 and 1600 to feeding and traveling in *Acacia* scrublands.

The proportion of time spent in each habitat type also varied across months (Figure 5.6). The baboons spent the most time – at least 35% – in *Acacia* scrublands in every month except for May, when they spent most of their time in palm forests. The baboons spent at least 15% of their time in palms during six months, corresponding with the contribution of palm fruit to monthly diets (section 4.3.2). It should be noted that during March, April, and May most of the time that the baboons spent in palm habitats

was in palm forests rather than palm clumps. In June, December, and February, by contrast, much of their time in palms was spent in palm clumps, as opposed to forests. The baboons did not utilize either palm forests or palm clumps at all in August. Band 1 spent at least 15% of its time on cliffs during every month of the year. The baboons spent the most time on cliffs in October (36.3%) and June (32.8%), corresponding with the larger proportion of time they spent resting and grooming during these months (section 4.4.1). The baboons did not spend more than 10% of their time in open grasslands or swamp vegetation in any month of the year.

Some of this variation in habitat use across months was related to seasonality (Figure 5.7). Band 1 utilized all five habitat types in the dry season in similar proportions to that of the entire study period. In the wet season, by contrast, Band 1 spent less than 1% of its time in both open grasslands and swamp vegetation, and only 4% of its time in palm forests. The baboons spent 75.7% of their time in *Acacia* scrublands, almost twice the amount of time they spent in this habitat during the dry season. This increased exploitation of *Acacia* scrublands during the wet season corresponds with a shift in home range use predominantly to the west of the Filoha Cliff, and in particular, an increased amount of time spent west of the Wasaro cliff (see section 5.4.4; Figure 5.14). Conversely, the band spent almost 10% less time on cliffs in the wet season than during the dry season, corresponding with decreased time spent resting and grooming during the wet season (section 4.4.1).

5.3.3 *Sleeping Sites*

Over 290 nights between March 2005 and February 2006, Band 1 slept on the Filoha cliff on 155 nights and on the Wasaro cliff at least 77 nights. The number of

nights that the baboons spent on each cliff during each month can be seen in Table 5.1.

There are clear seasonal patterns regarding the baboons' use of sleeping sites. The baboons slept on the Wasaro cliff on 22 of the 28 nights for which data exist in the wet season. Conversely, the baboons slept on the Wasaro cliff on only 12 of the 87 nights for which data exist in the dry season. Presumably, the baboons spent the majority of nights during the dry season on the Filoha cliff in order to have access to water which was not available in other parts of their home range. During the wet season, by contrast, the baboons had the flexibility to remain at the Wasaro cliff – and not return to the Filoha cliff at all during August – because standing water was available throughout their range (Swedell, 2002b, 2006).

The baboons split their time more evenly between the two sleeping cliffs during March, April, and May (Table 5.1). These months correspond to when the baboons ranged through the northern portion of their home range, feeding on palm fruit predominantly from the Hot Springs and Alibete palm forests (section 5.4.5; Figure 5.15). The baboons may have been able to spend almost half of their nights on the Wasaro cliff because of the permanent water available in the palm forests in which they spent so much of their time during these three months. It is also possible that they were able to regularly sleep on the Wasaro cliff because of the intermediate amount of rainfall during these months, and the resulting availability of standing water away from the Filoha region; half of the nights that the baboons slept on the Wasaro cliff during this three-month stretch occurred within two days following rain.

5.4 Results: Travel Patterns

5.4.1 Daily Paths

I recorded complete travel routes (i.e., from the morning sleeping site to the evening sleeping site) on 105 days. I completed the most travel routes in April (16), but only six in July and October 2005 and February 2006 (Table 5.2). Band 1's mean daily path length was 8.3 km (± 2.04 , $N=105$; range=4.6-14.2 km). Almost half of these travel routes ($N=49$) both started and ended at the Filoha cliff (Table 5.2, Figure 5.8). In almost a third of the travel routes ($N=29$), the baboons started their day on the Filoha cliff and traveled to the Wasaro cliff (Figure 5.9). On 15 days, the baboons both started and ended their day on the Wasaro cliff (Figure 5.10), and on the remaining 12 days the baboons began on the Wasaro cliff and traveled to the Filoha cliff (Figure 5.11).

The mean daily path length was 7.2 km when the baboons began and ended their day on the Filoha cliff, and 8.0 km when they began and ended their day on the Wasaro cliff. The baboons' path lengths were significantly longer when they started the day on one cliff and traveled to the other (one-way ANOVA, $F=12.10$, $p=0.00$). The mean daily path length was 9.6 km when Band 1 traveled from the Filoha cliff to the Wasaro cliff, and 9.3 km when it traveled from the Wasaro cliff to the Filoha cliff. It is interesting to note, however, that the two longest daily paths occurred when the baboons started and ended their day on the same cliff (Filoha→Filoha = 14.2 km; Wasaro→Wasaro = 14.2 km).

Overall, there were several common patterns in Band 1's travel routes. Regardless of whether the baboons started their day on the Filoha cliff or the Wasaro cliff, they almost always traveled either north or south along the cliff before turning east or west. The baboons usually took one of four routes when they both started and ended

their day on the Filoha cliff (Figure 5.8). On many days, the baboons traveled north along the cliff from their sleeping site, and then turned east and traveled into the Hot Springs palm forest. After feeding on palm fruit for several hours the baboons tended to either (1) travel farther north through the palm forest and then west into and through *Acacia* scrublands, before traveling southeast back to the Filoha cliff, or (2) travel west out of the palms and into *Acacia* scrublands, and then farther northwest through the *Acacia* before returning southeast to the Filoha cliff sleeping site. When the baboons began their travel route moving south from the Filoha cliff sleeping site, they generally followed one of two routes. First, the baboons traveled east into the Hot Springs palm forest, and then southeast through the palms into the large open grassland to the palm clumps southeast of Filoha, before traveling northwest back to the Filoha cliff in the afternoon. Second, the baboons continued south off the cliff and then traveled southeast through *Acacia* scrublands to the palm clumps southeast of Filoha. From here, the baboons traveled north into the southern portion of the Hot Springs palm forest before returning west to the Filoha cliff.

When Band 1 started at the Filoha cliff and traveled to the Wasaro cliff (Figure 5.9), the baboons most commonly traveled north from the sleeping site and then east into the northern portion of the Hot Springs palm forest. Similar to when the baboons started and ended their day on the Filoha cliff, they then traveled northwest through *Acacia* scrublands, or west into *Acacia* before then moving north. From their location in *Acacia* scrublands northwest of Filoha, the baboons then traveled southwest to the Wasaro cliff. On several occasions, the baboons traveled south from the Filoha cliff sleeping site and then turned east into the southern portion of the Hot Springs palm forest. From there, the

baboons tended to travel north through the palms before turning west and traveling to the Wasaro cliff sleeping site.

When the baboons started and ended their day on the Wasaro cliff, they generally followed one of two routes (Figure 5.10). First, the baboons traveled north along the cliff, and then northeast into and through *Acacia* scrublands, before returning to the Wasaro cliff along this same general route. In the second common route, the baboons traveled south along the cliff, and then west into *Acacia* scrublands. When the baboons reached the westernmost point of their route, they moved north, before traveling east back to the Wasaro cliff. On one day the baboons traveled east to the Filoha cliff but then returned to the Wasaro cliff sleeping site.

When the baboons traveled from the Wasaro cliff to the Filoha cliff (Figure 5.11), they also started the day traveling either north or south from the Wasaro cliff sleeping site. When the baboons went north, they then moved northeast into *Acacia* scrublands, before veering to the southeast back to Filoha. When the baboons began the day moving south, they continued south from the cliff into *Acacia* scrublands, before turning east toward Filoha. On each travel route from the Wasaro cliff to the Filoha cliff, the baboons either stopped to feed in the Alibete palm forest before returning to the Filoha cliff, or traveled farther east of the Filoha cliff and fed in either the Hot Springs palm forest or palm clumps southeast of Filoha, before returning west back to the Filoha cliff sleeping site. Swedell (2006) found that in 1996-1998 the baboons also tended to begin their daily travel by following their morning sleeping cliffs before turning east or west, suggesting a consistent travel pattern over time.

As discussed in Chapter 6, Band 1 fissioned along clan lines for six days in March 2005, for 31 consecutive days in September and October 2005. While this study pertains

to the band as a whole, I collected eight daily paths during these periods in which the band existed as two separate entities. The mean daily path length was 9.2 km (± 1.8 , $N=8$; range=7.3-11.7 km). While the average daily travel route was longer for half the band than for the band as a whole, this difference was not significant.

5.4.2 Departure from and Arrival at Sleeping Sites

On average, the band left their sleeping cliff between 0730 and 0745 in the morning. The baboons departed several times before sunrise, and as late as 1015 on one occasion. There was a significant inverse relationship between daily path length and the time that the baboons left their sleeping cliff; the longer the daily path length, the earlier the baboons left the cliff in the morning ($r_s = -0.261$, $p = 0.01$, $N = 105$). The baboons began daily travel significantly earlier when they started from the Filoha cliff (between 0700-0715) than from the Wasaro cliff (between 0745-0800) (Mann-Whitney test, $p = 0.00$). The baboons left the Filoha cliff earlier on days that they traveled to the Wasaro cliff than on days that they returned to the Filoha cliff, though this relationship was not statistically significant. On days that the baboons began their daily travel on the Wasaro cliff, there was no difference in the time that they left the cliff between the days that they returned to the Wasaro cliff and those in which they traveled to the Filoha cliff.

On average, the baboons reached their sleeping site between 1545 and 1600. On four afternoons the baboons reached their sleeping cliff by 1300, and four other times they did not reach their sleeping cliff until after 1730. On these latter days, the baboons were within 200 m and traveling toward the Filoha cliff by 1730. There was no relationship between daily path length and the time of arrival at the evening sleeping cliff. On average, the baboons arrived at the Filoha cliff at the same time regardless of which

cliff they began their day on. On most of the days that the baboons traveled to Wasaro I was unable to follow them all the way back to the cliff and therefore I can not examine the difference between arrival times at the two cliffs.

5.4.3 Travel Speed

The baboons' mean travel speed was 0.7 km per hour. The mean distance traveled per each hour of the day throughout the study period can be seen in Figure 5.12. The baboons traveled the greatest distance between 0800-0859, corresponding to the onset of their daily travel after leaving the sleeping cliff. Travel speed then decreased over the next five hours, before increasing again between 1400-1459 as the baboons began traveling toward their evening sleeping site. In the last two hours of the day, 1600-1800, travel speed declined substantially as the baboons reached their sleeping sites. These hourly travel speeds differed significantly from each other (one-way ANOVA, $F=7.64$, $p=0.00$). When both the first two hours (0600-0800) and last two hours (1600-1800) of the day were excluded from the analyses to account for early morning acceleration as the baboons leave their sleeping sites and late afternoon deceleration as the baboons arrive at their sleeping sites (Altmann and Altmann, 1970), these differences disappeared.

5.4.4 Temporal Variation in Travel Patterns

Mean daily path lengths varied across months (Table 5.2), and these differences were statistically significant (one-way ANOVA, $F=7.31$, $p=0.00$). The baboons traveled the shortest distances in October (6.0 km), while their daily paths were longest in July (11.0). It should be noted, however, that in both of these months, means are based on only six complete travel routes, and therefore they may not provide a full picture of the

baboons' travel patterns. Table 5.2 shows which sleeping sites the baboons began and ended their days on each month. All six travel routes in October started and ended on the Filoha cliff, as did 13 of the 14 travel routes in December. In August, by contrast, the baboons both started and ended all nine of their travel routes on the Wasaro cliff. The baboons traveled between the two cliffs most frequently in April and May.

There was also seasonal variation in travel patterns. The 43 dry season travel routes are shown in Figure 5.13, and the 15 wet season routes are shown in Figure 5.14. The mean daily path length in the dry season was 7.1 km, and ranged from 4.6 to 10.7 km. The mean daily path length in the wet was 8.8 km, and ranged from 5.0 to 14.2 km. The mean wet season daily path length was significantly longer than that of the dry season (Mann-Whitney test, $p=.02$). Because water was available throughout their home range during the wet season, the baboons likely had the flexibility to range widely throughout their home range, as they were not constrained by access to water (Swedell, 2002b, 2006).

Overall, the baboons spent more time away from Filoha during the wet season than the dry season, corresponding to the availability of water throughout their home range (section 5.3.3). The baboons spent an equal proportion of their time traveling in the wet and dry seasons (section 4.4.1), yet they traveled further during the wet season. This discrepancy is accounted for by the fact that the mean travel speed during the dry season was 0.60 km/hour, while that of the wet season was 0.74 km/hour. These differences, however, were not statistically significant (Mann-Whitney test, $p>0.05$).

These seasonal patterns are less straightforward, however, when looking at the wet season months separately. The mean daily path length in July was 11.0 km ($N=6$), the longest of any month. During this month, fresh leaves were available throughout their

range. The baboons had the highest feeding breadth, consuming 28 different plant species (section 4.3.2), and spent more time traveling than in any other month (section 4.4.1). The baboons likely ranged widely, therefore, to take advantage of the wide availability of both fresh leaves and water. On at least one day in July, the baboons began the day on the Wasaro cliff, traveled to the Filoha cliff, but then returned to the Wasaro cliff sleeping site late in the afternoon. While the baboons did travel to the Wasaro cliff from Filoha in the late afternoon once upon encountering another band near Filoha, on this day there appeared no obvious reason for the baboons' return to Wasaro. The availability of water en route to and at Wasaro likely accounts for this travel route.

The mean daily path length in August, by contrast, was only 7.3 km (N=9). In August the baboons did not return to Filoha at all, and during six of the nine travel routes the baboons ranged exclusively on the west side of the Wasaro cliff, an area of their home range they barely used during the rest of the year (Figure 5.14). During this month, the baboons fed on only 15 plant species (section 4.3.2), and spent more time feeding than in any other month (section 4.4.1). *Tribulus cistoides* flowers comprised 59.4% of the feeding records, a substantially higher percentage than any other plant species' contribution to any monthly diet (section 4.3.2). These flowers were available throughout the baboons' home range, yet the baboons remained in the Wasaro vicinity the entire month (section 5.3.1). The baboons may have taken advantage of the small window of opportunity in which both water and a preferred food resource were available in order to decrease their foraging effort. In July, when fresh leaves were available but flowers were not, the baboons ranged widely and increased their feeding breadth; when flowers became available in August, however, the baboons shifted their foraging strategy and remained near the Wasaro cliff, feeding on relatively few plant species.

5.4.5 Food Resources

Contrary to expectations, there was no relationship between daily path length and the proportion of the top three food species – *A. senegal*, *H. thebaica*, and *T. cistoides* – in the baboons' diet (Chapter 4). There was also no relationship between daily path length and either the proportion of each plant part in the diet or phenology. The baboons' ranging behavior, however, was clearly impacted by feeding behavior. Travel patterns appeared to reflect where the baboons fed on doum palm fruit (*H. thebaica*). In March, April, and May the baboons ate palm fruit most regularly from the Hot Springs and Alibete palm forests. In fact, Band 1 traveled to one of these palm forests during each one of its travel routes during these three months (Figure 5.15). On June 1, the baboons traveled to the Hot Springs palm forest as well, but by mid-June almost no palm fruit was available there. Instead, the band shifted its use of the home range to the south, and fed on palm fruit mostly from the palm clumps southeast of Filoha. The baboons ate very little palm fruit in July, August, October, and November. When they resumed eating palm fruit regularly again in December, they did so mainly from the palm clumps southeast of Filoha. The same was true in January and February, although by this time the baboons began to return to the Hot Springs and Alibete palm forests as fruit became available.

I observed the baboons eating palm fruit on 83 of the 105 days for which I have complete travel routes. On at least two-thirds of these routes (N=56), the farthest point from the evening sleeping site was located in a palm forest or palm clump. There were several additional days that palm trees likely marked the farthest point in the travel route, but I cannot be certain as I lost the baboons for periods ranging from 15 minutes to two

hours during which the baboons may have traveled to a further location that was not in palms. Sites in the Hot Springs palm forest were the farthest points in the baboons' travel routes at least 23 times, and palm clumps southeast of Filoha marked the farthest point from the evening sleeping site on at least 20 days. The Alibete palm forest contained the farthest point at least eight times, and the palm clumps 3 km northwest of the Filoha cliff sleeping site were farthest from the sleeping site on at least five days. In addition to influencing where the baboons range, therefore, their reliance on palm fruit also appears to play a role in determining daily path lengths.

The proportion of *A. senegal* in the baboons' diet did not seem to influence the baboons' travel patterns as much as that of *H. thebaica*. The proportion of *A. senegal* in the baboons' diet remained relatively constant throughout the study period, and the same phenophases were generally available at the same time throughout their home range (Chapter 3). Changes in the baboons' travel patterns thus do not appear to be a result of their use of *A. senegal*.

As discussed above in section 5.4.4, in August when *T. cistoides* flowers made up the bulk of Band 1's diet, the baboons ranged in the Wasaro region the entire month. On six of the nine complete travel routes the baboons remained exclusively on the west side of the Wasaro cliff, despite the fact that these flowers were available throughout their home range during this month. The baboons may have restricted their ranging area during this time to take advantage of the limited time period during the year when both a preferred food resource and water were available at Wasaro.

5.4.6 Access to Water

The influence of water on Band 1's ranging patterns manifested itself mostly in relation to the baboons' sleeping site use as opposed to their drinking behavior per se. As discussed in section 5.3.3, following expectations the baboons spent more time away from Filoha during the wet season, presumably due to the wider availability of standing water. As predicted, daily paths were also shorter during the dry season (section 5.4.4), likely a result of remaining in close proximity to the permanent water sources at Filoha.

The baboons were observed drinking on 83.4% of the complete observation days for which data exist (N=103). The baboons drank from hot springs and swamps in just over half (51.5%) of the total drinking scans (N=299). In fact, more than a third of the instances in which the baboons were observed drinking (36.8%) occurred in the hot springs and swamp just at the bottom of the Filoha cliff. The baboons drank in palm forests 26.1% of the time. It was less common for the baboons to drink in *Acacia* scrublands and open grasslands. The baboons drank from puddles in these habitats – as opposed to from the swamps and hot springs in and around the Filoha region – only 22.4% of the time. Almost all of these occasions occurred during the wet season or just after rains during other points of the year.

The baboons were observed drinking during their daily travel – after leaving their sleeping site in the morning and before arriving in the afternoon – 67.9% of the time. Almost every time that the baboons drank from the swamp at the bottom of the Filoha cliff (93.7%), they did so before leaving the cliff in the morning or after returning in the afternoon. During the remaining 6.3% of the time, the baboons stopped to drink at the bottom of the cliff in the afternoon, before traveling west to the Wasaro cliff.

A manmade water hole built by a humanitarian group for the Afar was located in *Acacia* scrublands ~3 km northwest of the Filoha cliff sleeping site. The baboons drank here on at least six days. On at least four of these days, the water hole was the farthest point in the travel route from the baboons' evening sleeping site. There were at least four other days in which the baboons traveled to the water hole but were unable to drink there because either Afar and their cattle were occupying it (section 5.4.9), or no water was available.

5.4.7 Predators

Out of a total of 290 nights spent at the Filoha camp, lions were heard on 80 nights, and hyenas on 174 nights. Both lions and hyenas were heard on 58 of these nights. Of the 78 complete travel routes in which the baboons began their day on the Filoha cliff, only hyenas were heard on 37 nights, only lions were heard on four nights, and both lions and hyenas were heard on 19 nights. On 18 of these days, neither hyenas nor lions were heard near Filoha the previous night. The presence of predators appeared to influence what time the baboons departed from the sleeping cliff. Band 1 left the Filoha cliff earliest – on average between 0645 and 0700 – when neither hyenas nor lions were heard the previous night. On nights when just one of the predators was heard, the baboons left the cliff between 0700 and 0715 the following morning. The baboons remained on the cliff latest on mornings after both hyenas and lions were heard close to Filoha; on these days the baboons did not leave the cliff, on average, until close to 0730. It appears, then, that the baboons remained on the relative safety of cliffs for longer on days when predators were known to be in the Filoha region the previous night. There were no differences, however, in daily path length or habitat use on days after predators

were heard overnight compared with times when no predator vocalizations were heard from the Filoha camp.

The baboons encountered predators during daylight hours on several occasions. While the baboons appeared to alter their behavior briefly, counter to predictions, their overall ranging patterns did not seem to be affected by encounters with predators. Band 1 came across spotted hyenas once at the bottom of the Filoha cliff after sunrise. While the baboons alarm called while resting on the bottom of the cliff, they did not climb back up to the top of the cliff. Band 1 also encountered spotted hyenas on the bottom of the Wasaro cliff on one morning. On this occasion, half of the band had remained on the top of the cliff, while the other half had climbed down the west side of the cliff into *Acacia* scrublands where they encountered a hyena. The baboons that had reached the *Acacia* scrublands climbed back up the cliff. Another hyena then appeared on the bottom of the cliff, before quickly running west through the *Acacia* trees. The baboons remained on the cliff until close to 0900, almost an hour later than they usually left the Wasaro cliff. While the baboons had originally begun traveling west from the cliff before encountering hyenas, when they finally all began daily travel they went east instead. On another morning on the Wasaro cliff, a lion was heard roaring loudly seemingly only a few hundred meters south of where the baboons were resting and grooming. The baboons began to travel north along the cliff, but after about 0.5 km they stopped and resumed resting and grooming. There were no differences in daily path lengths or habitat use on days that the baboons encountered predators compared with days in which no predators were present.

5.4.8 *Conspecifics*

Over the course of the study period, Band 1 and Band 3 shared a sleeping cliff on at least 89 nights; they both slept on the Filoha cliff on 83 nights and on the Wasaro cliff on at least six nights (Schreier and Swedell, 2008; section 6.2). Band 1 and Band 2 both slept on the Wasaro cliff on at least 22 nights and on the Filoha cliff one night. All three bands were never observed to sleep together on the same cliff on the same night (section 6.2).

There were no consistent patterns regarding daily travel when Band 1 began the day on the same cliff as another band. Of the 105 complete travel routes, Band 1 began the day on the same cliff as Band 2 on 18 mornings, all but one of which on the Wasaro cliff. On 14 mornings the two bands did not travel together at all. While on several of these occasions they remained near each other on the cliff while resting and grooming, by 0700 one of the bands had started traveling while the other remained on the cliff. On the other four mornings Band 1 and Band 2 traveled from 0.8 to 1.7 km together, before separating each time by 0900.

On 31 of the complete travel routes, Band 1 and Band 3 both started on the same cliff, all but one of these mornings on the Filoha cliff. The two bands began daily travel together on 15 mornings. On 11 of these mornings the baboons traveled from 0.4 to 2.0 km together, and separated by 0900. On three occasions, however, the two bands traveled together until midday, traveling almost 3 km together twice and 7 km together once. On the final day, Band 1 and Band 3 traveled 6.6 km together and did not separate until 1600. At this time the baboons were about 1 km northwest of the Filoha cliff sleeping site – after traveling on the east side of the cliff with Band 3 all day – and Band 1 then traveled 5 km to the Wasaro cliff sleeping site while Band 3 returned to Filoha. When the two

bands traveled together, one band started traveling either north or south along the cliff, and the other band followed. This band then caught up, and the baboons all traveled together until one band pulled ahead. This pattern continued, and there was no clear 'leader' band.

I never observed either band depart when Band 1 and Band 3 met each other at the Filoha cliff sleeping site in the late afternoon. Twice, however, Band 1 slept at least 100 m farther north on the cliff than they normally did. Furthermore, on one occasion Band 1 and Band 3 encountered each other in the Hot Springs palm forest 0.4 km north of the Filoha cliff sleeping site at 1500. Although the baboons did not interact across band lines, Band 1 subsequently left the palms and traveled 5 km to sleep on the Wasaro cliff and Band 3 slept on the Filoha cliff. While I cannot be certain that Band 1 traveled to the Wasaro cliff to avoid sharing a sleeping site with Band 3, it is rare for the baboons to travel such a far distance so late in the day.

I observed Band 1 and Band 3 encounter each other during daily travel on two other occasions. Both times band members – both males and females – fought with one another for about 15 minutes before separating and traveling in different directions. Band 1 encountered Band 2 during daily travel at least four times, each of these occasions occurring as both bands approached the Wasaro cliff in the late afternoon. On all but one of these afternoons, both bands in their entirety continued to and slept on the Wasaro cliff. Once, however, Band 1 encountered Band 2 about 1.5 km northeast of the Wasaro cliff at 1530. The band had been traveling WSW toward the Wasaro cliff since 1345. By 1545, however, about 75% of Band 1 (~150 individuals) changed directions and began traveling east over 3 km back to the Filoha cliff, while the remainder of the band traveled to the Wasaro cliff with Band 2. I cannot be certain that most of the band changed their

travel route, and eventual sleeping site, due to their encounter with Band 2, but again, it is rare for the baboons to both change directions and travel such a far distance so late in the day.

5.4.9 Afar Nomads

Band 1 encountered Afar nomads 232 times from March 2005 through February 2006, at rates of 1.5 encounters per day and 0.2 encounters per hour. These encounters consisted of Afar passing by or through areas in which the baboons were ranging. Frequently, there were cows, goats, donkeys, and/or camels with the nomads, and other times the Afar traveled without animals. The nomads usually did not harass the baboons, although on at least 10 occasions I observed the nomads throwing stones and sticks at the baboons.

While the Afar nomads did temporarily alter the baboons' activity patterns, travel directions, and speed of travel as predicted, overall the presence of Afar in the Filoha region did not seem to greatly impact the baboons' ranging behavior. More than half of the Afar encounters (N=120) occurred when the baboons were resting, grooming, and/or feeding. On half of these occasions (N=65), the baboons moved 50-200 m and then continued to rest, groom, and/or feed. Thirty-six times the baboons began to travel from a stationary position. At least 18 times the baboons were feeding in palm trees, and they ran down from the trees and out of the palm forest when Afar approached. On these occasions it appeared that the baboons cut their feeding bout short due to the presence of Afar. This same pattern occurred at least seven times when the baboons were feeding in *Acacia* spp. trees, and twice when the baboons were foraging in open grasslands.

The other half of Afar encounters (N=113), occurred while Band 1 was traveling. On more than half of these occasions (N=49) the baboons changed directions, but then reversed and continued traveling in their original direction after the Afar passed. Seventeen times, the baboons stopped and waited for the Afar to pass before continuing their travel. On 15 occasions, the baboons briefly sped up when they encountered Afar, but they did not change directions. Eleven times, the baboons circumvented the Afar, veering around them. On the remaining 11 occasions, the baboons had recently left the sleeping cliff to begin their daily travel; upon encountering Afar the baboons climbed back up the cliff and continued resting and grooming until the Afar passed and then began their travel in earnest.

There was only one occasion in which the baboons permanently changed directions upon encountering Afar nomads. This occurred in *Acacia* scrubland about halfway between the Filoha and Wasaro cliffs. The baboons had been traveling west toward Wasaro for at least an hour. When they encountered Afar and cattle, they reversed directions and began traveling east, and continued in this direction back to the Filoha cliff where they slept that night. While I cannot be certain that the baboons were en route to the Wasaro cliff and changed their eventual sleeping site due to Afar, the baboons appeared to change directions in response to the nomads and their cattle.

There were several occasions on which it appeared that the baboons were prevented from drinking because of the presence of Afar and cattle. On these occasions the baboons approached a water hole or swamp from which they regularly drank, but upon reaching the location and seeing Afar, the baboons continued on without stopping. It should be noted that there were at least eight times that the baboons encountered Afar

nomads with goats, camels, or donkeys and did not react at all. Overall, the baboons' response to Afar did not differ based on the age, sex, or number of nomads encountered.

In addition to the encounters described above, the baboons sometimes came across cattle, goats, or camels without Afar nomads. The baboons generally did not react to the animals when they were unaccompanied by humans – except for moving aside if they were in the direct path of a herd of cattle – suggesting that the baboons fear the Afar people and not the animals (Swedell, 2006). It was common during the last few months of the dry season for the Afar to water their cattle at the hot springs at the base of the Filoha cliff sleeping site for several hours in the afternoon. On several occasions the baboons returned to Filoha in the early afternoon, presumably to drink, but climbed to the top of the cliff upon encountering the cattle. As soon as the cattle vacated the area, the baboons climbed down the cliff to drink at the bottom of the cliff. There were also at least six times in which gunshots could be heard nearby, but no Afar were seen. On these occasions, the baboons did not react.

5.5 Comparisons with other hamadryas studies

Band 1's minimum annual home range size of 38.6 km² is larger than that previously reported for hamadryas baboons. Swedell (2002b, 2006) reported that Band 1 ranged over at least 30 square kilometers in 1996-1998, but noted that its home range was probably substantially larger as they disappeared from the Filoha and Wasaro regions for several weeks during the wet season. Contrary to expectations, home range size at Filoha was not smaller than those at other sites, despite the accessibility of food and water close to the Filoha Cliff sleeping site. Sigg and Stolba (1981) reported a home range size of 28 km² at Erer Gota, Ethiopia. The home range in the Alhada Mountains of Saudi Arabia

was 9.3 km² (Boug et al., 1994). Home range sizes have not been reported for any other hamadryas population. Band 1's home range, therefore, is substantially larger than that reported for other hamadryas sites, despite the presence of a permanent water source and palm fruit in close proximity to the Filoha cliff sleeping site.

Band 1 at Filoha used its home range unevenly, corresponding with the distribution of important resources (section 5.3.2). Similarly, Kummer's (1968a) observations suggested that the baboons at Erer Gota spent more time in areas of their home range that contained sleeping cliffs, water holes, and acacia trees than in areas without these resources. In the only other study that systematically investigated hamadryas home range use, Sigg and Stolba (1981) also reported that the baboons' displayed a pattern of non-random use of their home range determined by the location of both large feeding areas and water holes.

Band 1's mean daily path length of 8.3 km in 2005-2006 is slightly longer than the 7.5 km reported for Band 1 in 1996-1998 (N=27) (Swedell, 2002b, 2006). At Awash Station, Ethiopia, Nagel (1973) mapped seven travel routes and the mean daily path length was 6.5 km. Conversely, Kummer and Kurt (Kummer, 1968a) mapped nine complete travel routes at Erer Gota and the mean daily path length was 13.2 km (range=4.1-19.2, N=9). Band 1's daily path lengths, however, are comparable to those reported by Sigg and Stolba (1981) at Erer Gota: 8.6 km for Band I (N=57) and 10.4 for Band II (N=13). Daily paths ranged from 1.04 – 14.03 km in Saudi Arabia, but no mean was reported (Biquand et al., 1992; Boug et al., 1994). It should be noted that my results are most similar to those of Sigg and Stolba (1981), the study with the largest sample size. The other studies' smaller samples are probably not large enough to provide valid estimates of mean daily path length.

On average, Band 1 departed from the sleeping cliff between 0730 and 0745 in the morning. The baboons at Erer Gota also left their sleeping site between 0729 and 0743 during the winter months. While there were no seasonal differences in departure time at Filoha, at Erer Gota the baboons left the cliff an hour earlier during the summer months. As at Filoha, the baboons at Erer Gota almost always reached their evening sleeping site between 1600 and 1700. In both studies, travel speed peaked when the baboons left their sleeping cliff in the morning and began daily travel. Similarly, the afternoon spike in travel speed corresponded with the baboons' return to their evening sleeping site. Overall, my results correspond closely with those of Sigg and Stolba (1981), suggesting that aspects of timing during daily travel are consistent across sites, regardless of differences in habitats.

Swedell (2002b, 2006) found similar seasonal patterns in the travel patterns of Band 1 in 1996-1998 to those in the current study. Namely, the mean daily path length was slightly shorter in the dry season than the wet season. Furthermore, the baboons spent more time away from Filoha during the wet season, as they did in 2005-2006. Sigg and Stolba (1981) did not examine seasonal differences in home range use and travel patterns. In Saudi Arabia, Boug et al. (1994) found that home range was smallest and daily path length shortest during the driest month of the year, while the baboons traveled the longest distances in April when vegetation was abundant.

5.6 Chapter Summary and Conclusions

Band 1's home range size from March 2005 through February 2006 was 38.6 km². As expected, the baboons did not use their home range evenly, spending less time than expected in *Acacia* scrublands, and more time than expected in palm forests. This pattern

of use reflects the concentration of doum palm fruit in only a few relatively small regions of the baboons' home range. The baboons also spent more time than expected on cliffs, corresponding with the large proportion of time that the baboons spent resting and grooming in the relative safety afforded by sleeping cliffs.

The baboons' mean daily path length was 8.3 km. Contrary to expectations, despite the presence of both a permanent water source and doum palm fruit in close proximity to the Filoha cliff sleeping site, Band 1's home range size was not smaller and daily path lengths were not shorter than those at other hamadryas sites. Although they were not constrained by food and water resources, the baboons still traveled up to 14.2 km each day. I did not observe the baboons feeding on any food species away from Filoha that were not also available in the Filoha region, suggesting that the baboons did not range over such a large area or travel such long distances solely to obtain critical resources. Furthermore, the mean daily path length, time of departure from and arrival at sleeping sites, and patterns of travel speed throughout the day at Filoha were comparable to those reported at Erer Gota (Sigg and Stolba, 1981), despite the differences in resource distribution and availability between the two sites.

Band 1's large home range size and long daily paths may be a consequence of its large band size. Bands are larger at Filoha than at other hamadryas sites (section 6.3.1), and such an increase in group size is expected to increase the distance group members must travel each day in order to meet their energetic and nutritional requirements (Eisenberg et al., 1972; Altmann, 1974; Chapman and Chapman, 2000). However, the mean daily path length when clans traveled independently was 9.2 km (N=9), larger than when Band 1 traveled as a cohesive band. Furthermore, I was able to map complete travel routes for Band 3 in its entirety – about 400 individuals (section 6.3) – on seven

days. Despite the fact that Band 3 is twice as large as Band 1, its mean daily path length (7.3 km) was shorter than that of Band 1. Finally, Band 1's mean daily path length was comparable to those reported at Erer Gota, despite the larger band sizes at Filoha. These results suggest that group size does not influence travel distances at Filoha.

Instead, it is possible that the baboons are constrained by their phylogenetic history (Swedell, 2002b, 2006). It is thought that hamadryas baboons evolved in harsh semi-desert environments characterized by a sparse distribution of resources (Kummer, 1971, 1990). As suggested by Swedell (2002b), may thus have a genetic predisposition to travel far distances even when the current availability of resources deems such ranging unnecessary. Several aspects of hamadryas behavior such as herding and notifying have, in fact, been shown to be invariable over a range of environmental conditions, including ranging behavior (Lackman-Ancrenaz, 1994) and male social behavior (Kummer and Kurt, 1965; Colmenares, 1990).

Seasonal patterns in Band 1's ranging behavior were evident. As predicted, the baboons spent more time away from Filoha during the wet season than the dry season. Presumably, it was not necessary to stay near Filoha due to the availability of standing water throughout their home range during the wet season. Furthermore, as expected, the mean daily path length was significantly shorter in the dry season than the wet season, likely a reflection of the baboons' need to remain in close proximity to the permanent water sources at Filoha.

When looking at variation across months, however, these seasonal patterns are not as straightforward as they initially appear. While the mean daily path lengths across dry season months were relatively consistent, the mean daily path lengths in the two wet season months were significantly different (Mann-Whitney test, $p=0.02$). The mean daily

path length in July was 11.0 km, the longest of any month. During this month, both standing water and fresh leaves were available throughout the baboons' home range. The baboons ranged widely and fed on more plant species than in any other month. In August, by contrast, the mean daily path length was 7.3 km, comparable to those of the dry season. During this month, water, fresh leaves, and flowers were available throughout their home range. The baboons traveled shorter distances and ranged mostly on the west side of the Wasaro cliff, foraging predominantly on the flowers of *T. cistoides* – a preferred food resource (Chapter 4) – despite the fact that these flowers were available throughout the baboons' home range. The baboons, therefore, employed two disparate ranging strategies during the wet season. When water and fresh leaves were available, the baboons ranged widely and increased their dietary breadth, taking advantage of the widespread resources. When water and a preferred food resource were available, however, the baboons ranged over a smaller area that they were unable to utilize as intensively during the rest of the year.

Contrary to expectations, daily path lengths did not decrease as the proportion of doum palm fruit in the baboons' diet increased. The baboons' reliance on palms, however, did appear to influence their travel patterns. The band's use of its home range was tied to where the baboons fed on palm fruit; the baboons used the northern part of their home range when they foraged in the Hot Springs and Alibete palm forests, and they used the southern portion of their home range when they fed from the palm clumps southeast of Filoha. Furthermore, the farthest point from the evening sleeping site was located in palms in over two-thirds of the complete travel routes in which the baboons were observed eating palm fruit.

While the presence of predators influenced when Band 1 departed from the Filoha cliff in the morning, overall it did not appear to affect the baboons' ranging patterns. Similarly, no consistent patterns emerged regarding the influence of other bands on Band 1's travel patterns. Finally, while the presence of Afar nomads in the Filoha region did temporarily alter the baboons' activity patterns, travel directions, and speed of travel as predicted, overall the Afar did not impact the band's ranging behavior.

Table 5.1 Band 1's home range size and sleeping site use by month and overall

<i>Month</i>	<i>Observation Days</i>	<i>Home Range (km²)</i>	<i>Nights Filoha Cliff</i>	<i>Nights Wasaro Cliff</i>
March 05	19	10.5	12	12
April 05	19	15.0	19	9
May 05	15	11.6	13	13
June 05	13	22.1	15	5
July 05	10	19.1	6	7
August 05	10	5.0	0	15
September 05			3	4
October 05	9	4.8	23	1
November 05	11	15.8	13	4
December 05	17	12.9	24	1
January 06	13	11.5	16	5
February 06	10	12.7	11	1
Total	146	38.6	155	77

Table 5.2 Attributes of Band 1's complete travel routes by month and overall

<i>Month</i>	<i>Complete Travel Routes</i>	<i>Mean Daily Path Length (km)</i>	<i>Filoha→ Filoha</i>	<i>Filoha→ Wasaro</i>	<i>Wasaro→ Wasaro</i>	<i>Wasaro→ Filoha</i>
March 05	8	9.7	1	6	1	0
April 05	16	8.7	7	6	0	3
May 05	12	9.3	2	6	1	3
June 05	11	9.3	8	3	0	0
July 05	6	11.0	0	3	2	1
August 05	9	7.3	0	0	9	0
October 05	6	6.0	6	0	0	0
November 05	7	7.5	4	0	2	1
December 05	14	6.4	13	0	0	1
January 06	10	8.5	4	4	0	2
February 06	6	7.1	4	1	0	1
Total	105	8.3	49	29	15	12

Figure 5.1 Cumulative area used by Band 1 over study period

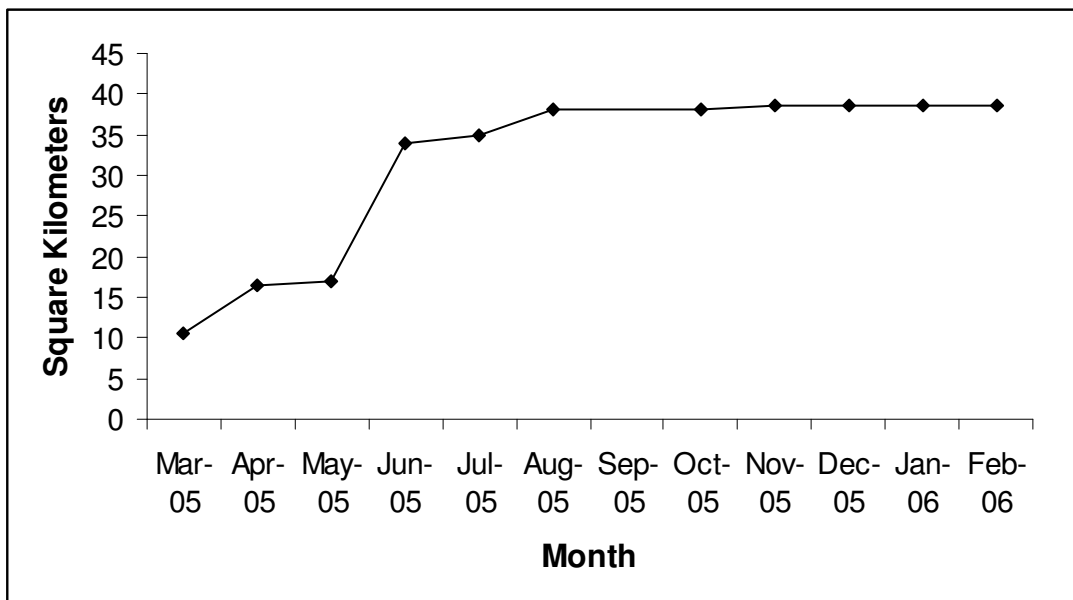


Figure 5.2 Annual habitat budget for Band 1

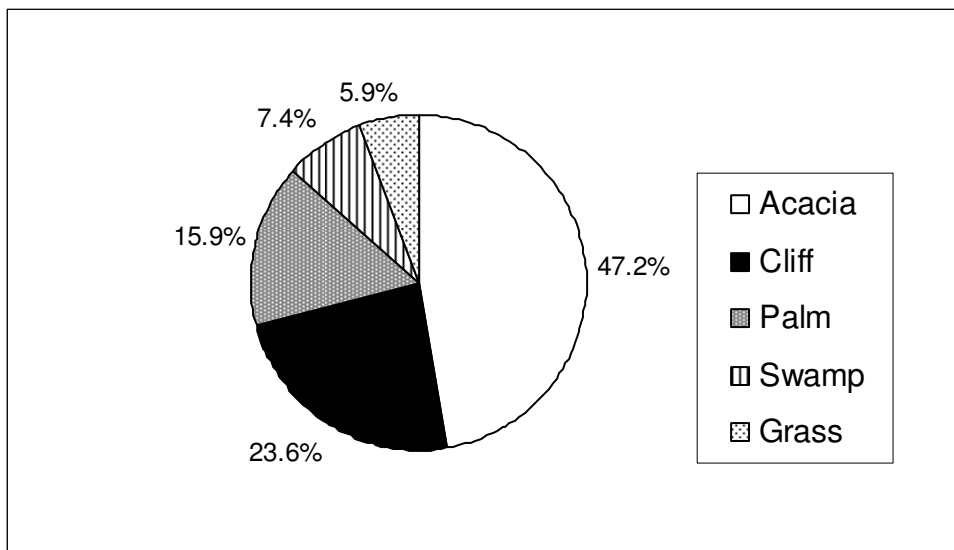


Figure 5.3 Observed versus expected time spent in each habitat type

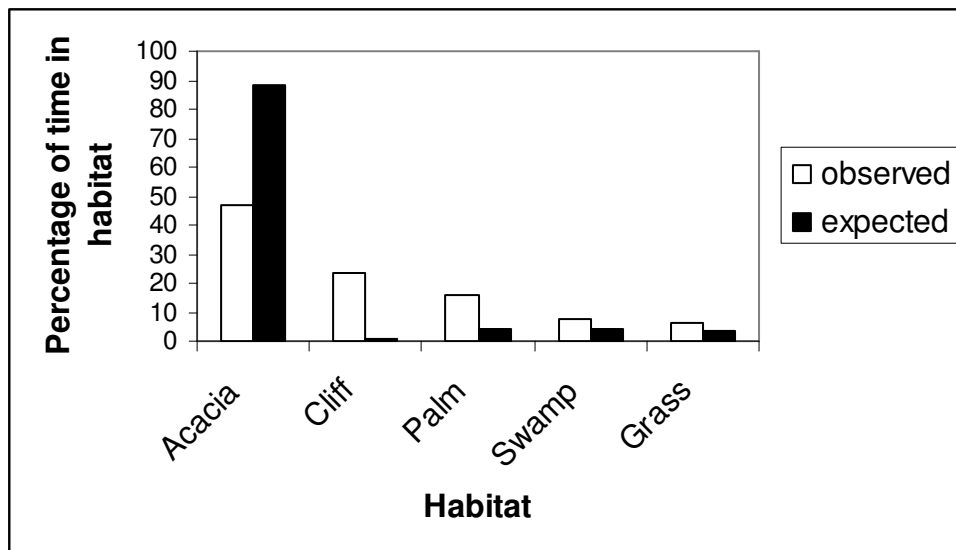


Figure 5.4 Activity budget by habitat type

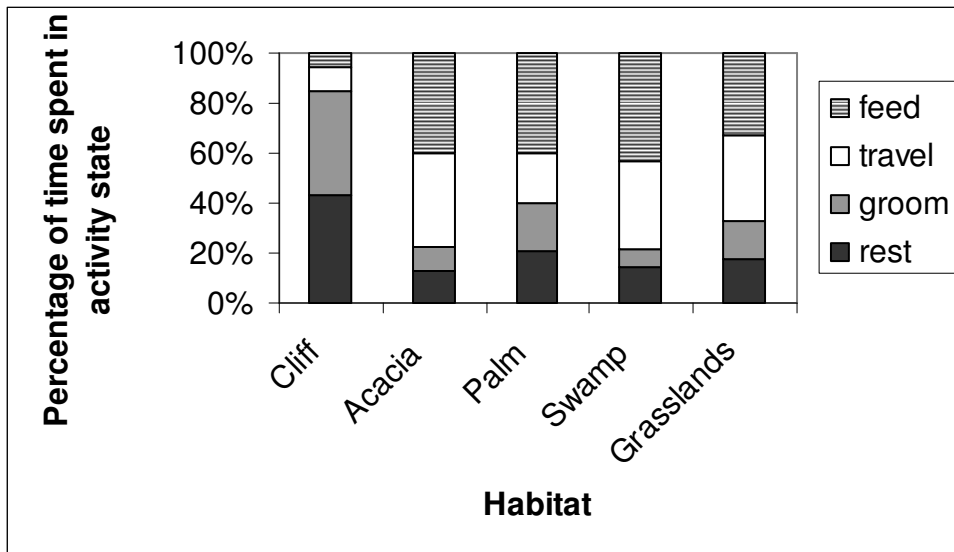


Figure 5.5 Habitat budget by hour of the day

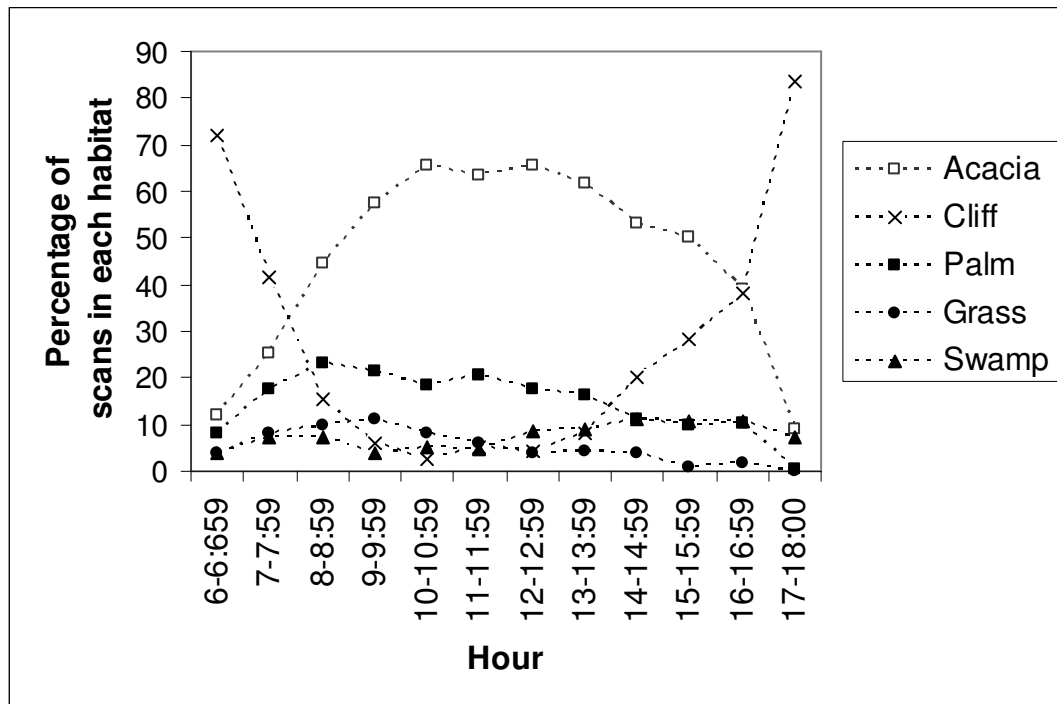
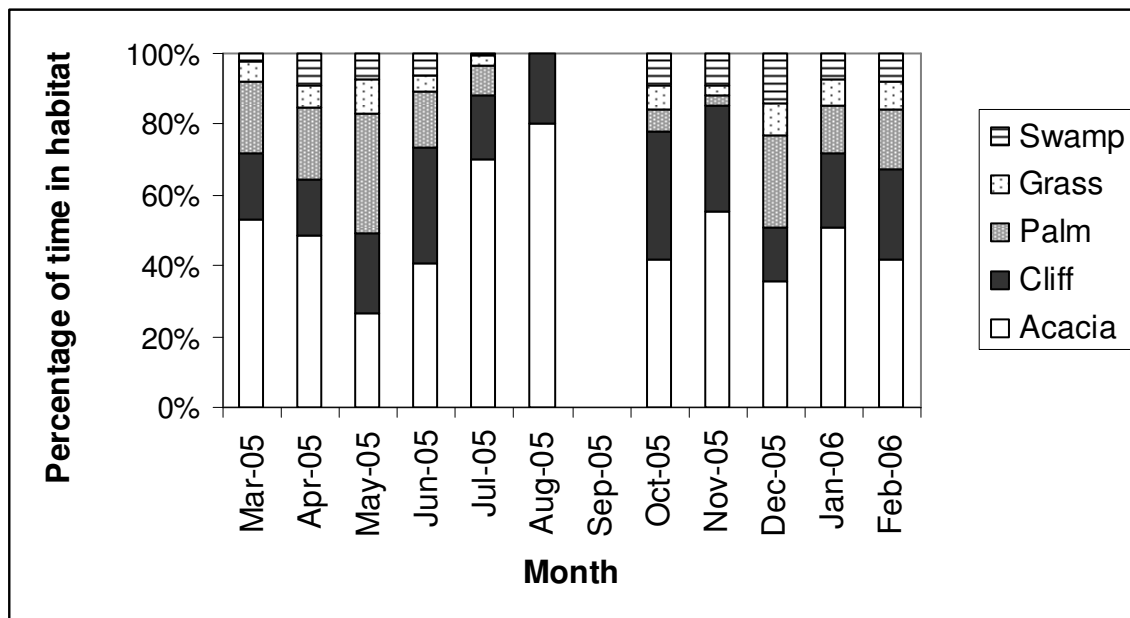


Figure 5.6 Monthly variation in habitat use



Dry Season = October, November, and December 2005; January and February 2006

Wet Season = July and August 2005

Figure 5.7 Seasonal use of habitat types

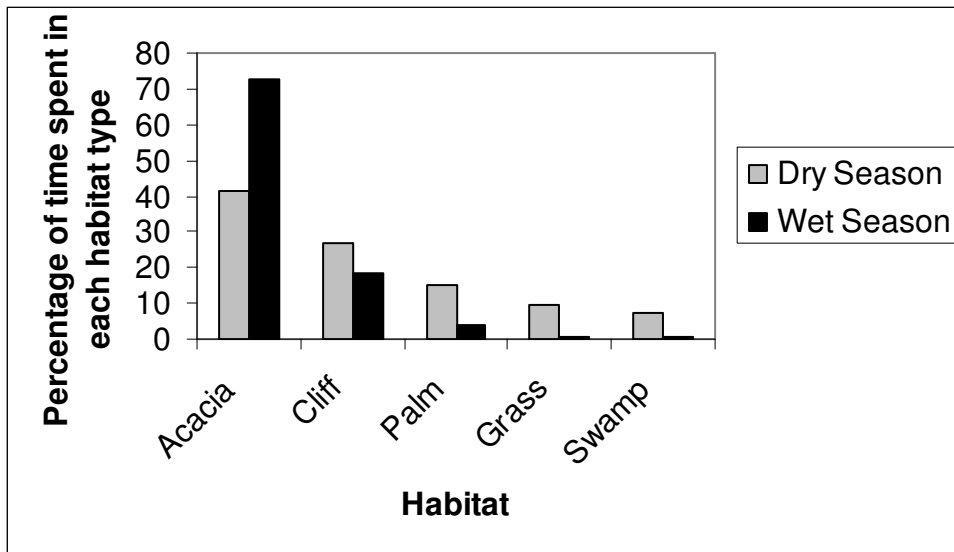


Figure 5.8 Travel routes beginning and ending at the Filoha cliff (N=49)



Figure 5.9 Travel routes from the Filoha cliff to the Wasaro cliff (N=29)

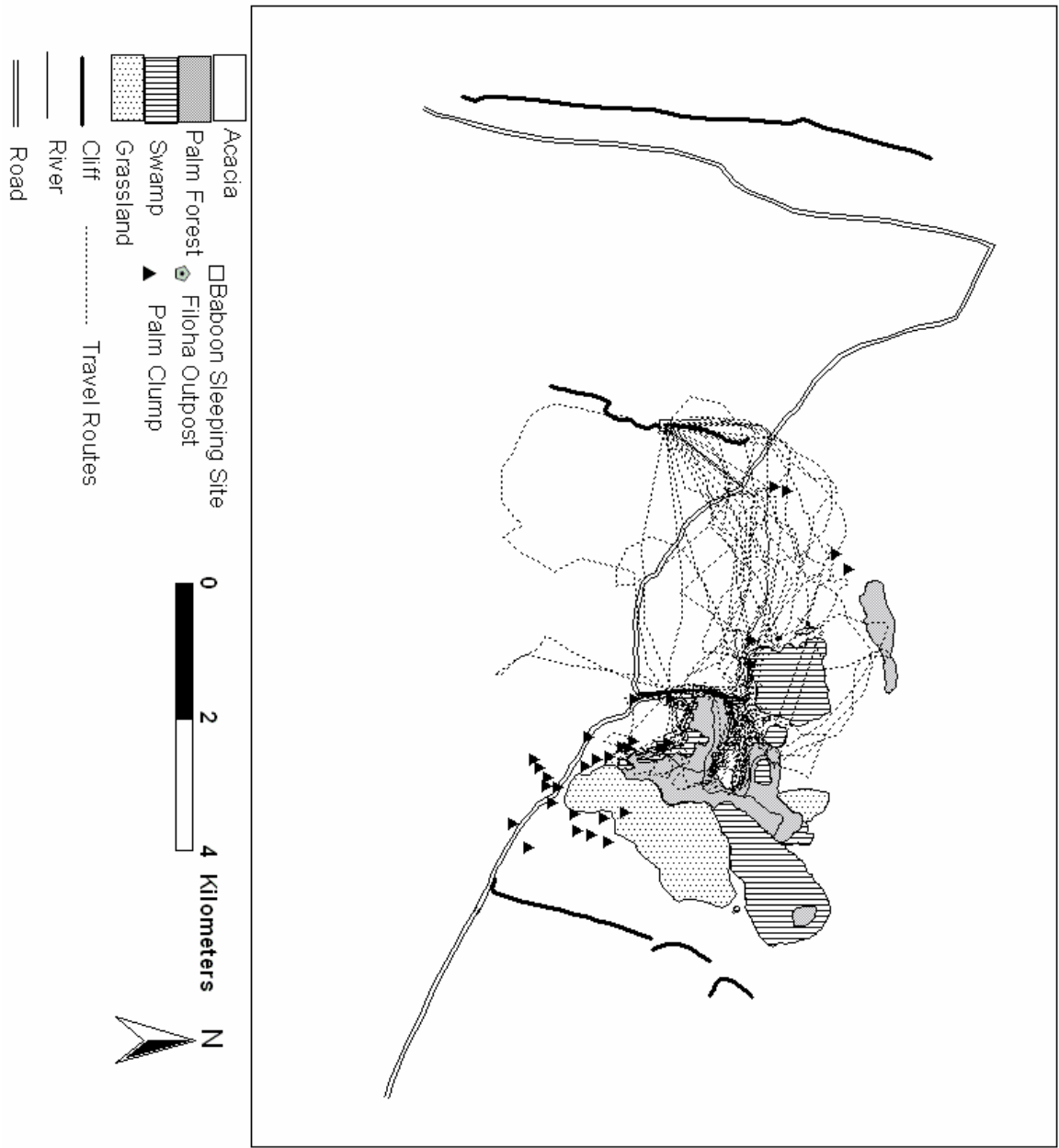


Figure 5.10 Travel routes beginning and ending at the Wasaro cliff (N=15)

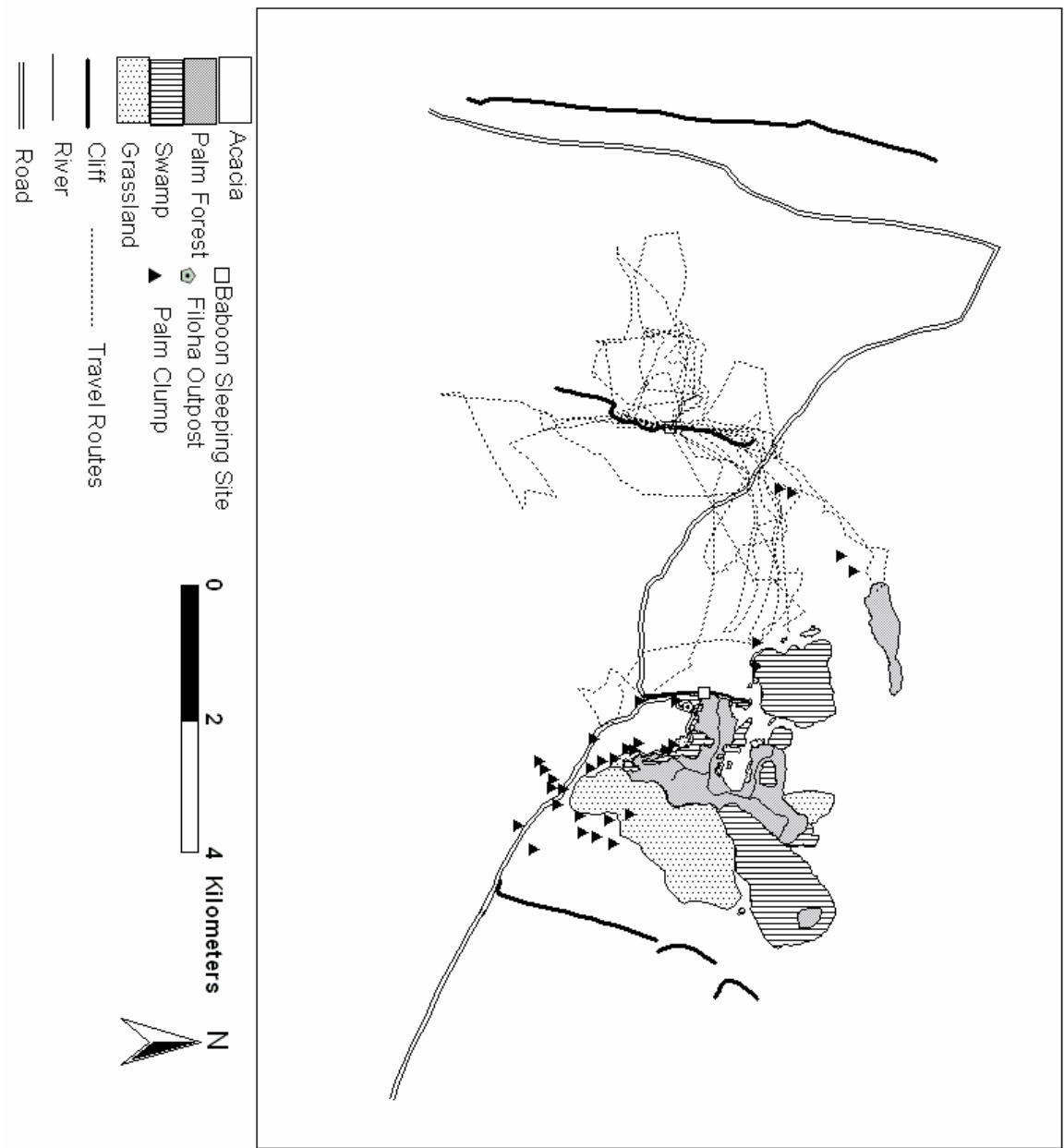


Figure 5.11 Travel routes from the Wasaro cliff to the Filoha cliff (N=12)



Figure 5.12 Average distance traveled by Band 1 each hour of the day

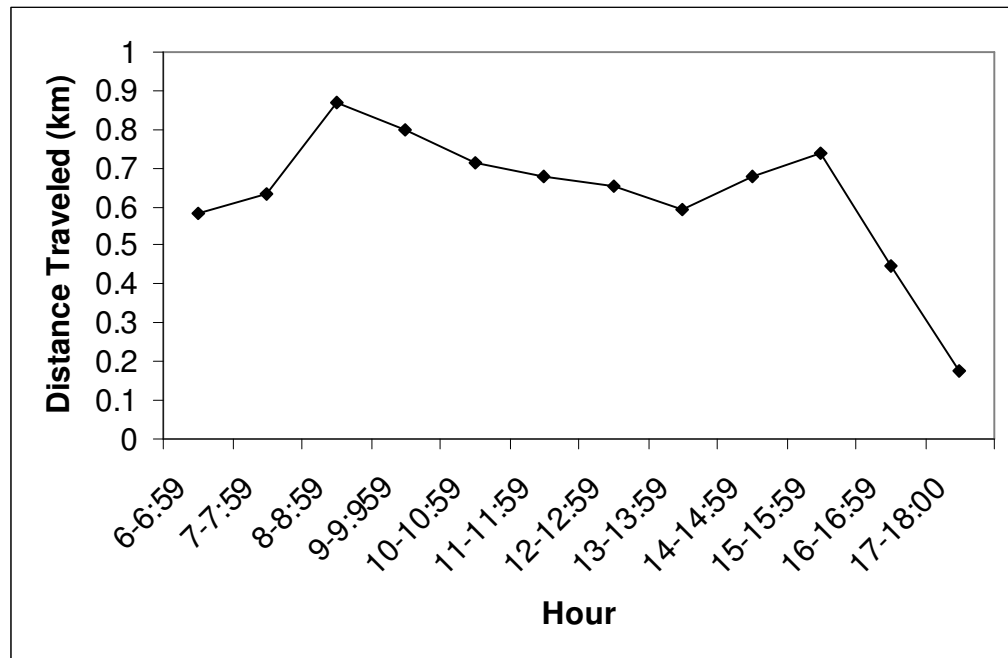


Figure 5.13 Dry season travel routes (N=43)



Figure 5.14 Wet season travel routes (N=15)

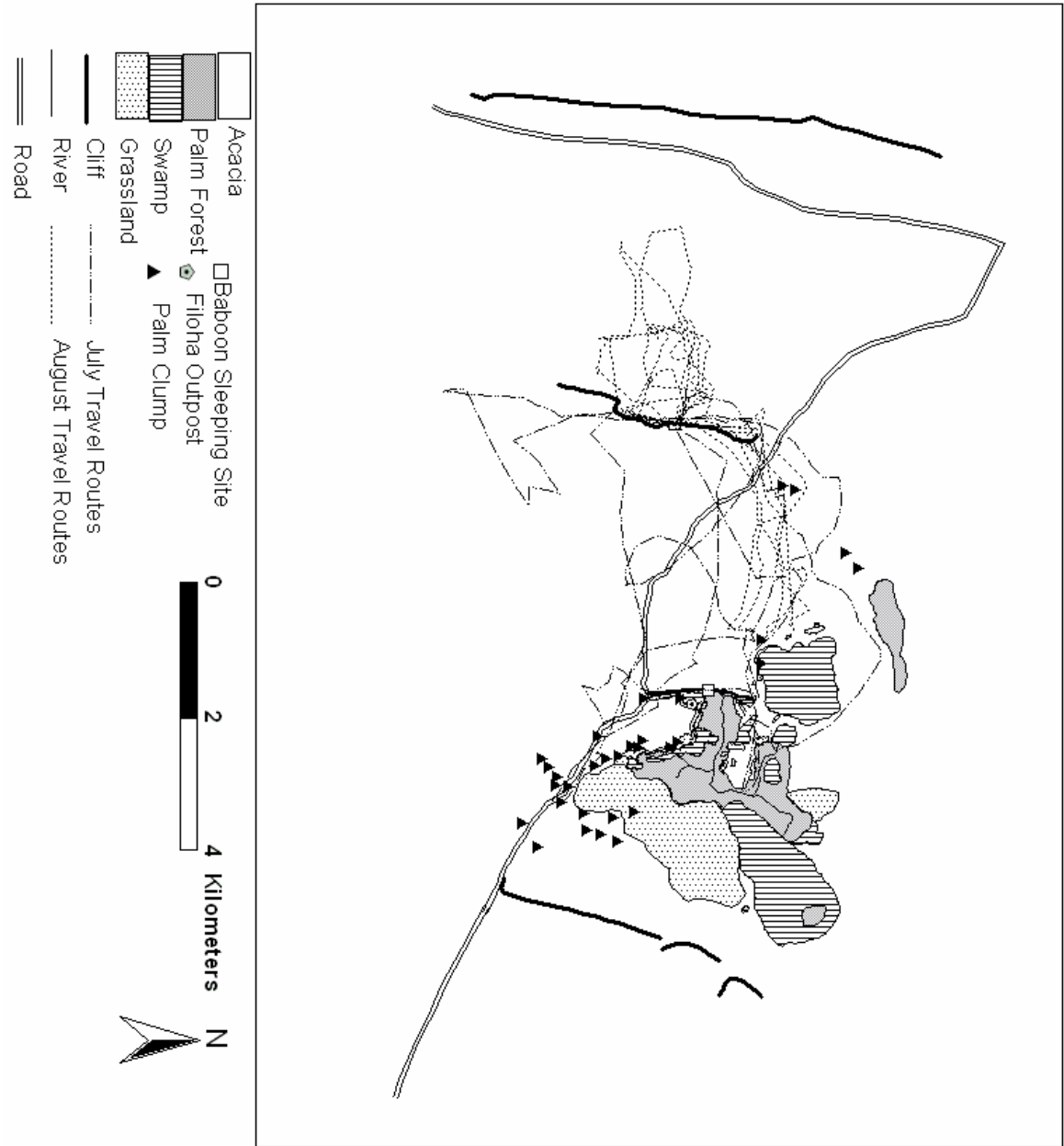
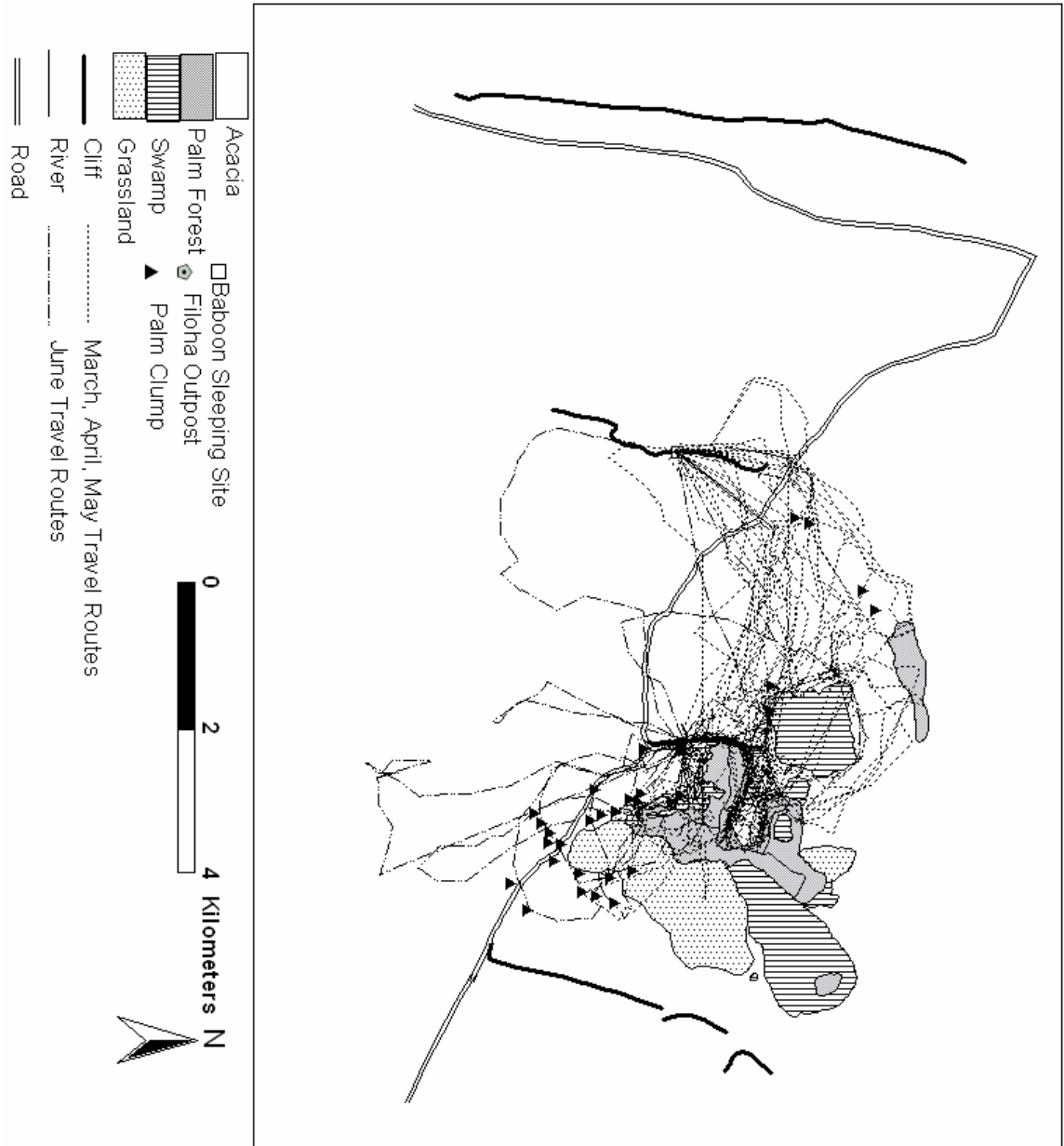


Figure 5.15 Travel routes in March, April, and May (N=36) compared to June (N=11)



CHAPTER 6

SOCIAL STRUCTURE AND SOCIAL ORGANIZATION

In this chapter, I describe and discuss the social structure and social organization of Band 1 at Filoha. Following Rowell (1972, 1979), social structure is defined as the size, composition, and spatiotemporal cohesion of a social group. As such, I will describe the size and composition of Band 1 and its component one-male units and clans. Social organization, in turn, refers to the pattern of interactions and association among members of a social group, which I will describe at each level of hamadryas society – the troop, the band, the clan, and the one-male unit. The relationship between the hamadryas multilevel social system and the distribution of resources in their home range will be explored in Chapter 7.

6.1 Hamadryas Social Structure and Organization

Hamadryas baboons are known for their unique multilevel social structure in which large groups break into smaller foraging parties during daily travel. It is thought that this nested social structure is related to the sparse distribution of resources in hamadryas habitats in that it allows a large group to break up during daily travel so that all group members can access sufficient food resources (Kummer, 1968a,b, 1971, 1990, 1995). Three main levels of organization characterize hamadryas society. The *band* is the fundamental unit that displays coherence over time. It is a stable social unit that travels together during the day, coordinates its overall movement and activities, and generally sleeps at the same cliff each night. The band is homologous to the ‘troop’ in other *Papio* subspecies, and hamadryas social interaction as a whole occurs almost

exclusively among members of the same band. The hamadryas *troop* is a temporary cluster of bands (up to several hundred baboons) that assembles at sleeping cliffs, but otherwise does not function as a single unified social group. Jolly (2007) attempts to resolve the semantic confusion between hamadryas and other baboons by coining the term “MTA” (multi-troop association) for what have formerly been called “troops,” and then using “troop” to refer to a hamadryas band. To maintain consistency with previous work on hamadryas baboons, I will follow Kummer’s (1968a) terminology here. *One-male units* (OMUs) are divisions of bands, each consisting of a leader male, several females, their dependent offspring, and occasionally one or more “follower” males. OMUs are socially and spatially cohesive, and most social interaction occurs within these units rather than among them (Kummer and Kurt, 1963; Kummer, 1968a, 1971; Abegglen, 1984; Swedell 2002a, 2006).

Abegglen (1984) was the first to document a fourth level of social structure in hamadryas society, which he called “clans.” He noticed that certain OMUs in the Erer Gota population in Ethiopia rested near one another on the sleeping cliff, foraged together during the day, and occasionally traveled as subgroups independently from the rest of the band. Based on physical resemblance among males, Abegglen suggested that these associations of OMUs and unaffiliated males consisted of male relatives, although this was never substantiated.

In the following sections, I will describe the social structure and organization of the troop at Filoha, followed by that of Band 1 and its constituent OMUs. In the final section, I will quantify and describe Band 1’s clan structure and discuss the functions of this fourth level of social structure.

6.2 The Troop

The troop structure is evident at Filoha and, as reported previously (Kummer, 1968a, 1971; Abegglen, 1984; Swedell, 2006), emerges mainly at sleeping sites. Three bands at Filoha, Band 1, Band 2, and Band 3 (see section 6.3 for details on band composition), sometimes share sleeping sites but do not otherwise behave as a single cohesive social unit. Band 1 and Band 3 shared a sleeping cliff on at least 89 nights; they both slept on the Filoha cliff on 83 nights and on the Wasaro cliff on at least six nights (Schreier and Swedell, 2008). Band 1 and Band 2 both slept on the Wasaro cliff on at least 22 nights and on the Filoha cliff one night. On at least one night Band 2 and Band 3 both slept on the cliff 4 km west of the Wasaro cliff. All three bands were never observed to sleep together on the same cliff on the same night.

When more than one band shared a sleeping site, each band slept at a particular location on the cliff, and all baboons were spatially situated within their own band. When Band 1 and Band 3 both slept on the Filoha cliff, Band 1 slept north of a regularly used walkway and Band 3 slept south of it, with only several meters separating the members of the two bands closest to the walkway. When they slept alone on the Filoha cliff, however, each band spread across both sides of the walkway. The bands' sleeping sites on the Wasaro cliff were located near a *Delonix elata* tree. Band 1 slept south of the tree, Band 3 slept north of it, and Band 2 slept right at the tree; in this arrangement, Band 1 and Band 3 were separated by about 200 m. The bands appeared to sleep in these positions regardless of whether or not another band was present.

Hamadryas bands are typically quite tolerant of one another on sleeping cliffs (Kummer, 1968a; Swedell, 2006), but relationships among bands can sometimes be agonistic as well (Swedell, 2006). Band 1 and at least part of Band 3 slept together on the

Filoha cliff on 40% of the nights for which data exist, and I never observed either band depart when they met each other at the Filoha cliff sleeping site in the late afternoon. Twice, however, Band 1 slept at least 100 m further north on the cliff than they normally did. Furthermore, on one occasion Band 1 and Band 3 encountered each other in a palm patch 0.4 km north of the Filoha cliff sleeping site at 1500. Although the baboons did not interact across band lines, Band 1 subsequently left the palms and traveled 5 km to sleep on the Wasaro cliff and Band 3 slept on the Filoha cliff. While I cannot be certain that Band 1 traveled to the Wasaro cliff to avoid sharing a sleeping site with Band 3, it is rare for the baboons to travel so far so late in the day. These instances suggest that bands may occasionally attempt to avoid each other at sleeping sites.

When two bands share a sleeping site, they often begin daily travel together the following morning (Kummer, 1968a; Sigg & Stolba, 1981; Swedell, 2006). Band 1 and Band 3 departed from sleeping cliffs together on several occasions, and once traveled together all day (section 5.4.8). Band 1 and Band 2 departed from the Wasaro cliff together on several mornings. I observed Band 1 and Band 3 encounter each other during daily travel only twice. Both times band members – both males and females – fought with one another for about 15 minutes before separating and traveling in different directions. These fights consisted of growling, threat yawns, chasing, screaming, and biting. Band 1 encountered Band 2 during daily travel at least four times as both bands approached the Wasaro cliff in the late afternoon; the baboons did not interact across band lines.

6.3 The Band

Several bands of hamadryas baboons populate the Filoha region, two of which, Band 1 (“Group 1” in Swedell 2000, 2002a,b, 2006) and Band 3 (“Group 3”), have been studied intermittently since 1996 (Swedell, 2000, 2002a, 2002b, 2006). In February 2006, Band 1 and Band 3 consisted of approximately 210 and 400 individuals, respectively. A third band, Band 2, was sometimes observed on and near the Wasaro cliff, and numbered about 150 baboons. Another group of less than 100 baboons was also occasionally observed on the Wasaro cliff, but it was unclear whether it constituted a fourth band or was a clan or small fragment of another band.

6.3.1 Band Size

The band sizes at Filoha are considerably larger than those reported for other Ethiopian hamadryas populations. At Erer Gota, Kummer (1968a) reported bands of 30 to 90 baboons, Sigg and Stolba (1981) reported bands of 62 to 95 baboons, and Abegglen (1984) reported bands of 52 to 90 individuals. At Awash Station, the two hamadryas bands studied by Nagel (1973) consisted of 51 and 57 individuals. Band sizes at Filoha are also much larger than those in hamadryas populations in the Arabian peninsula. In Saudi Arabia, Kummer et al. (1981) reported bands ranging from 13 to 70 individuals, and Biquand et al. (1992) reported groups of 9 to 102 individuals. Bands of 22 to 89 baboons were found in Yemen (Al-Safadi, 1994). It should be noted, however, that the Arabian populations were not followed long enough to be certain that these groups were not just clans. The large band sizes at Filoha reflect the high abundance and availability of doum palm fruit, a preferred food resource (Swedell, 2002b; Swedell, 2006; Swedell et al., 2008; Chapter 4).

6.3.2 *Band Demography*

At the start of the study period in March 2005, Band 1 consisted of about 190 individuals: 24 leader males, 5 follower males, about 15 adult and subadult males unaffiliated with an OMU, 54 adult females, 9 adolescent females, and at least 80 juveniles and infants. At the end of the study period in February 2006, Band 1 consisted of approximately 210 individuals: 24 leader males, 7 follower males, about 20 adult and subadult unaffiliated males, 53 adult females, 13 adolescent females, and at least 90 juveniles and infants (see Table 2.2 for age classes). All adult and adolescent females were members of OMUs. Leader males, adult females, and adolescent females were all recognized individually, but the identities of most follower males, unaffiliated males, and juveniles were unknown.

The ratio of adult and adolescent females to adult and subadult males ranged from 1.43 to 1.50 over the study period. This female-biased sex ratio is consistent with those reported previously for hamadryas baboons (1.3 to 1.8 at Filoha in 1996-1998, 1.13 at Erer Gota, 2.07 in Eritrea, 1.73 in wild Arabian groups, and 1.96 in commensal Arabian groups; Swedell, 2006; Kummer, 1968a; Zinner et al., 2001; Biquand et al., 1992), and can be attributed to the longer periods of development in males than females. Females begin reproductively cycling when they are about four years old and reach their adult body size when they are five or six. Males, by contrast, do not reach the subadult stage of development until they are about six years old, and the adult stage until they are about ten (Swedell, 2006).

The size of Band 1 increased in numbers by 11% over the study period. This increase in size is similar to that reported for Band 1 between 1997 and 1998 (Swedell,

2006). The rate of increase in band size over one year at Filoha, however, is higher than the 12% reported for the hamadryas population at Erer Gota over 5.5 years (Sigg et al., 1982).

Of the possible proximate mechanisms affecting group size – births, deaths, immigration, and emigration – the increase in band size at Filoha is likely related to a high birth rate coupled with a low rate of infant mortality. Thirty-two infants were born over the study period. Three of these infants died: the first died less than a month after birth and appeared to be the victim of infanticide (described in section 6.4.3), the second infant died within two weeks of birth and seemed to be abandoned by her mother, and the third infant died at six months old, after appearing thin with patchy hair for the preceding two months.

Several other members of Band 1 are known or presumed to have died as well. (Throughout this chapter, the names of leader males are written in capital letters and the names of females are in italics.) One leader male, MORRIS, disappeared while all of his females remained in Band 1. As MORRIS appeared to be healthy leading up to his disappearance, it was presumed that he died from a sudden injury, perhaps a snake bite. Another leader male, FRUIT, disappeared and, based on his old appearance, including wrinkles and sagging skin, was presumed to have died. One adult female, *Natalie*, was also presumed to have died. She appeared to be sick for several months prior to her disappearance, and displayed rapid physical deterioration in the final few weeks. At least two juvenile males are presumed to have died after their legs atrophied to the point at which they could no longer travel.

Immigration and emigration also contribute to changes in group size. At Filoha, such changes were recorded mainly for females. The transfer of females between bands

is almost exclusively the result of aggressive takeovers by males (Swedell and Schreier, in press). Over the study period, at least 13 adolescent and adult females immigrated into Band 1 from another band. Their tenure in Band 1 ranged from a few days to ten months during this period. Four of these females then emigrated out of Band 1, but it is unclear if they returned to the same band from which they came. One female emigrated from Band 1 to Band 3, but several months later immigrated back into Band 1. No leader males immigrated to Band 1 during the study period; it is possible that unaffiliated males immigrated into the band but this cannot be confirmed as their identities were, for the most part, unknown. Likewise, accurate counts of the number of juveniles that immigrated into the band could not be obtained because juveniles were not individually identified.

Several members of Band 1 emigrated into other bands over the study period. Two OMUs (consisting of a total of two leader males, three adult females, two juveniles, and one infant) disappeared from Band 1 and were presumed to have emigrated into another band as they were last seen when Band 1 was mixed with another band. Another leader male's two females disappeared from Band 1, presumably taken over by a male from another band, while he stayed in Band 1 and became a follower male. One adult female left Band 1 and was later observed in Band 3, and five other females were presumed to have emigrated into Band 3 as they were last seen when the two bands were both on the Filoha cliff.

The number of both gains and losses of individuals in Band 1 at Filoha from March 2005 through February 2006 was far greater than that reported for other Ethiopian hamadryas populations. Band 1 at Erer Gota gained 23 individuals between May 1971 and February 1974. This included 20 births and three immigrations. Conversely, they

lost 17 individuals over this time period, but it is unclear how many of these disappearances were due to death or emigration, respectively (Abegglen, 1984). Band 1 at Filoha, by contrast, gained 45 individuals and lost 21 individuals in a third of the time. As the number of known and presumed immigrations and emigrations at Filoha were equal at 13, the increase in band size at Filoha appeared to be primarily a result of the high birth rate and high infant survival rate in this population.

6.3.3 Band Fissions

Band 1 separated for periods of three hours up to 31 days at a time from March 2005 through February 2006. The general circumstances surrounding the band fissions will be described here. The OMU membership of subgroups, and whether they constitute clans, will be discussed in section 6.5.4.

The first such temporary fission occurred for six consecutive days from 19 March to 25 March 2005. On 19 March, Band 1 started the day on the Wasaro cliff with Band 2. About half of the band (11 OMUs) traveled west from the Wasaro cliff with Band 2, while the other half (9 OMUs) traveled east back to the Filoha cliff. The 9-OMU subgroup was followed and observed over the next four days, while the whereabouts of the 11-OMU subgroup was unknown. On the afternoon of 25 March the entire band reunited and slept on the Filoha cliff.

The second band fission occurred at the beginning of the dry season in September and October 2005. Band 1 was followed all day on 5 September, and then could not be located over the following ten days. On the night of 16 September about half of the band (11 OMUs) slept on the Filoha cliff, and was followed several days that week. All members of Band 1 then disappeared again until the morning of 6 October, when the

other half of Band 1 (9 OMUs) was located at the Wasaro cliff sleeping site. This subgroup was followed and observed through 17 October, and that night the entire band reunited and slept on the Filoha cliff. Two OMUs were not seen at all during this month-long fission, but returned to Band 1 several days after the band reassembled. In addition to these extended fissions, Band 1 separated for a minimum of three hours during daily travel on at least nine days: 17 June, 23 June, 29 November, 30 November, 1 December, 4 December, 13 December, 16 December, and 25 December.

Despite the apparent abundance of food resources at Filoha (i.e., the presence of doum palms) compared to other areas inhabited by hamadryas baboons, periods of relative food scarcity may underlie band fissions. Palm fruit comprised over 20% of Band 1's monthly feeding records during seven months, but it constituted less than 5% of feeding records in both September and October when ripe fruit was not available throughout the baboons' home range (Chapter 4). These months correspond to the band's longest fission. It is possible, therefore, that the band separated into independent subgroups during this period of low palm fruit availability to ensure feeding success for all members of the band. Furthermore, all nine days that the baboons separated for at least three hours during daily travel occurred during the dry season when fresh *Acacia senegal* flowers, leaves, and pods were scarce. Band fissions, therefore, seem to provide an extra level of flexibility during periods of relative resource scarcity.

6.4 The One-Male Unit

6.4.1 OMU Composition

Each of the OMUs in Band 1 consisted of a leader male, one to eight adult and/or adolescent females, their dependent offspring, and occasionally one or more follower

males. All adult and adolescent females were members of an OMU, while only 47% of adult and subadult males were leader males. About a third of the OMUs over the course of the study period (38%) had follower males. The rest of the adult and subadult males were not affiliated with a particular OMU and instead interacted mostly with other unaffiliated males and juveniles in the band.

From March 2005 through February 2006, a total of 32 adult and subadult males were leaders of an OMU. Table 2.3 shows the OMU composition of Band 1 over this time period. Females that belonged to different OMUs at different points in the study period are listed as members of each OMU to which they belonged. The number of juveniles listed in each OMU is approximate as it was difficult to both obtain accurate counts due to their small size and be certain of which OMU they belonged to.

Furthermore, it was sometimes difficult to ascertain whether OMUs had follower males, and if they consistently affiliated with the same OMU over the course of the study period. Eight of the 32 males were no longer leader males by the end of the study period. Four of them disappeared from Band 1. MORRIS and FRUIT were both presumed to have died, while POPE's and OMO's OMUs presumably emigrated into another band. The other four leader males – ASHEBER, MERCURY, JACK, and NELSON – lost their females and remained in Band 1 as unaffiliated males.

The number of OMUs at any one point during the study period ranged from 20 to 24. At the end of the study period the average number of females per unit was 2.8, with a range of 1 to 8. Figure 6.1 shows a frequency distribution of the number of females per OMU in February 2006. When all OMUs that existed at any point over the study period were included, and with leader males counting as separate OMUs when they had different

numbers of females at different points in time, the average number of females per OMU was still 2.8.

6.4.2 Changes in OMU Composition

During the study period, membership in OMUs at Filoha was consistent in 19 of the 32 (59%) OMUs. The number of females in the remaining 13 OMUs varied over time. In six of these 13 OMUs, at least two females remained constant throughout the study period, while one or more females transferred to new OMUs (once or more). The transfer of females among OMUs occurred as it typically does in hamadryas baboons, i.e., via aggressive takeovers by males characterized by frequent neckbiting and herding of new females (Kummer 1968a; Swedell and Schreier, in press).

During the study period, at least 17 females were transferred into new OMUs in Band 1. Two leader males, PEACH and TEDDY, each took over a female from another leader male in Band 1. In addition, two leader males, LEN and PEACH, gained three and one females respectively when their previous leader males disappeared from Band 1. Eight leader males – YIRDAW, PARK, FORD, EVANGADI, NELSON, SAMI, TITI, and TEDDY – all of whom except SAMI already had at least one female, gained at least one additional female from another band.

Conversely, at least ten females were lost by Band 1 leader males during the study period. Two leader males, FRUIT and MERCURY, lost a female to another male in Band 1, while at least five other leader males – Jack, Evangadi, Nelson, Park, and Mac – lost at least one female to males from other bands.

The majority of transfers at Filoha during the study period thus occurred among rather than within bands. In most of these cases, either new females were observed in

Band 1 OMUs or previous females from Band 1 were noticed to be absent, and such observations took place after nights in which Band 1 shared a sleeping cliff with another band, most commonly Band 3.

OMU composition in Band 1 was less consistent over time than reported previously for other Ethiopian hamadryas populations. Overall, there were at least 25 transfers of females at Filoha from March 2005 through February 2006, a rate of 0.07 transfers/OMU/month. By contrast, over two years between November 1996 and September 1998, there were at least 10 takeovers in Band 1 at Filoha (0.01 transfers/OMU/month) (Swedell, 2006). However, it should be noted that in Swedell's (2006) earlier study, Band 1 was not nearly as well habituated as it was in 2005 and not all of the individuals in Band 1 were known; thus many transfers among OMUs, clans, and bands may have been overlooked. At Erer Gota, where all individuals in a band were known over 5.5 years, there were 18 transfers of females over this period (0.01 transfers/OMU/month) (Sigg et al., 1982). Comparable data for Arabian and Eritrean hamadryas populations are not available, as there are no bands in these areas in which individual identities have been known over time.

6.4.3 Takeovers and Transfers

As mentioned above, I observed two takeovers within Band 1. (In the following descriptions, the names of leader males are written in capital letters and the names of females are in italics.) The first involved PEACH, a follower male, taking over the female *Papaya* from the leader male FRUIT. Before the takeover, FRUIT had two females – *Mango* and *Papaya* – and PEACH was his follower male. *Mango* had a

yearling, and *Papaya* had a black infant who was estimated to be about four months old at the time of the takeover. FRUIT appeared to be old, with wrinkles and sagging skin.

FRUIT was last seen with both *Mango* and *Papaya* on the afternoon of 25 May 2005. On the morning of 28 May, the next observation day of Band 1, FRUIT and *Mango* were observed resting 1 m apart while 10 meters away from them, *Papaya* was resting within 1 m from PEACH. PEACH had a fresh wound on his face, suggesting that the takeover included a fight. Throughout the day, FRUIT and PEACH (with their females) were consistently observed about 10 m apart from one another. On several occasions PEACH was observed herding *Papaya* when she strayed more than 3 m from him. PEACH was *Papaya*'s leader male for the rest of the study period. On 18 June *Papaya* had a small sexual swelling, and she and PEACH were observed copulating several times over the following two weeks while she was swollen. By the middle of January 2006 *Papaya* appeared to be pregnant.

PEACH and FRUIT continued to associate spatially over the following 3.5 months when they each had one female: they were each other's nearest-neighbor leader male in 13 of 29 scans, or 45% of the time for which such data exist. *Mango* belonged to FRUIT's OMU through 5 September, when FRUIT was last seen. On the next observation day – 17 September – *Mango* was observed with PEACH and *Papaya*, though I did not witness any of the aggressive behavior typical of hamadryas takeovers (Swedell and Schreier, in press). *Mango* remained in PEACH's OMU for the rest of the study period. For *Mango*, joining PEACH's OMU thus appeared to be related to her previous relationships with both *Mango* and PEACH from when they all belonged to FRUIT's OMU. *Mango* was observed with a sexual swelling for the first time during the

study period on 19 October, and she was seen copulating with PEACH over the following several days. She did not, however, become pregnant before the end of the study period.

The second takeover that I observed occurred in June 2005, when the leader male TEDDY took over the female *Daisy* from the leader male MERCURY. Before the takeover, TEDDY had one female, *Patch*; MERCURY also had one female, *Daisy*, and an infant that was born on 13 March 2005. A follower male was associated with MERCURY's OMU but not TEDDY's.

On the morning of 18 June, MERCURY and *Daisy* were traveling together through swamp vegetation. TEDDY followed them, and MERCURY bit *Daisy* on her lower back, and looked back at TEDDY. At mid-day, TEDDY, *Patch*, MERCURY, and *Daisy* were all eating palm fruit on the ground in a palm patch; TEDDY and MERCURY were about 3 m away from one another. TEDDY approached MERCURY, who moved away while embracing and covering *Daisy*. TEDDY continued to approach MERCURY, who pushed *Daisy* into palm fronds. TEDDY followed them and a fight between TEDDY and MERCURY ensued, including screaming, chasing, and biting each other's faces. MERCURY then ran out of the palm fronds screaming, without *Daisy*. After several minutes, *Daisy* came out of the palm fronds and began to groom TEDDY, who was being groomed by *Patch* simultaneously. Over the next hour and a half, TEDDY and *Daisy* groomed one another while MERCURY sat several meters away. During this time, MERCURY attempted to 'kidnap' *Daisy's* infant several times.

Over the following five days, TEDDY, *Daisy*, and *Patch* rested, groomed, and traveled together. MERCURY was consistently observed within 10 m of them, and was seen grabbing the infant several times. Thereafter, and through July, MERCURY was

not seen within 15 m of TEDDY's OMU, of which both *Daisy* and *Patch* were clear members.

Patch was last seen on 31 July. On the morning of 6 August, the next observation day of Band 1, MERCURY and *Daisy* were observed grooming each other on the bottom of the Wasaro cliff, while TEDDY sat alone about 20 m away. Throughout the day, MERCURY and *Daisy* were never observed further than a few meters apart, while TEDDY maintained a distance of 10 to 20 m from them. None of them had any visible scratches or wounds. *Daisy*, and her infant, stayed with MERCURY through 14 August, during which time TEDDY was not consistently observed within 15 m from them.

On the morning of 15 August, TEDDY and *Daisy* were observed grooming on the bottom of the Wasaro cliff, while MERCURY rested several meters away. Through 21 August, TEDDY and *Daisy* were observed together, with MERCURY consistently about 20 m away from them. On 5 September, after a two-week gap in observations, *Daisy* and her infant were still with TEDDY. MERCURY was not observed within a 10 m radius of TEDDY and *Daisy* for the rest of the study period, during which time he remained in Band 1 as an unaffiliated male. *Daisy* did not resume reproductive cycling during the study period.

It is unclear what prompted MERCURY's briefly taking *Daisy* back from TEDDY in August. It is possible that *Patch*, TEDDY's first female, was taken over by a male from another band, at which point MERCURY may have taken advantage of TEDDY's vulnerability and taken over *Daisy*. Alternatively, it is possible that TEDDY sustained an injury or illness that led to his losing both of his females at that time.

The third transfer of females observed during the study period did not involve an aggressive takeover but rather the incorporation of three females into a new OMU after

the disappearance of a leader male. Before his disappearance, MORRIS had three females – *Maxine*, *Mary*, and *Maggie*. *Maxine* had a yearling, and *Maggie* was pregnant. LEN had one adolescent female, *Lila*. MORRIS was last seen on 23 May 2005 with all three of his females. As all of his females remained in Band 1, and MORRIS appeared healthy leading up to his disappearance, it was presumed that he died from a sudden injury, perhaps a snake bite.

On 25 May, *Maxine* was observed traveling with LEN's OMU. She was consistently observed within 1 m from *Lila*, but never closer than 8 m from LEN. Over the next several days, *Maxine* continued to both spatially and socially associate with *Lila*, and by June 1, both *Maggie* and *Mary* were consistently observed within a 10 m radius of them. Interestingly, LEN was never observed engaging in the typical herding or neck-biting behavior that generally characterizes hamadryas takeovers (Swedell and Schreier, in press). *Maxine*, *Mary*, and *Maggie*'s entry into LEN's OMU appeared to be based on *Maxine*'s previous relationship with *Lila*, and in turn, *Mary*'s and *Maggie*'s previous relationship with *Maxine*.

Mary had a small sexual swelling when she entered LEN's OMU and she continued her regular reproductive cycle until she became pregnant in the middle of December. *Maggie* was pregnant when she entered LEN's OMU, and her infant was born on 30 September. The infant remained with her in LEN's OMU for the rest of the study period, during which time *Maggie* did not resume ovarian cycling. *Maxine* did not resume cycling until February 2006.

I also observed two takeovers that occurred across bands. Until 17 March 2005 the female *Hasna* belonged to ASHEBER's OMU; she had an infant that was born in October 2004. By 22 March *Hasna* was no longer with ASHEBER, and was observed in

Band 3. On 21 June, *Hasna* and her infant were seen back in Band 1 with a new leader male, SAMI. They remained in SAMI's OMU for the rest of the study period. *Hasna* resumed reproductive cycling on 21 December.

Additionally, the leader male PARK took over the female *Candy* from Band 3 on 20 April 2005 when she was pregnant. Her infant was born on 28 May. On 21 June, PARK was observed trying to grab the infant from *Candy*, who screamed and tightly held on to the infant. On the morning of 22 June, PARK was observed squeezing the infant and hitting it against a rock, while *Candy* screamed. The infant was last seen alive at 1030. At 1355 *Candy* was observed carrying the dead infant, which presumably PARK killed. She continued to carry, and then drag, the infant for the following two days. On 5 July, 38 days after the birth of her infant and 13 days after its death, *Candy* had a small sexual swelling. *Candy* and PARK were first observed copulating in mid-July. By the end of January 2006 she was pregnant.

Of the five infants involved in the above takeovers and transfers, only *Candy's* died, presumably a victim of infanticide. The other four remained unharmed in their new OMUs through the remainder of the study period. TEDDY was observed carrying *Daisy's* infant several times, whereas PEACH, SAMI, and LEN were not observed specifically interacting with the infants. This pattern contrasts with that reported by Swedell (2006) and Swedell and Tesfaye (2003), who described several takeovers that occurred in Band 1 between 1996 and 2002. During this time period, all four infants involved in the takeovers died or disappeared shortly afterwards.

Takeovers may influence female reproductive cycles. *Candy* came into estrus just 38 days after her infant was born, a much shorter time period than the typical 9-16 month lactational amenorrhea described in wild hamadryas baboons (Sigg et al., 1982; Swedell,

2006). Her interbirth interval, then, likely decreased by at least eight months as a result of her takeover and the resulting death of her infant. Additionally, *Papaya* had a small swelling only 21 days after she was taken over by PEACH, even though her infant was just five months old at the time and remained alive for the rest of the study period. Her interbirth interval, therefore, appeared to decrease by at least four months as a result of her takeover, despite the fact that her infant did not die. Takeovers did not seem to affect the reproductive cycles of the other three females with infants. *Daisy* did not resume cycling during the study period, and *Hasna* resumed cycling six months after her takeover, which occurred 14 months after her infant's birth. *Daisy's* and *Hasna's* takeovers, therefore, did not appear to have an effect on the length of lactational amenorrhea. After the birth of her infant, *Maggie* did not resume cycling for the rest of the study period; as this was only a period of five months, however, it is unclear if her interbirth interval was affected by her takeover.

Whereas takeovers had an effect on the reproductive condition of only two of the five females described above, in other studies takeovers had a more consistent effect on female reproduction. In the takeovers described in Band 1 at Filoha in previous studies, all five females for which data are reported came into estrus within several weeks of their takeover (Swedell, 2006; Swedell & Tesfaye, 2003). Furthermore, four females from the Erer Gota hamadryas population came into estrus much sooner after their takeovers than would be expected based on the typical period of lactational amenorrhea (Sigg et al., 1982).

6.4.4 Social Interaction Within OMUs

Almost all social interaction in hamadryas society occurs among individuals belonging to the same OMU, and among juvenile and unaffiliated males (Kummer, 1968; Swedell, 2006). Within OMUs, social interaction occurs most commonly between leader males and their females, among females, and between females and their offspring, and grooming is the most prevalent social interaction in each of these combinations of individuals. Leader males also behave aggressively toward their females, herding and neck-biting them when they stray too far away (Kummer 1968a; Swedell and Schreier, in press). Interactions among leader males and other males consist of aggressive behavior such as threats and fights, as well as notifying behavior in which a male approaches another male, presents to him, and then quickly moves away (Kummer, 1968a; Abegglen, 1984).

Grooming interactions were quantified for leader males and their females from the 31 OMUs for which I had at least 10 scan samples separated by 10 minutes. Table 2.4 shows the OMUs included in these analyses. When the size and composition of an OMU varied over the study period, they were considered separate OMUs. For example, if a leader male had three females but then gained a fourth, data from the period of time in which he had three females were considered separately from when he led a four-female OMU. Thus, the 31 OMUs in the analyses represent just 24 different leader males. Five males – Peach, Shato, Yirdaw, Mac, and Len – had two OMUs each; one male – Teddy – had three OMUs, two with one female, and one with two females. The distinction between a leader male's different OMUs is indicated by the number following his name, which represents the number of females in the OMU. Teddy's two one-female OMUs

are distinguished as Teddy1a for when Patch was his only female and Teddy1b for when Daisy was his only female.

Table 6.1 displays the percentage of overall grooming scans that each individual leader male spent grooming or being groomed by his female(s), as well as with males from different age classes. The results from each leader male were combined to produce an overall average of the grooming interactions of Band 1 leader males, as well as for leader males from each OMU size (Table 6.2). Leader males spent 91% of their overall grooming scans grooming with the females in their OMU; they were never observed grooming with females that did not belong to their OMU. On average, males were groomed by their females twice as frequently (59%) as their females were groomed by them (31%). The number of females in a unit was positively correlated with the percentage of scans a leader male spent grooming with (both grooming and being groomed by) his females ($r_s=0.496$, $p=0.005$, $N=31$). Furthermore, the percentage of scans that leader males were groomed by their females was positively correlated with OMU size ($r_s=0.418$, $p=0.019$, $N=31$); the opposite pattern emerged for the percentage of scans that leader males groomed their females, but this relationship was not significant.

Overall, leader males spent just 8% of their overall grooming scans grooming with other males: 2% grooming other males and 6% being groomed by other males. Leader males with fewer females in their unit groomed more with other males than did leader males with more females ($r_s = -0.464$, $p=0.009$, $N=31$).

Table 6.3 shows the percentage of overall grooming scans that adult and adolescent females spent grooming with 1) other adult and adolescent females, 2) their leader males, and 3) their offspring. The identity of each female within an OMU was not always recorded during grooming interactions, and for OMUs with more than one female

I randomly selected one female from each scan. These results, therefore, represent a sample of each OMU's females as opposed to each individual female. As with the leader males, the percentage of grooming interactions of females from each OMU were tabulated to obtain averages for each OMU size, as well as an average for Band 1 females as a whole (Table 6.4). Overall, adult and adolescent females spent 19% of their grooming scans grooming with other females; on average, they spent almost as much time being groomed by other females (8%) as they did grooming them (11%). The number of females in a unit was positively correlated with the likelihood of grooming with other adult and adolescent females ($r_s=0.703$, $p=0.000$, $N=31$). On several occasions females groomed with adult and adolescent females across OMU boundaries; these interactions are described in section 6.5.5 below.

Adult and adolescent females spent, on average, half (48%) of their overall grooming scans grooming with their leader males. They groomed their leader males almost twice as frequently (30%) as they were groomed by them (18%). The more females in an OMU, the less likely a female was to groom her leader male ($r_s=-0.607$, $p=0.000$, $N=31$) and be groomed by him ($r_s=-0.582$, $p=0.001$, $N=31$). Females were never observed grooming with leader males other than their own. Overall, adult and adolescent females spent just 1% of their grooming scans grooming with subadult males, 0.5% with unaffiliated males, and 2% with follower males.

Females spent almost one-third of their overall grooming scans (28%) grooming with juveniles and infants. They groomed their juveniles four times as much (22%) as they were groomed by them (6%). Females from larger OMUs tended to groom with juveniles more than females from smaller units did, but this relationship was not significant.

These results confirm that the majority of social interaction in hamadryas society occurs within OMUs. Leader males spend most of their social time grooming with their females, while adult and adolescent females split their grooming time between other females, their leader males, and their offspring.

Aggressive interactions between leader males and their females were observed 27 times over the study period, during both focal samples of OMUs and on an *ad libitum* basis. These behaviors were not recorded consistently outside of focal samples, and qualitative observations suggest that they were more common than these results indicate. Half of these aggressive interactions (N=14) consisted of males biting females on their necks or lower backs. Most of these instances (N=11) occurred on the day of or the days just following takeovers. Males were also observed grabbing their females (N=4), pushing or hitting females (N=4), chasing females (N=3), growling at females (N=1), and holding females in a possession grip (N=1). Overall, two-thirds of these aggressive behaviors (N=18) occurred on the day of or the days just after takeovers (Swedell and Schreier, in press).

Aggression among males consists of threats (i.e., threat-yawns, lunges) and fights. Quantitative data on male-male aggression were not collected, but qualitative observations suggest that it was fairly common. Although some fights included many males and lasted up to 30 minutes, the majority of aggressive interactions lasted for just a minute or two, and occurred between only two males. While some aggression did take place between leader males, the majority of male-male aggression occurred between leader males and non-leader males (i.e., juvenile, subadult, unaffiliated, and follower males), as well as among only non-leader males. The majority of these aggressive interactions appeared to occur over access to females. Data are not available to examine

whether leader males exhibited aggressive behavior more or less frequently with other males from their OMU than with males not belonging to their OMU.

6.4.5 A Solitary Female

Consistent with previous observations of wild hamadryas baboons, all adult and adolescent females in Band 1 at Filoha were members of an OMU. One female, however, was essentially solitary for the last month before she disappeared. *Natalie* was NELSON's only female from the beginning of the study period through 27 October 2005, at which point she began to appear sick with a protruding belly and patches of translucent skin. On 28 October, *Natalie* was no longer with NELSON; she was seen grooming *Sue* (TITI's OMU), but she did not interact with TITI and was not seen with his OMU again that day. *Natalie* continued to travel alone through 21 November. During this time period, several unaffiliated males were observed chasing and/or neck-biting her. *Natalie* was never seen with any male, however, for longer than 10 minutes. She was also seen grooming *Sue* twice more; during one of these grooming bouts TITI chased her away. At this point she was extremely thin, was missing patches of hair, and had scabs on her back. *Natalie* was last seen on 22 November; due to her physical condition, it was presumed that she died.

A female hamadryas baboon has not previously been reported to travel as a solitary female. It is unclear what caused the end of *Natalie*'s association with NELSON, as no aggression was observed between them, and she was not taken over by another male. Several males appeared to try to take her over during the month that she was alone but, interestingly, it seemed that the males did not want her, walking away from her or even chasing her away. Furthermore, *Natalie* did not seem interested in belonging to an

OMU, with the possible exception of TITI's. Her association with TITI's OMU, however, seemed to be based on a previous relationship with *Sue* rather than any motivation to interact socially or sexually with TITI.

In sum, Band 1 at Filoha during this study was composed of many one-male units, consistent with all other hamadryas populations to date. OMU composition was, however, less consistent over time than in previous studies of this and another nearby Ethiopian population (Kummer, 1968; Abegglen, 1984; Sigg et al., 1982; Swedell, 2006). Several takeovers and transfers of females occurred over the study period; they appeared to have had less of an effect, however, on infant survival and female reproduction than those described previously (Swedell, 2006; Swedell & Tesfaye, 2003; Sigg et al., 1982). Finally, Band 1 at Filoha had the unique presence of a solitary adult female for a month-long period before she died.

6.5 The Clan

As described previously, Abegglen (1984) documented a fourth level of social structure in hamadryas society, which he called "clans." He noticed that groups of three to four OMUs rested near one another on the sleeping cliff, traveled together during their daily foraging route, and occasionally traveled as subgroups independently from the rest of the band. Based on physical resemblance among males, Abegglen suggested that these associations of OMUs and unaffiliated males consisted of male relatives.

While a clan structure has been described for two bands at Erer Gota (Abegglen, 1984; Kummer, 1995; Sigg & Stolba, 1981; Sigg et al., 1982), it has not been identified in any other population to date (Saudi Arabia: Biquand et al., 1992; Kummer et al., 1985; Mori et al., 2007; Eritrea: Zinner et al., 2001b). Clans have been described for captive

hamadryas baboons in the Madrid Zoo colony (Colmenares, 1992, 2004; Colmenares et al., 2006), though it should be noted that this population includes hybrids (*P. h. hamadryas* x *P. h. cynocephalus*). While Abegglen's supposition that clans consisted of related males was never tested with genetic evidence in the Erer Gota population, clans in the captive Madrid colony have been shown to consist only of related males, most commonly fathers and sons and full or maternal brothers (Colmenares, 1992; Colmenares et al., 2006). Males in different clans were more likely to be unrelated; when they were related, they tended to be paternal brothers (Colmenares, 1992).

6.5.1 Methods Used to Establish Clans

The spatial arrangement of animals reflects their social organization (Kummer, 1968a; Whitehead, 1997), and thus spatial data can be used to represent patterns of interactions among members of a social group (Whitehead & Dufault, 1999). Observations of associations of individuals in space have been used to quantify social structure across a wide range of primate taxa (pygmy chimpanzees, *Pan paniscus*: White & Burgman, 1990; proboscis monkeys, *Nasalis larvatus*: Yeager, 1990; spider monkeys, *Ateles belzebuth belzebuth*: Shimooka, 2003; howler monkeys, *Alouatta palliata*: Dias & Luna, 2006; Lemur spp., *Lemur catta*, *Eulemur fulvus*, *E. coronatus*: Kappeler, 1993), including baboons (chacma baboons, *P. h. ursinus*: Byrne et al., 1989; hamadryas baboons, *P. h. hamadryas*: Colmenares et al., 2006; Mori et al., 2007).

For each leader male, I calculated the number of times that each other leader male was within a 10 m radius of him, and the samples in which male A was within 10 m of male B were pooled with the samples in which male B was within 10 m of male A. In an effort to measure associations and relationships that were consistent over time, these

analyses are based only on the 22 males that were leader males for at least eight consecutive months (Table 6.5). The dataset includes scans during which the baboons rested and groomed on sleeping cliffs and foraged during daily travel (N=1942).

Association indices were then computed for each dyad of leader males via the half-weight index (Cairns & Schwager, 1987), which accounts for differences in observations between individuals: $I_{AB} = \#AB / A + B$. I_{AB} is the dyadic association index for dyad AB; #AB is the number of scans in which A and B were within a 10 m radius of one another; A is the total number of scans for A; and B is the total number of scans for B. Association data were analyzed by hierarchical cluster analysis, using the complete-linkage method and Euclidean distances (e.g., De Gheff, 1978; Morgan et al., 1976; Whitehead and Dufault, 1999).

Because cluster analysis is a descriptive method, the number of true clusters in a dataset is often unclear (Dudoit and Fridlyand, 2002; Tibshirani et al., 2001). I used the gap statistic, therefore, to validate the number of clusters in the data (Tibshirani et al., 2001). The gap statistic uses the output from any clustering algorithm, and compares the change in within-cluster dispersion (W_k) to that expected under a null distribution. The optimal number of clusters, then, is the value of k for which $\log(W_k)$ falls farthest below the reference curve. The gap test was performed using Mathematica 6 software (Wolfram Research, Inc., Champaign, IL).

6.5.2 *Clan Composition*

The resulting dendrogram of the cluster analysis indicates a clear pattern of spatial organization among OMUs, as reflected by association among leader males. The dendrogram displays two main subgroups of 13 and nine OMUs, respectively (Figure

6.2). As groups of OMUs that associate more frequently with certain other OMUs, these subgroups represent clans (cf. Abeggelen, 1984). Therefore, the subset of 13 OMUs on the left side of the dendrogram was termed Clan A and included the following leader males: CLODIO, CORY, DJ, EVANGADI, FORD, MAC, MIKE, NELSON, PARK, PEACH, TEDDY, TITI and TRIPP. Three subsets with two, five, and six OMUs existed within Clan A. The subgroup of nine males on the right side of the dendrogram was termed Clan B and included the following males: ANDY, HERB, KALID, LEN, PETE, REDFACE, SAMI, SHATO, and YIRDAW. Like Clan A, three smaller subsets of OMUs also existed within Clan B, with three OMUs each. The results of the gap test verified the existence of two clusters with 13 and nine OMUs each (Figure 6.2). When association indices from when the baboons rested and groomed were analyzed separately from when they traveled and fed, the same two large subgroups described above emerged for both conditions but the smaller subgroups within them were not consistent.

In general, physical similarities among the males at Filoha were not obvious. Fecal samples have been collected from many of the males so future genetic analyses should reveal whether clan members are related.

6.5.3 Clans and Band Fissions

All of the band fissions described in section 6.3.3 occurred along clan lines. During the six-day fission in March, Band 1 was composed of 20 OMUs: of these, 17 were led by males included in the subset of 22 in the cluster analyses described above, and three of them were headed by males who were no longer leader males by June and thus were not included in the analyses. (The additional five OMUs included in the cluster analyses had not yet been identified in March). The OMU composition of subgroups

during the March fission corresponded to that of Clan A and Clan B. Of the 17 males who were leader males throughout the study period, only MIKE's OMU traveled with the opposite clan during the March fission.

During the month-long split in September and October, Clan A was the subset of OMUs observed between 16 and 23 September, and Clan B was the subgroup observed between 6 October and 17 October. Neither FORD's nor TITI's OMUs were seen between 16 September and 17 October, but they were both observed in Band 1 several days after the band reassembled. Furthermore, each time the band fissioned for at least three hours during daily travel, they did so along clan lines. TITI's and FORD's OMUs traveled as part of Clan A on each of these nine days, corresponding with their clan membership indicated by the cluster analysis.

6.5.4 Takeovers and Clan Membership

Behavioral evidence suggests that takeovers are more likely to occur between males belonging to the same clan. PEACH and FRUIT appeared to belong to the same clan both before and after PEACH's takeover over of *Papaya*. (FRUIT was not included in the cluster analyses as data exist for only five months when he was a leader male). Before the takeover, PEACH was FRUIT's follower male (and thus by definition in the same clan). As described in section 6.4.3, PEACH and FRUIT continued to associate spatially over the following 3.5 months when they each had one female. *Ad libitum* observations of FRUIT at sleeping sites also suggest that his OMU belonged to Clan A when he was a leader male.

Evidence also suggests that TEDDY and MERCURY belonged to the same clan both before and after TEDDY took over *Daisy*. TEDDY and MERCURY were within a

10 m radius as nearest-neighbor leader males at least three times during focal-OMU samples over the two days prior to the takeover. For a week following the takeover MERCURY was consistently observed within 10 to 15 m of TEDDY's OMU. During the March fission, MERCURY's OMU traveled with Clan A, and TEDDY was not yet a leader male. In the cluster analyses and all later fissions TEDDY's OMU belonged to Clan A. Similarly, during all band fissions after the takeover, MERCURY remained in Clan A as an unaffiliated male.

MORRIS and LEN also belonged to the same clan. MORRIS' OMU traveled with Clan B during the March fission, when LEN was not yet a leader male. In the cluster analysis and all later band fissions, LEN and his females also belonged to Clan B.

Although SAMI did not take over *Hasna* directly from ASHEBER (she spent three months in Band 3 before returning to Band 1), it is interesting to note clan membership surrounding her transfers. During the March fission ASHEBER traveled with Clan B and SAMI was not yet a leader male. In the cluster analyses and all other band fissions SAMI (with *Hasna*) belonged to Clan B. ASHEBER remained in Clan B as an unaffiliated male for the rest of the study period.

6.5.5 Extra-OMU Interactions and Clan Membership

While the vast majority of social interaction occurred among members of the same OMU, extra-OMU interactions were observed on several occasions during both focal samples of OMUs and on an *ad libitum* basis. The primary grooming partners of leader males were females in their own OMUs, and no leader male was ever observed grooming with a member of another OMU (either another leader male or his females) (section 6.4.4). Leader males did occasionally groom with other males (unaffiliated and

follower males), but this occurred in less than 5% of the total number of scans in which they were observed grooming (N=1839). As the identities of non-leader males were not known, whether these male grooming partners were members of the same clan cannot be addressed.

Adult and subadult females were observed interacting across OMU boundaries 17 times over the study period. These interactions consisted of grooming and infant inspecting. *Marta* (KALID's OMU) groomed with *Tulip* (REDFACE's OMU) on three different occasions, and once with *Monica* (SHATO's OMU). *Mabel* (YIRDAW's OMU) and *Iris* (HERB's OMU) were grooming partners on at least seven different dates, with grooming bouts lasting up to 15 minutes. *Natalie* (NELSON's OMU) and *Sue* (TITI's OMU) groomed each other at least four times. *Elsie* (PARK's OMU) and *Daisy* (TEDDY's OMU) groomed each other once, as did *Lizzy* (PETE's OMU) and *Rose* (HERB's OMU). *Betty* (PARK's OMU) played with *Clea's* (CLODIO'S OMU) infant once, as did *Fugee* (DJ's OMU). All of these interactions occurred between females (and infants) belonging to the same clan.

6.5.6 Comparisons with Other *Hamadryas* Populations

Results indicate that Band 1 at Filoha is divided into two distinct units based on spatial associations among males and social interaction among females. Following previous descriptions of hamadryas social organization at Erer Gota (Sigg et al., 1981; Abegglen, 1984), I interpret these two groupings to be clans. As in the clans described for the Erer Gota population, OMUs within each clan at Filoha rested near one another on sleeping cliffs, foraged together during daily travel, and sometimes traveled independently from the rest of the band.

The sizes of the clans, however, differed from those described elsewhere. Band I at Erer Gota consisted of three clans, with two, three, and four OMUs respectively (Abegglen, 1984), and clans in the captive Madrid colony also consist of between two and four OMUs (Colmenares, 1992; Colmenares et al., 2006). Band 1 at Filoha, by contrast, was composed of two large clans with 13 and 9 OMUs, respectively. As two large clans existed in 2005-2006, as well as in 1997-1998, large clan size appears to be a characteristic of the Filoha population (Schreier and Swedell, in review).

The large clan size at Filoha may be a function of band size. As described above, the band sizes in the Filoha population are larger than those described for other hamadryas populations (Erer Gota, Ethiopia: Kummer, 1968a; Sigg and Stolba, 1981; Abegglen, 1984; Awash River, Ethiopia: Nagel, 1973; Saudi Arabia: Kummer et al., 1981; Biquand et al., 1992; Yemen: Al-Safadi, 1994), and this is likely related to the high abundance and consumption of doum palm fruit at Filoha (Swedell, 2002b, 2006; Swedell et al., 2008). It is possible, therefore, that the distribution of palm trees allows the baboons to forage as clans rather than OMUs, and this will be explored in Chapter 7. The clan sizes at Filoha may simply be the largest size that the band can split into and still obtain enough food during periods of palm scarcity (see below).

6.5.7 Functions of Clans

Previous research has suggested two possible, and potentially overlapping, functions of the clan layer of the hamadryas social system. The first possibility is that clans simply provide an additional cleavage point for band subdivision during daily travel, thereby enabling greater foraging flexibility and increasing access to widely dispersed and limited food resources. The second possibility is that the clan structure

strengthens male-male relationships within clans, which may enable males to better cooperate over access to and control of females (Abegglen, 1984; Kummer, 1995).

Results support both of these hypotheses.

First, the multilevel social structure of hamadryas baboons has been attributed to the sparse distribution of resources in their habitats: coming together as troops at sleeping sites provides necessary protection from predators, while separating into OMUs during the day enables the baboons to find sufficient food (Kummer, 1968a, 1971, 1995).

Despite the apparent abundance of food resources at Filoha compared to other areas inhabited by hamadryas baboons, periods of relative food scarcity may underlie band fissions into clans for extended periods. As discussed in Chapter 4, palm fruit's contribution to the baboons' monthly feeding records corresponded to its seasonal availability; palm fruit comprised over 20% of the monthly feeding records during seven months, but it constituted less than 5% of feeding records in both September and October when ripe palm fruit was not available throughout the baboons' home range. It is possible, therefore, that Clan A and Clan B functioned as independent subgroups during this period of low palm fruit availability because resource abundance was not high enough for the baboons to forage as a cohesive band. Further, a peak in birth rate occurred during this period. Of 32 births over the study period, nine occurred between 30 September and 10 October. Traveling as independent clans may have enabled females to obtain sufficient nutrition during the critical first days of an infant's life. Lastly, all nine days that the baboons separated along clan lines for at least three hours during daily travel occurred during the dry season when fresh *A. senegal* flowers, leaves, and seeds were scarce. The ability to fission into clans, therefore, seems to provide an extra level of flexibility during periods of resource scarcity.

The presence of doum palms in the Filoha region appears to allow larger band sizes than elsewhere due to greater food abundance. The consequence of this, however, is that during periods of low abundance of palms, bands must split into clans for longer periods of time in order to obtain enough food. During these periods, *clans* at Filoha may fill the ecological role of *bands* in other areas of hamadryas range where doum palms are not present. The clan sizes at Filoha (Clan A = ~100 baboons, Clan B = ~84 baboons) are comparable to the band sizes of 62 to 95 individuals at Erer Gota (Sigg and Stolba, 1981; Abegglen, 1984). Clan A and Clan B at Filoha spent periods of several hours to several weeks apart and slept at different sleeping sites on at least 38 nights during the 2005-2006 study period. Band I at Erer Gota, by contrast, spent only one night over 18 months split into separate clans at different sleeping sites. Clans at Erer Gota thus appear to be mainly social units rather than foraging units. This lends support to the idea that clan size is determined by band size and social relationships, whereas band size is determined by local ecology.

Second, male-male relationships that develop among clan members may enable a degree of cooperation over access to females that enhances each male's fitness (Abegglen, 1984; Colmenares, 2004; Kummer, 1995). Abegglen (1984) suggested that clans consisted of related males and reported that social interaction among males occurred more frequently among males in the same clan than among males without this association. Colmenares (1992) reported that clans in the captive Madrid colony consisted only of related males and the strongest associations occurred between fathers and sons, as well as between half-brothers sharing the same mother. Clan males in this colony had greater success taking over females (Colmenares et al., 2006), longer tenures

as leader males, and larger OMUs than leader males who led single OMUs not belonging to a clan (Colmenares, 1997).

While I do not yet have genetic data to assess kin relationships among clan males at Filoha, behavioral evidence suggests that takeovers are more likely between males belonging to the same clan. All males and females involved in the four takeovers and transfers that occurred within Band 1 (excluding MORRIS who disappeared) remained in the same clan before and after the takeover. It thus appears that relationships among males in the same clan facilitate access to females. Future research on relationships among leader, follower, and unaffiliated males should elucidate the social and kin bonds among males that underlie these patterns.

It has also been reported that female kinship and familiarity facilitate the existence of clans (Colmenares, 1992). In other populations, females who once belonged to the same OMU tend to reunite later in life in new OMUs (Abegglen, 1984; Kummer, 1990). In captivity, related females or those that have been members of the same OMU for many years tend to interact with one another even if they no longer belong to the same OMU (Colmenares, 1992). At Filoha, all extra-OMU interactions occurred between females belonging to the same clan. While available data do not allow me to determine whether these pairs of females belonged to the same OMU earlier in life or were close relatives, the tendency of takeovers to occur between OMUs in the same clan suggests that this possibility is very likely. Female relationships also appeared to play a role in the takeover by LEN in 2005 in that he did not exhibit the neck-biting and aggressive herding that is typical of hamadryas males during takeovers of females (Swedell and Schreier, in press). Instead, *Maxine's* entry into LEN's OMU appeared to be based on her relationship with *Lila*; additionally, *Mary* and *Maggie* seemed to then join LEN's OMU due to their

previous relationship with *Maxine*. Similarly, *Mango*'s transfer into PEACH's OMU after her leader male disappeared seemed to be based on her previous relationship with *Papaya* from when they were members of the same OMU. Future genetic analyses will reveal whether pairs of females such as these – as well as those that interact across OMUs – are close relatives.

In summary, Band 1 at Filoha comprised two clans, consisting of 13 and 9 OMUs, respectively. The large clans at Filoha appear to be related to band size: clans may simply be the largest size that the band can split into and still get enough food during periods of palm scarcity. Clans at Filoha, therefore, appear to provide an extra level of flexibility to deal with the pressures of feeding competition during periods of low food availability. In addition, behavioral evidence suggests takeovers occur between males belonging to the same clan, and that female social relationships, and perhaps kinship, play a role in clan membership. Future research on the roles and reproductive success of follower and unaffiliated males at Filoha should lend insight into the benefits that clan membership affords males and females in this population of hamadryas baboons.

6.6 Chapter Summary and Conclusions

Overall, the baboons at Filoha displayed the multilevel social structure typical of hamadryas baboons. Several differences, however, emerged between Band 1 at Filoha and other hamadryas populations at the band, one-male unit, and clan levels (Kummer, 1968a; Abegglen, 1984; Biquand et al., 1992; Zinner et al., 2001b).

Consistent with previous studies at Filoha (Swedell, 2002b), the band sizes during this study were larger than those described elsewhere, and this can be attributed to the high abundance and availability of food resources compared to other hamadryas sites.

The increase in the size of Band 1 over the study period reflects a high birth rate and its corresponding high infant survival rate.

The size and composition of OMUs in Band 1 in this study period were similar but less consistent over time compared to other Ethiopian hamadryas populations. Females transferred in or out of almost half of the OMUs in Band 1 over the study period, at a rate of 0.07 transfers/OMU/month. The majority of these changes were due to immigration and emigration to and from other bands, while three transfers occurred among OMUs within Band 1. Only one of the five infants involved in takeovers died, and the reproductive cycles of females were affected in only two of the five mothers. The takeovers in Band 1 during this study period, therefore, did not have as much of an effect on female reproduction as in previous studies of this band (Swedell, 2006; Swedell & Tesfaye, 2003) and other hamadryas populations (Sigg et al., 1982).

Clans have been described previously in only one wild hamadryas population (Abegglen, 1984). During the study period, Band 1 at Filoha consisted of two large clans. Clan size appears to be determined by band size and social relationships, whereas band size is determined by local ecology. Clans at Filoha appear to provide an extra level of flexibility to deal with the pressures of feeding competition during periods of low food availability. Genetic analyses should reveal whether clan members are related, as Abegglen (1984) suggested.

With the social structure of Band 1 at Filoha quantified and described, the possible functions of this unique multilevel social structure of hamadryas baboons can be examined. The relationship between hamadryas social structure and the distribution of resources in their habitats as well as other ecological variables will be explored in the following chapter.

Table 6.1 Percentage of overall grooming scans leader males spent grooming with females and males

Leader Male	Number of Females	Total Grooming and Groomed By (Grooms Scans	Grooming with Adult Females			Grooming with Males						
			Grooms and Groomed by (GR)	Grooms (GM)	Groomed By (GB)	GR All Males	GM All Males	GB All Males	GR Juvenile	GR Subadult	GR Unaffiliated	GR Follower
Ciodio	1	39	92	38	54	8	0	8	0	0	8	0
DJ	1	11	82	18	63	9	0	9	9	0	0	0
Ethan	1	6	83	33	50	17	17	0	0	17	0	0
Fruit	1	5	100	100	0	0	0	0	0	0	0	0
Kalid	1	39	67	41	26	33	2	31	18	8	8	0
Mercury	1	11	82	27	55	18	9	9	9	9	0	0
Mike	1	28	86	46	39	14	3	11	3	0	3	7
Nelson	1	14	86	50	36	14	7	7	7	0	7	0
Peach1	1	7	100	0	100	0	0	0	0	0	0	0
Pete	1	23	70	22	48	9	0	9	9	0	0	0

Table 6.1 (cont.)

Leader Male	Number of Females	Total Grooming (Grooms and Groomed By) Scans	Grooming with Adult Females			Grooming with Males							
			Grooms and Groomed by (GR)	Grooms (GM)	Groomed By (GB)	GR All Males	GM All Males	GB All Males	GR Juvenile	GR Subadult	GR Unaffiliated	GR Follower	
Sami	1	14	93	43	50	0	0	0	0	0	0	0	
Shato1	1	5	60	20	40	40	0	40	0	40	0	0	
Teddy1a	1	5	60	20	40	40	0	40	20	20	0	0	
Teddy1b	1	7	100	29	71	0	0	0	0	0	0	0	
Peach2	2	2	100	50	50	0	0	0	0	0	0	0	
Pope	2	8	100	25	75	0	0	0	0	0	0	0	
Shato2	2	26	92	38	54	8	4	4	0	0	0	8	
Teddy2	2	12	100	42	58	0	0	0	0	0	0	0	
Yirdaw2	2	18	83	44	39	17	17	0	0	17	0	0	
Andy	3	56	100	11	89	0	0	0	0	0	0	0	
Cory	3	18	100	50	50	0	0	0	0	0	0	0	

Table 6.1 (cont.)

Leader Male	Number of Females	Total Grooming (Grooms and Groomed By) Scans	Grooming with Adult Females			Grooming with Males						
			Grooms and Groomed by (GR)	Grooms (GM)	Groomed By (GB)	GR All Males	GM All Males	GB All Males	GR Juvenile	GR Subadult	GR Unaffiliated	GR Follower
Evangadi	3	12	83	25	58	17	0	17	0	17	0	0
Mac3	3	19	89	32	58	5	0	5	5	0	0	0
Titi	3	6	100	17	83	0	0	0	0	0	0	0
Tripp	3	35	100	37	63	0	0	0	0	0	0	0
Yirdaw3	3	32	91	34	56	9	6	3	9	0	0	0
Len4	4	9	100	44	56	0	0	0	0	0	0	0
Mac4	4	6	100	0	100	0	0	0	0	0	0	0
Herb	5	6	100	0	100	0	0	0	0	0	0	0
Len5	5	13	100	69	31	0	0	0	0	0	0	0
Redface	5	45	100	16	84	0	0	0	0	0	0	0

Table 6.2 Average of leader males' grooming interactions, overall and by OMU size

Size of OMU	Total Grooming (Grooms and Groomed By) Scans	Grooming with Adult Females			Grooming with Males						
		Grooms and Groomed by (GR)	Grooms (GM)	Groomed By (GB)	GR All Males	GM All Males	GB All Males	GR Juvenile	GR Subadult	GR Unaffiliated	GR Follower
1-Female OMUs	214	82	36	45	15	2	13	7	4	4	1
2-Female OMUs	79	94	33	61	6	5	1	0	4	0	3
3-Female OMUs	178	96	28	69	3	1	2	2	1	0	0
4-Female OMUs	15	100	27	73	0	0	0	0	0	0	0
5-Female OMUs	16	100	25	75	0	0	0	0	0	0	0
ALL OMUs	550	91	31	59	8	2	6	3	2	1	1

Table 6.3 Percentage of overall grooming scans females (by OMU) spent grooming females, males, and juveniles

OMU that the Females Belong To ¹	Number of Females	Total Grooming (Grooms and Scans of all Females in OMU)	Grooming with Adult Females			Grooming with Males							Grooming with Juveniles (including Infants)		
			GR	GM	GB	GR ² Lead ²	GM Lead	GB Lead	GR ² Sub ²	GR ² Un ²	GR ² Foil ²		GR	GM	GB
Ciodio	1	56	0	0	0	87	50	37	2	0	2		32	23	9
DJ	1	10	0	0	0	90	70	20	0	0	0		10	10	0
Ethan	1	5	0	0	0	100	60	40	0	0	0		0	0	0
Fruit	1	9	0	0	0	56	0	56	0	0	0		44	44	0
Kalid	1	30	0	0	0	87	50	37	3	0	0		10	3	7
Mercury	1	14	0	0	0	64	43	21	7	0	0		29	29	0
Mike	1	29	0	0	0	83	38	45	0	3	3		10	10	0
Nelson	1	14	0	0	0	86	36	50	0	0	0		14	14	0
Peach1	1	9	0	0	0	78	78	0	0	0	0		22	22	0
Pete	1	31	0	0	0	51	35	16	10	0	0		39	23	16

Table 6.3 (cont.)

OMU that the Females Belong To ¹	Number of Females	Total Grooming (Grooms and Scans of all Females in OMU)	Grooming with Adult Females			Grooming with Males							Grooming with Juveniles (including Infants)		
			GR	GM	GB	GR Lead ²	GM Lead	GB Lead	GR Sub ²	GR Un ²	GR Fol ²		GR	GM	GB
Sami	1	18	0	0	0	72	39	33	0	0	0		28	28	0
Shato1	1	4	0	0	0	75	50	25	0	0	0		25	25	0
Teddy1a	1	3	0	0	0	100	67	33	0	0	0		0	0	0
Teddy1b	1	11	0	0	0	63	45	18	0	0	0		36	9	27
Peach2	2	24	37	33	4	42	42	0	0	0	0		21	17	4
Pope	2	5	40	20	20	0	0	0	0	0	0		60	40	20
Shato2	2	21	14	5	9	62	33	29	0	0	0		24	24	0
Teddy2	2	7	28	14	14	71	14	57	0	0	0		0	0	0
Yirdaw2	2	17	12	12	0	29	12	17	0	0	0		59	41	18
Andy	3	38	58	45	13	37	34	3	0	0	0		5	5	0

Table 6.3 (cont.)

OMU that the Females Belong To ¹	Number of Females	Total Grooming (Grooms and Groomed By) Scans of all Females in OMU	Grooming with Adult Females			Grooming with Males							Grooming with Juveniles (including Infants)		
			GR	GM	GB	GR Lead ²	GM Lead	GB Lead	GR Sub ²	GR Un ²	GR Foil ²	GR	GM	GB	
Cory	3	22	54	18	36	9	0	9	0	0	0	36	32	4	
Evangadi	3	14	43	21	22	43	36	7	0	0	7	7	7	0	
Mac3	3	13	30	15	15	15	15	0	0	0	0	54	23	31	
Titl	3	10	30	20	10	20	20	0	0	0	0	50	50	0	
Tripp	3	46	35	17	17	39	22	17	0	2	0	24	22	2	
Yirdaw3	3	15	20	13	7	7	7	0	7	0	0	67	67	0	
Len4	4	3	67	33	33	33	0	33	0	0	0	0	0	0	
Mac4	4	5	40	0	40	0	0	0	0	0	0	60	60	0	
Herb	5	18	6	6	0	0	0	0	0	0	55	39	22	17	
Len5	5	3	33	0	33	33	33	0	0	0	0	33	33	0	

Table 6.3 (cont.)

OMU that the Females Belong To ¹	Number of Females	Total Grooming (Grooms and Scans of all Females in OMU)	Grooming with Adult Females			Grooming with Males							Grooming with Juveniles (including Infants)		
			GR	GM	GB	GR ² Lead	GM Lead	GB Lead	GR ² Sub ²	GR ² Un ²	GR ² Foll ²		GR	GM	GB
Redface	5	37	38	27	11	16	16	0	0	0	0		46	35	11

¹For OMUs with more than 1 female I randomly selected one female from each scan; results, therefore, represent a sample of each OMU's females as opposed to each individual female

²Lead = leader male; Sub = subadult male; Un = unaffiliated male; Foll = follower male

Table 6.4 Average of adult females' grooming interactions, overall and by OMU size

Size of OMU ¹	Total Grooming (Grooms and Groomed By) Scans of all Females in OMU	Grooming with Adult Females			Grooming with Males							Grooming with Juveniles (including Infants)		
		GR	GM	GB	GR ² Lead ²	GM Lead	GB Lead	GR ² Sub ²	GR ² Un ²	GR ² Foll ²	GR	GM	GB	
1-Female OMUs	243	0	0	0	72	42	30	2	0	1	24	18	6	
2-Female OMUs	74	24	18	7	45	27	18	0	0	0	31	24	7	
3-Female OMUs	158	42	24	18	28	21	7	1	1	1	28	24	4	
4-Female OMUs	8	50	13	37	12	0	12	0	0	0	38	38	0	
5-Female OMUs	58	28	19	9	12	12	0	0	0	17	43	31	12	
ALL OMUs	541	19	11	8	48	30	18	1	0	2	28	22	6	

¹For OMUs with more than 1 female I randomly selected one female from each scan; results, therefore, represent averages of a sample of each OMU's females as opposed to each individual female

²Lead = leader male; Sub = subadult male; Un = unaffiliated male; Foll = follower male

Table 6.5 Leader males included in clan analyses

Leader Male	Code¹	Number of Scans
Andy	An	124
Cllodio	Cl	106
Cory	Co	123
DJ	Dj	52
Evangadi	Ev	71
Ford	Fo	47
Herb	He	103
Kalid	Ka	124
Len	Len	72
Mac	Mac	64
Mike	Mi	93
Nelson	Ne	43
Park	Pa	41
Peach	Pea	101
Pete	Pet	95
Redface	Re	106
Sami	Sa	91
Shato	Sh	87
Teddy	Te	75
Titi	Ti	71
Tripp	Tr	110
Yirdaw	Yi	143
Total Scans =		1942

¹abbreviation displayed in dendrogram

Figure 6.1 Frequency distribution of number of females per OMU in February 2006

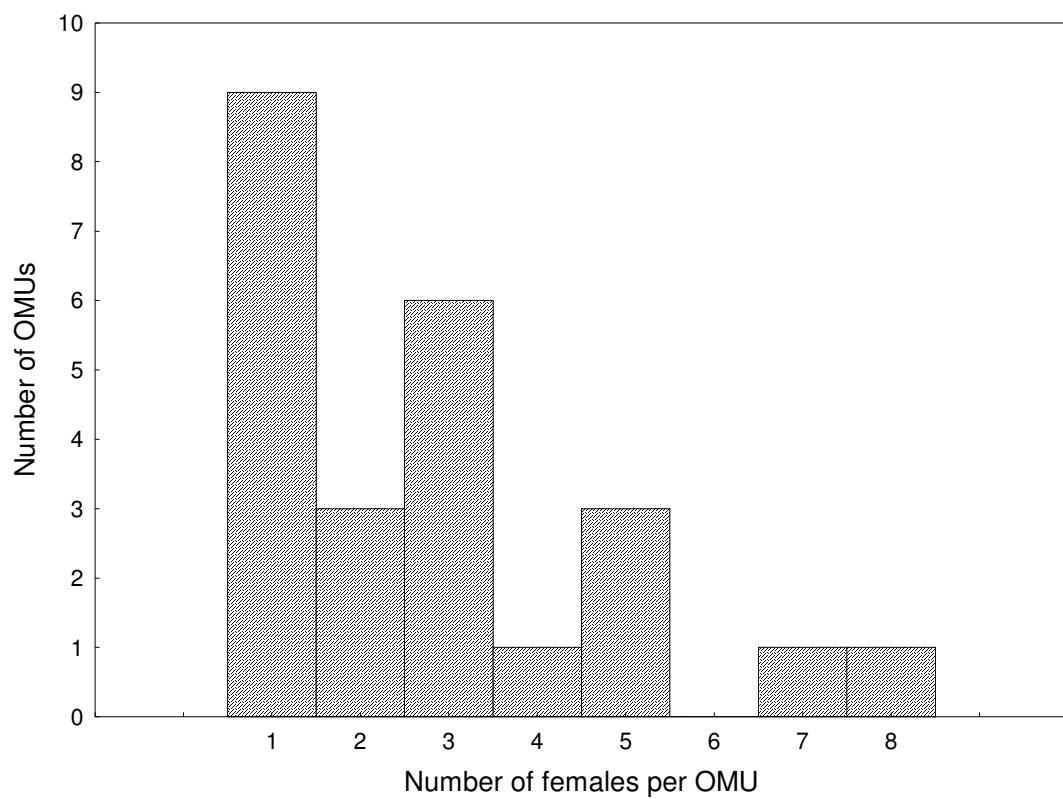
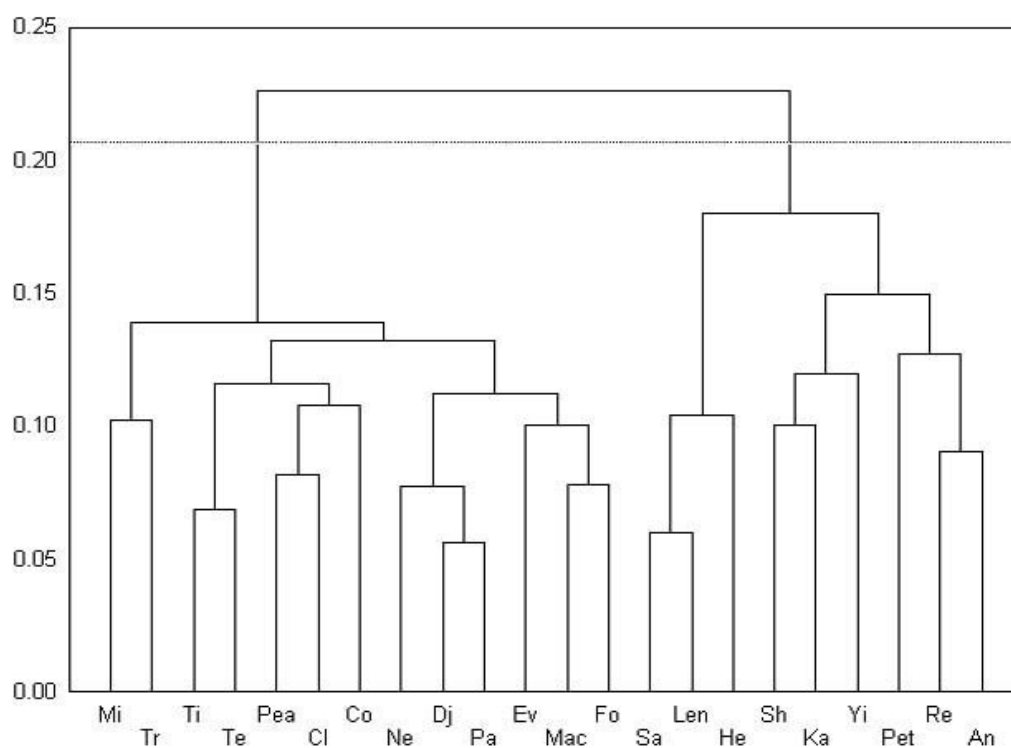


Figure 6.2 Complete-linkage cluster analysis of association indices among leader males



Complete-linkage cluster analysis of association indices among leader males (N=1942). Association indices based on the number of scans in which 2 leader males were within a 10 m radius of one another. X-axis = leader males; Y-axis = linkage distance. Stronger clusters are lower in the figure. The dotted line cuts the tree, leaving two clusters as suggested by the gap statistic.

CHAPTER 7

SPATIAL COHESION

7.1 Introduction

As described in Chapter 6, the Filoha hamadryas population displayed the multilevel social structure typical of hamadryas baboons in which large groups (bands) break into smaller foraging parties (clans) during daily travel. The evolution of this flexible, multi-level social structure unique to hamadryas is possibly related to the wide dispersion and low availability of resources in their habitats (Kummer 1968a,b, 1995), enabling the baboons to split up into individual OMUs when resource density and abundance is lowest. However, this idea has never been explicitly tested.

The distribution and relative abundance of food resources is commonly thought to be a primary determinant of primate social structure and social organization (Wrangham, 1980; van Schaik, 1983; Terborgh & Janson, 1986; Isbell, 1991; Sterck et al., 1997). Many primate species alter the size of their feeding parties in relation to the size and dispersion of food patches to reduce intragroup feeding competition (e.g., Chapman et al., 1995; Newton-Fisher et al., 2000). In fission-fusion social groups, members of a community split up when food patches are small and then come together when resources are abundant enough to accommodate more individuals. Thus, spatial cohesion of group members is reduced when patches are small and is greater in areas of higher resource abundance.

The fission-fusion system is typified by chimpanzees (*Pan troglodytes* spp.) and spider monkeys (*Ateles* spp.). A variety of studies have indicated that the size of chimpanzee foraging parties was correlated with food patch size (e.g., Isabirye-Basuta,

1988; Chapman et al., 1994; Boesch, 1996). Party size in spider monkeys is also positively related to patch size (Symington, 1990; Chapman et al., 1995; Robbins et al., 1991). A fission-fusion social system, thus, seems to be an effective means of adapting to the spatial and temporal distribution of resources in both chimpanzees and spider monkeys. An important distinction between the fission-fusion system typical of chimpanzees and spider monkeys and the multilevel social structure of hamadryas, however, is that, in the former, subgroups are variable in both size and composition over time. By contrast, the OMUs and clans of hamadryas baboons are consistent in their composition over time.

Kummer (1968a,b, 1995) suggested that the size and spatial cohesion of hamadryas groupings at each level of social structure are related to resource density and distribution. Kummer's observations suggested that only sleeping cliffs supported troops; permanent water holes and *Acacia* forests with groundwater supported bands; patches of roots covering 500 square feet accommodated clans; and areas of bushes and trees separated by 100 meters or more accommodated only OMUs. Thus, both total band cohesion and individual OMU cohesion would be greatest in areas with high resource density and lowest in less dense locales. In a study of captive hamadryas baboons at the Madrid Zoo, members of individual OMUs were more cohesive when food was clumped than when it was dispersed (Gil-Burmann et al., 2001). This general association, however, has neither been explicitly tested nor quantitatively described in wild hamadryas populations.

In this chapter, I describe variation in spatial cohesion at the OMU, clan, and band levels of hamadryas social structure for Band 1 at Filoha from March 2005 through February 2006 and test the idea that social cohesion is related to resource distribution and

abundance. Due to the presence of palm forests in the Filoha region, important food resources are less dispersed than in other parts of hamadryas' range, which consist primarily of *Acacia* scrublands, open grasslands, and cliffs (Kummer, 1968a; Sigg and Stolba, 1981; Biquand et al., 1992; Al-Safadi, 1994; Zinner et al., 2001a; Swedell, 2006). Filoha is therefore an ideal site at which to examine the influence of resource distribution on the baboons' multilevel social structure.

Over the study period, Band 1 most frequently fed from *Acacia senegal* and *Hyphaene thebaica* (section 4.3.1). As described in Chapter 3, food availability is higher in palm forests than in *Acacia* scrublands. Therefore, I expected the baboons to be more cohesive at each level of social structure when foraging in palm forests than in *Acacia* scrublands. Within habitat types, I expected the baboons to be more cohesive in those areas with a higher density and availability of *A. senegal* or *H. thebaica*. Similarly, I expected cohesion to be higher in the wet season than the dry season when foraging in *Acacia* scrublands because of the higher abundance of *Acacia* spp. flowers and young leaves during and just after the long rains (section 3.2.1).

7.2 Methods

I collected data on spatial cohesion by conducting instantaneous scan-samples of focal OMUs at 2-minute intervals. At the start of each 30-minute focal OMU sample, I recorded the GPS location of the leader male, the identities of the leader male and each adolescent and adult female, and the habitat type(s) in which each adolescent and adult OMU member was located.

I defined OMU cohesion as the spread in meters between the two farthest individuals in the OMU, excluding juveniles and infants. I estimated this spread at each

2-minute interval. I also calculated the average distance between leader males and each of their females at any one time as an alternative measure of OMU cohesion.

To measure the spread among OMUs and obtain an estimate of clan cohesion, I used an estimated 10 m radius of the focal leader male as a spatial cohesion index (e.g., Chapman, 1990b). Within this radius, I recorded the number of OMUs and estimated the distance between the focal OMU's leader male and the leader males of the other OMUs. A 10 m radius was the largest size in which I could consistently monitor and accurately identify multiple OMUs and their individuals. While the number of OMUs within a 10 m radius and the distance between pairs of leader males do not provide estimates of cohesion across entire clans, they do provide consistent measures of between-OMU, or within-clan, cohesion.

As described in Chapter 2, cohesion within and between OMUs was quantified for leader males and their females from the 31 OMUs for whom I had at least 50 2-minute instantaneous scan-samples. Table 2.4 shows the OMUs included in these analyses. To increase independence of samples, I used only scans separated by 10 minutes; the number of scans shown in the table, therefore, represents the number of scans at 10-minute intervals.

I defined band spread as the distance in meters between the two farthest individuals in the band. When the baboons rested and groomed, they were commonly arranged in an oblong formation and the individuals that were farthest apart could frequently be seen from one vantage point. During these times, my field assistant and I took GPS points at the locations of the two farthest individuals. When foraging, by contrast, the baboons typically spread out in a linear formation. During these times, my field assistant stayed toward the front or back of the band, and I stayed on the other end.

Communicating via hand-held radios, whenever possible, we each located the baboon that was at the very front or back of the band, and recorded their GPS locations. I computed the distance between two points via the great circle formula:

Distance = $\text{acos}(\sin(\text{lat1}) * \sin(\text{lat2}) + \cos(\text{lat1}) * \cos(\text{lat2}) * \cos(\text{lon1} - \text{lon2}))$. The GPS unit provided positional coordinate readings to the ten-thousandth of a minute, and was accurate to within 10 meters.

It was often difficult to determine where the edge of the band was, particularly when the band was traveling and feeding and when they were located in dense *Acacia* scrublands, swamp vegetation, or areas of palm forests that encompassed rivers. In these areas, even if we could see where the farthest baboon was, it was often impossible to reach these locations and record GPS points. Further, radio reception was poor when the distance between me and my field assistant approached 1 km, and we were often unable to communicate with one another at or farther than this distance. The band spreads used in these analyses, therefore, consist only of those times in which we were certain that we were at either end of the band and were able to reach those locations and record GPS points. Thus, all reported band spreads should be viewed as minimum distances.

To examine variation in cohesion within habitat types, I used those *Acacia* scrublands and palm forest patches in which I collected at least 10 OMU distance estimates. As described in Chapter 3, I conducted vegetation transects (50 m x 4 m) in patches of *Acacia scrublands* and palm forests. Within *Acacia* scrublands, I calculated availability only for *A. senegal* as it was the most commonly eaten food species by Band 1, comprising 23.0% of the total feeding records, while the second most eaten *Acacia* species, *A. nubica*, constituted only 7.6% of the total feeding records (section 4.3.1). The baboons most frequently consumed the leaves, seeds, and flowers of *A. senegal* (section

4.3.3). As a measure of *A. senegal* availability, I multiplied the density of *A. senegal* (i.e., the number of *A. senegal* individuals per square meter) by the mean DBH of *A. senegal* shrubs in that transect (section 3.1.2). In palm forests, I calculated “density” as the number of palm trees per square meter. As a measure of palm fruit availability, I multiplied the density by the mean DBH of palm trees in the transect (section 3.1.3).

7.3 Results: One-Male Unit Cohesion

I analyzed OMU cohesion using two measures: OMU spread, and the average distance between a leader male and each of his females at any one time. Patterns of results were the same, and therefore, in this section I report only the results of the OMU spread analyses. Table 7.1 displays the mean OMU spread for Band 1’s 31 OMUs from March 2005 through February 2006. The mean OMU spread was 5.0 m (N=1323), and ranged from 0 to 45 m. There was a significant positive relationship between OMU spread and OMU size (i.e., the number of females in the OMU) ($r_s=0.22$, $p=0.00$, N=1323), and I will therefore discuss OMU cohesion by OMU size for the remainder of this section.

7.3.1 One-Male Unit Cohesion and OMU Size

Table 7.2 shows the mean OMU spread for each OMU size. One-female OMUs were the most cohesive with a mean OMU spread of 3.8 m, and cohesion decreased as OMU size increased to four females. Five-female OMUs were more cohesive than OMUs with four females. The minimum OMU spread ranged from 0 m in 1-female OMUs (i.e., the leader male and his female were in physical contact) to 2 m in 4- and 5-female OMUs (Table 7.2). The maximum OMU spread varied more extensively, and

inversely, with OMU size (Table 7.2). One-female OMUs spread out up to 45 m, while the maximum OMU spread for 5-female OMUs was 25 m.

Variation in OMU cohesion also existed among OMUs of the same size (Table 7.1). These differences may be due to a variety of factors including the presence of infants and the number of cycling females in an OMU which are predicted to increase cohesion (Swedell, 2006). I examined OMU cohesion before and after the birth of an infant for the following six OMUs for which I had data for both conditions: Clodio, Kalid, Mike, Pete, Evangadi, and Redface. There were no differences in mean OMU spread for five of them before and after the birth of an infant. Only Redface's OMU was significantly more cohesive after the birth of an infant (Mann-Whitney test, $p=0.04$). In this OMU, however, three infants were born over the last several months of the study period, and the increased cohesion may have been due to multiple infants as opposed to the presence of just one. The number of cycling females in an OMU had no effect on OMU cohesion.

7.3.2 *One-Male Unit Cohesion, Activity, and Habitat Type*

The mean OMU spread was significantly lower when all OMU members were resting and/or grooming than when they were all traveling and/or feeding for all OMU sizes (one-way ANOVA, $p=0.00$) (Figure 7.1). For each OMU size, the range of OMU spreads was greater when OMU members were all resting and/or grooming than when they were all traveling and/or feeding.

Across OMU sizes, significant differences existed in mean OMU spreads among habitat types (one-way ANOVA, $p=0.00$). Post-hoc LSD tests showed that OMUs were significantly more cohesive when they were on cliffs than when they were in *Acacia*

scrublands ($p=0.00$), palm forests ($p=0.00$), and open grasslands ($p=0.00$). OMU cohesion, however, did not differ significantly between *Acacia* scrublands and palm forests. I have too few OMU cohesion data for comparative purposes for 4- and 5-female OMUs or when the baboons were in swamps and grasslands; Figure 7.2, therefore, shows the mean OMU spreads for 1-, 2-, and 3-female OMUs on cliffs, and in *Acacia* scrublands and palm forests. The mean OMU spread was significantly lower on cliffs than in *Acacia* scrublands and palm forests for all three OMU sizes (one-way ANOVAs, $p=0.00$).

One- and 3-female OMUs displayed the same patterns of OMU cohesion when resting and/or grooming in various habitat types (Figure 7.3). Specifically, these OMUs were most cohesive when resting and/or grooming on cliffs, and least cohesive when resting and/or grooming in palm forests, although these differences were not significant. When the baboons rested and/or groomed in *Acacia* scrublands and palm forests, they generally did so while sitting together underneath trees. The shade cast by *Acacia* spp. is smaller than that of *H. thebaica*, and the baboons therefore must remain closer together in *Acacia* scrublands when underneath one shrub to remain in the shade. Two-female OMUs were most cohesive when resting and/or grooming in palm forests and least cohesive when resting and/or grooming in *Acacia* scrublands. The only significant difference in cohesion, however, was between *Acacia* scrublands and cliffs (LSD test, $p=0.01$).

Because the majority of the time the baboons spent foraging occurred while they were in *Acacia* scrublands and palm forests (section 5.3.2), I examined variation in OMU cohesion when all OMU members were traveling and/or feeding only between these two habitat types (Figure 7.4). In 1- and 3-female OMUs, the mean OMU spread when traveling and/or feeding was higher in *Acacia* scrublands than in palm forests. These

differences were significant, however, only for 1-female OMUs (Mann-Whitney test, $p=0.03$). In 2-female OMUs, by contrast, the mean OMU spread was higher in palm forests than in *Acacia* scrublands but this difference was not significant. The maximum OMU spread in 1-, 2-, and 3-female OMUs was greatest in *Acacia* scrublands (compared to palm forests and cliffs) for all activity states.

I also examined variation in OMU cohesion within habitat types. There were no differences in OMU cohesion between the Filoha cliff and the Wasaro cliff overall, by OMU size, or by activity state.

Within *Acacia* scrublands, I compared OMU cohesion among the five patches from which I collected at least 10 OMU spreads. These areas are represented by *Acacia* Scrublands Transects 1, 4, 9, 13, and 21 (Tables 3.2, 3.3; Figure 3.1). *A. senegal* was the dominant *Acacia* species in all five patches. Table 7.3 shows the mean OMU spread in each of these patches, as well as the total density, *Acacia* spp. density, and availability of *A. senegal*. While the mean OMU spread ranged from 4.3 to 8.3 m, OMU cohesion did not vary significantly among *Acacia* patches. There were also no relationships between mean OMU spread and total density, *A. senegal* density, or *A. senegal* availability.

Within palm forests, I examined variation in OMU cohesion among the three palm forest patches for which I collected at least 10 OMU spreads. These patches are represented by Palm Forest Transects 2, 3, and 5 (Table 3.6; Figure 3.2). Table 7.4 displays the mean OMU spread, as well as the mean density of palm trees and availability of palm fruit in each patch. OMU cohesion varied significantly among these palm patches (one-way ANOVA, $p=0.01$). OMU cohesion was positively correlated with both the availability and density of palms, but only the former relationship was significant.

7.3.3 Seasonal Variation in One-Male Unit Cohesion

Overall, OMUs of all sizes were more cohesive in the dry season than the wet season (Figure 7.5). These differences were significant, however, only for 3-female OMUs (Mann-Whitney test, $p=0.01$). The baboons spent most of their time during the wet season in *Acacia* scrublands and on cliffs (section 5.3.2). During the wet season of 2005 there were no 2-female OMUs in Band 1 and I collected only limited data on 4- and 5-female OMUs. Seasonal comparisons, therefore, can be made only for 1- and 3-female OMUs. There were no seasonal differences in OMU spread for these OMUs when they were on cliffs. When 1-female OMUs were in *Acacia* scrublands, OMU spread was lower in the wet season than the dry season, but this difference was not significant. Three-female OMUs, by contrast, were significantly more spread out in the wet season than the dry season (Mann-Whitney test, $p=0.01$). These seasonal patterns remained when looking only at when all OMU members were traveling and/or feeding in *Acacia* scrublands, but the difference for 3-female OMUs was no longer significant.

As discussed in section 5.4.4, seasonal patterns in ranging behavior – in which the baboons traveled greater distances per day and spent more time away from Filoha in the wet season than the dry season – were less clear-cut when examining the two wet season months separately. Overall, both 1- and 3-female OMUs were more cohesive in July than in August, although these differences were not significant. When 1- and 3-female OMUs were in *Acacia* scrublands, OMU spread was lower in July than in August, although only the former relationship was significant (Mann-Whitney test, $p=0.00$).

7.4 Results: Clan Cohesion

As described in section 6.5, two large clans consisting of 13 and nine OMUs existed in Band 1. Table 7.1 shows the mean number of OMUs within a 10 m radius of the focal male and the mean distance from the focal OMU's leader male to his nearest neighbor leader male for each OMU. The mean number of OMUs within a 10 m radius was 2.0 (N=1276), and ranged from 1 to 7. The mean distance between a leader male and the next closest leader male was 6.4 m (N=703), with a range of 1 to 15 m. There was no relationship between either of these measures and the size of the focal male's OMU.

7.4.1 Clan Cohesion, Activity, and Habitat Type

The mean number of OMUs within a 10 m radius of the focal male when all members of the focal OMU were resting and/or grooming was 2.3, significantly more than when focal OMU members were all traveling and/or feeding (1.5) (t-test, $p=0.00$) (Table 7.5). Similarly, leader males remained significantly closer to one another on average when they were resting and/or grooming than when they were traveling and/or feeding (t-test, $p=0.00$) (Table 7.3).

The number of OMUs within a 10 m radius varied significantly across habitat types (one-way ANOVA, $p=0.00$) (Table 7.5). The average of 2.5 OMUs on cliffs was significantly more than in *Acacia* scrublands (1.5), palm forests (2.0), open grasslands (1.9), and swamp vegetation (1.5) (LSD tests, $p=0.00$). There were also significantly fewer OMUs in *Acacia* scrublands than in both palm forests (LSD test, $p=0.00$) and open grasslands (LSD test, $p=0.01$).

The distance between a leader male and the next closest leader male also varied significantly across habitat types (one-way ANOVA, $p=0.01$) (Table 7.5). Leader males

remained significantly closer on cliffs than in *Acacia* scrublands (LSD test, $p=0.01$). No other significant differences between habitat types were detected.

When the focal leader male was resting or grooming, the mean number of OMUs within a 10 m radius varied significantly across habitat types (one-way ANOVA, $p=0.00$). There were significantly fewer in *Acacia* scrublands than in either palm forests or on cliffs (LSD tests, $p=0.00$). Furthermore, there were significantly more close OMUs when the baboons were traveling and/or feeding in palm forests than in *Acacia* scrublands (Mann-Whitney test, $p=0.00$).

When the focal leader male was resting or grooming, the mean distance between him and the next closest leader male was 6.6 m in *Acacia* scrublands, 5.7 m in palm forests, and 6.1 m on cliffs. These differences were significant only between *Acacia* scrublands and palm forests (Mann-Whitney test, $p=0.01$). When traveling and/or feeding, the mean distance between nearest neighbor leader males was 7.5 m in *Acacia* scrublands and 6.9 m in palm forests, but this difference was not significant.

I also examined variation in clan cohesion within habitat types. There were no differences in either the number of OMUs within a 10 m radius of the focal male or the distance between nearest neighbor leader males between the Filoha cliff and the Wasaro cliff.

Table 7.3 shows clan cohesion measures for the five *Acacia* scrublands patches used in these analyses. The number of OMUs within a 10 m radius varied significantly among these patches (one-way ANOVA, $p=0.01$). There were no relationships, however, between the number of OMUs and the total density, *Acacia* spp. density, or the availability of *A. senegal*. The mean distance between nearest neighbor leader males did

not vary significantly among *Acacia* patches, and there were no relationships between this distance and any of the density and availability measures.

Table 7.4 displays clan cohesion measures, the density of palm trees, and the availability of palm fruit for the three palm patches used in these analyses. Both the number of OMUs within a 10 m radius and the distance between a leader male and the next closest leader male varied significantly among palm patches (one-way ANOVAs, $p=0.00$). All but one of the observations in Transect 3, however, occurred while all OMU members were resting and grooming. When this transect was excluded from the analysis, these differences in clan cohesion disappeared.

7.4.2 Seasonal Variation in Clan Cohesion

When all habitats and activity states are combined, there were 2.0 OMUs within a 10 m radius in the dry season, and 1.8 OMUs in the wet season, and this difference was statistically significant (Mann-Whitney test, $p=0.00$). The mean distance between nearest neighbor leader males in the wet season (6.6 m) was comparable to that of the dry season (6.4 m). There were no seasonal differences in the number of OMUs in a 10 m radius when the baboons were resting and/or grooming on cliffs or in *Acacia* scrublands, or when they were traveling and/or feeding in *Acacia* scrublands. There were also no seasonal differences in the mean distance between nearest neighbor leader males when the baboons were resting and/or grooming on cliffs or in *Acacia* scrublands. The mean distance between leader males when traveling or feeding in *Acacia* scrublands in the wet season (9.2 m) was, by contrast, significantly higher than that of the dry season (6.9 m) (Mann-Whitney test, $p=0.01$).

Within the wet season, clans were more cohesive in July than in August. The number of OMUs within a 10 m radius was 1.9 in July and 1.6 in August, but this difference was not significant. The mean distance between nearest neighbor leader males, however, was significantly higher in August (7.2 m) than in July (5.8 m) (Mann-Whitney test, $p=0.02$). These same patterns held when looking only at when the baboons were foraging in *Acacia* scrublands, although none of the relationships were significant.

7.4.3 Spatial Cohesion of Independent Clans

As discussed in Chapter 6, Band 1 fissioned along clan lines for six days in March 2005, for 31 consecutive days in September and October 2005, and for a minimum of three hours during daily travel on at least nine days. All data used in this dissertation thus far are for the band as a whole. To examine if the cohesion of OMUs and clans varied depending on whether the baboons behaved as a cohesive band or as independent clans, I looked at cohesion during the month-long period over September and October when Band 1 was separated into clans. Spatial cohesion did not differ between Clan A and Clan B during this time, so I pooled their data. Because this separation occurred during the dry season, I used data from the entire band only from the dry season to control for seasonal variation.

There were no differences in OMU cohesion overall, by activity state, or by habitat type between the time when the band behaved as a cohesive unit and when clans traveled independently. Likewise, the distance between nearest neighbor leader males did not differ between these conditions. The only difference in the number of OMUs within a 10 m radius of the focal male occurred while the baboons were resting and grooming on cliffs: there were significantly more close OMUs for the band as a whole (2.5) than when

the baboons were separated into clans (2.0) (Mann-Whitney test, $p=0.01$). The baboons consistently used the same locations on the Filoha and Wasaro cliffs as sleeping sites throughout the study period. Therefore, OMUs needed to remain closer to one another when the baboons behaved as a cohesive band than when they were separated into independent clans so that all individuals were in the confines of the sleeping site. Overall, OMU and clan cohesion remained the same regardless of whether or not Band 1 was separated into clans.

7.5 Results: Band Cohesion

From March 2005 through February 2006, Band 1's spread averaged 220.5 m ($N=235$), and ranged from 51.0 to 685.9 m. Most of these distances ($N=210$) were recorded when all band members were in the same habitat. Almost half of the band spreads ($N=106$) were recorded when the entire band was in *Acacia* scrublands, about a quarter ($N=67$) when all of the baboons were on a cliff, and about 15% ($N=29$) when the baboons were all located in a palm forest. I recorded band spreads only four times each when the entire band was located in either open grasslands or swamp vegetation.

7.5.1 Band Spread and Habitat Type

Band spread varied significantly among habitat types (one-way ANOVA, $p=0.00$). The mean band spread in *Acacia* scrublands was 269.1 m, followed by palm forests (161.1 m), cliffs (158.6 m), grasslands (144.6 m), and swamps (135.0 m) (Table 7.5).

I also examined variation in band spread within habitat types. Mean band spread was significantly greater when all of the baboons were on the Wasaro cliff (195.0 m, $N=23$) than when they were on the Filoha cliff (145.1 m, $N=50$) (Mann-Whitney test,

$p=0.00$), corresponding with the fact that the Wasaro cliff is about 1 km longer than the Filoha cliff (section 3.1.6). There were only two *Acacia* scrublands patches for which I had at least 7 band spreads (Transects 4 and 9 – Tables 3.2, 7.3), and band cohesion did not differ between them. Similarly, band spread did not differ significantly among the three palm patches for which I had data (Transects 2, 3, and 5 – Tables 3.6, 7.4).

7.5.2 Band Spread and Activity State

Band spread varied significantly across activity states (one-way ANOVA, $p=0.00$) (Table 7.5). Band spread was lowest when all band members were resting and/or grooming (136.5 m). When the entire band was traveling they spread out an average of 159.7 m. When band members were all traveling and/or feeding, by contrast, the mean band spread was 270.7 m, significantly farther than when resting and/or grooming (Mann-Whitney test, $p=0.00$) and traveling ($p=0.02$) I have too little information to compare band spread by activity states within and among habitat types.

7.5.3 Seasonal Variation in Band Spread

Overall, the mean band spread in the wet season (296.3 m, $N=29$) was significantly higher than in the dry season (212.5 m, $N=206$) (Mann-Whitney test, $p=0.00$). Within habitat type, Band 1 was more spread out during the wet season than the dry season when the entire band was on cliffs, as well as when it was in *Acacia* scrublands and palm forests (Figure 7.6). None of these differences, however, was significant. There were also no significant seasonal differences in mean band spread across activity states, although the band was slightly less cohesive while foraging in *Acacia* scrublands during the wet season than the dry season.

7.6 Chapter Summary and Conclusions

From March 2005 through February 2006, the mean OMU spread for Band 1 OMUs was 5.0 m. The mean number of OMUs within a 10 m radius of the focal male was 2.0 and the mean distance between nearest neighbor leader males was 6.4 m. The mean band spread over the study period was 220.5 m.

At the OMU, clan, and band levels of hamadryas social structure, cohesion was higher when they were resting and grooming than when they were traveling and feeding. Furthermore, at each of these levels, the baboons were more cohesive on cliffs than in any other habitat types.

Relationships between spatial cohesion and the distribution of resources in Band 1's home range were less clear. I predicted that the baboons would be more cohesive at each level of social structure when foraging in palm forests than in *Acacia* scrublands. At the OMU level, however, the association between mean OMU spread when foraging in these two habitat types was weak and inconsistent across OMU sizes. This inconsistency is likely due to limited sample size for 2-female OMUs compared to those for 1- and 3-female OMUs. At the clan level, by contrast, the baboons were more cohesive when foraging in palm forests than in *Acacia* scrublands: there were significantly fewer OMUs within a 10 m radius in *Acacia* scrublands than in palm forests, and leader males remained in proximity to one another on average in palm forests more so than in *Acacia* scrublands. These results suggest that, overall, Band 1 was more likely to break up into individual OMUs in *Acacia* scrublands than in palm forests. Too few band spreads were available to examine differences at this level in cohesion when foraging in *Acacia* scrublands versus in palm forests.

Secondly, within habitat types, I expected the baboons to be more cohesive in those areas with a higher density and availability of *A. senegal* or *H. thebaica*. OMU cohesion did not differ significantly across patches of *Acacia* scrublands with varying densities of *Acacia* trees and availability of *A. senegal*. OMU cohesion was positively related to the density of palm trees, but this relationship was weak. At the clan level of social structure, no relationships were detected between cohesion and the density and availability of resources within *Acacia* scrublands or palm forests. The lack of such relationships within *Acacia* scrublands patches may be due to the limited cohesion data available to compare across *Acacia* patches. Furthermore, the three palm patches that could be compared in terms of band cohesion had similar densities of palm trees and availability of palm fruit, and therefore do not provide a particularly useful basis for comparison.

Third, I predicted that cohesion would be higher in the wet season than the dry season when foraging in *Acacia* scrublands because of the higher abundance of *Acacia* spp. flowers and young leaves during and just after the long rains. Contrary to expectations, OMU spread was higher in the wet season. While the number of OMUs in a 10 m radius did not vary across seasons when traveling or feeding in *Acacia* scrublands, the mean distance between leader males in the wet season was significantly higher than that of the dry season. Similarly, band spread was higher during the dry season than the wet season, although this relationship was not significant. Although the relationship between cohesion and seasonality when foraging was relatively weak across levels of social structure, the pattern of higher cohesion during the dry season was consistent despite the wet season's more abundant food resources.

In examining why these seasonal relationships did not conform to expectations, it is important to distinguish between different patterns of dispersion displayed by the baboons. When foraging in *Acacia* scrublands, the band tended to separate into smaller parties (OMUs and clans) with each OMU going to a different shrub. This clumped pattern of dispersion corresponds to the distribution of *Acacia* spp. shrubs. Unlike the clumped distribution of these shrubs, *Tribulus cistoides* is more uniformly distributed. Therefore, when foraging on *T. cistoides* flowers the baboons were able to spread out more evenly.

As discussed in section 4.3.3, *T. cistoides* made up 60% of the feeding records in August, a substantially higher percentage than any other plant species' contribution to any month's feeding records. *T. cistoides* flowers were widespread and uniformly distributed in August, covering all areas of the ground (aside from those consisting solely of rock and devoid of vegetation) in *Acacia* scrublands and open grasslands. During the wet season, therefore, when the baboons concentrated their feeding on these flowers, they were able to spread out while eating them, instead of increasing their cohesion in relation to the abundance of *A. senegal* leaves and flowers as I predicted.

This relationship between the spatial distribution of the baboons and that of frequently consumed food species is further confirmed by examining the differences in cohesion within the wet season. While band 1 concentrated on *T. cistoides* flowers in the second wet season month (August), they were not yet available in July, the beginning of the wet season. During this time, the baboons foraged predominantly on the fresh leaves and flowers of *A. senegal*. Both OMU and clan cohesion was higher in July than in August. In other words, OMU members remained closer to one another when foraging in *Acacia* shrubs and spread out more when feeding on *T. cistoides* flowers. Clans also

spread out more in August than in July, reflecting the widespread, uniform distribution of *T. cistoides* flowers.

As discussed in Chapter 6, the presence of doum palms appears to allow both larger band and clan sizes at Filoha than at other hamadryas sites. Despite the fact that Band 1 at Filoha was more than twice as large as bands at Erer Gota (Kummer 1968a), results from this study suggest that the baboons did not spread out as far during daily travel as did their counterparts at Erer Gota (Kummer, 1968a). Furthermore, bands at Erer Gota separated into OMUs and clans after departing from the sleeping cliff in the morning and often reunited only at water holes and as they approached the evening sleeping site (Kummer, 1968a; Sigg and Stolba, 1981; Abegglen, 1984; Stambach, 1987). Band 1 at Filoha almost never traveled as independent OMUs, or in groups of fewer than nine OMUs (i.e., an entire clan), for more than an hour during daily travel. There was just one night when as few as six OMUs slept on the Filoha cliff while the rest of the band slept on the Wasaro cliff. On this day, these OMUs got separated from the rest of the band late in the day by Afar and their cattle as the band began traveling towards Wasaro. By the time all of the cattle passed, these six OMUs traveled back to the Filoha cliff instead of catching up with the rest of the band en route to the Wasaro cliff; they reunited with the rest of the band the following morning.

While Band 1 members associated along OMU and clan lines during daily travel, the band remained as a cohesive unit for most of the study period. The richer environment at Filoha, therefore, appears to allow the baboons to forage as a cohesive band for most of the year. When limited availability of palm fruit and fresh *A. senegal* leaves, flowers, and seeds necessitated separating into independent clans, cohesion within and between OMUs remained the same. This suggests that the availability of resources

does not influence whether the baboons break into individual OMUs. Rather, clans appear to be more important than OMUs as foraging units at Filoha.

When Band 1 did separate into independent clans for extended periods, there was no prior indication that they were going to split. Furthermore, there were no differences in OMU, clan, or band cohesion between the week(s) or month just prior to the split and those just after the band reunited. In addition, the presence of predators in the Filoha region during the month-long split was one of the highest of any four week period over the study period. This suggests that the baboons did not travel as independent clans due to lower predation threat.

Table 7.1 OMU and clan cohesion by OMU

OMU	Number of Females	Mean OMU Spread (m) All Scans (N)	Mean Number OMUs Within 10 m Radius of Leader Male (N)	Mean Distance Between Leader Male and Next Closest Leader Male (m) (N)
Clodio	1	4.5 (104)	1.8 (102)	6.9 (46)
DJ	1	3.2 (37)	1.6 (35)	7.8 (14)
Ethan	1	1.7 (20)	2.5 (20)	6.6 (17)
Fruit	1	3.0 (23)	2.2 (23)	7.5 (17)
Kalid	1	4.2 (95)	1.8 (91)	5.7 (39)
Mercury	1	2.9 (29)	1.7 (91)	6.4 (15)
Mike	1	4.7 (92)	1.8 (89)	6.5 (42)
Nelson	1	4.9 (56)	1.5 (55)	6.9 (21)
Peach1	1	3.0 (28)	1.5 (26)	8.6 (12)
Pete	1	2.2 (50)	2.6 (44)	5.0 (33)
Sami	1	3.6 (33)	2.5 (33)	6.4 (21)
Shato1	1	2.9 (14)	1.4 (14)	7.5 (4)
Teddy1a	1	1.9 (19)	1.6 (18)	5.1 (7)
Teddy1b	1	4.5 (26)	1.9 (26)	5.8 (17)
Peach2	2	4.6 (45)	2.7 (43)	6.7 (31)
Pope	2	9.0 (17)	1.6 (17)	6.0 (8)
Shato2	2	5.1 (32)	2.4 (30)	6.9 (21)
Teddy2	2	3.4 (29)	1.9 (29)	6.4 (18)

Table 7.1 (cont.)

<i>OMU</i>	<i>Number of Females</i>	<i>Mean OMU Spread (m) All Scans (N)</i>	<i>Mean Number OMUs Within 10 m Radius of Leader Male (N)</i>	<i>Mean Distance Between Leader Male and Next Closest Leader Male (m) (N)</i>
Yirdaw2	2	4.5 (37)	2.1 (36)	5.8 (22)
Andy	3	5.5 (106)	1.9 (103)	6.6 (53)
Cory	3	7.3 (69)	2.0 (65)	6.5 (33)
Evangadi	3	6.9 (40)	2.3 (40)	5.8 (25)
Mac3	3	5.6 (35)	2.5 (34)	6.1 (27)
Titi	3	6.9 (32)	2.5 (31)	4.7 (18)
Tripp	3	4.3 (104)	1.8 (97)	7.3 (53)
Yirdaw3	3	8.0 (39)	2.6 (36)	5.6 (25)
Len4	4	10.0 (11)	1.7 (11)	8.0 (4)
Mac4	4	9.9 (22)	1.5 (21)	8.5 (8)
Herb	5	9.1 (16)	2.5 (16)	4.6 (13)
Len5	5	6.5 (11)	2.6 (11)	6.1 (6)
Redface	5	7.5 (52)	2.0 (51)	6.4 (33)

Table 7.2 Mean OMU spread by OMU size

<i>OMU Size</i>	<i>Mean OMU Spread (m)</i>	<i>N</i>	<i>Standard deviation</i>	<i>Range (m)</i>
1-female	3.8	626	6.0	0-45
2-females	4.9	160	5.5	0.5-40
3-females	6.0	425	5.9	0.5-32
4-females	9.9	33	7.3	2-27
5-females	7.7	79	4.7	2-25

Table 7.3 OMU and clan cohesion, density, and availability within *Acacia* scrublands patches

<i>Transect</i>¹	<i>Mean OMU Spread (m) (N)</i>	<i>Mean Number OMUs Within 10 m Radius of Focal Male (N)</i>	<i>Mean Distance Between Leader Male and Next Closest Leader Male (m) (N)</i>	<i>Total Density</i>²	<i>Acacia spp. Density</i>³	<i>A. senegal Availability</i>⁴
1	4.3 (14)	1.7 (14)	7.2 (9)	0.05	0.04	0.4
4	5.7 (17)	1.8 (16)	6.1 (9)	0.31	0.16	0.5
9	4.9 (47)	1.3 (45)	7.4 (14)	0.17	0.11	0.7
13	8.3 (10)	1.0 (10)	n.d.	0.17	0.08	n.d.
21	6.7 (20)	1.5 (20)	6.2 (6)	0.12	0.05	0.3

¹See Tables 3.2 and 3.3 for details of transects

²Total Density = Number of individuals of all woody species per square meter

³*Acacia* spp. Density = Number of individuals of *Acacia* spp. per square meter

⁴*A. senegal* Availability = *A. senegal* density (# *A. senegal* individuals per square meter)

X mean DBH of *A. senegal*

individuals

n.d.=no data

Table 7.4 OMU and clan cohesion, and density and availability of palm trees (*Hyphaene thebaica*) among palm patches

<i>Transect</i>¹	<i>Mean OMU Spread (m) (N)</i>	<i>Mean Number OMUs Within 10 m Radius of Focal Male (N)</i>	<i>Mean Distance Between Leader Male and Next Closest Leader Male (m) (N)</i>	<i>Density</i>²	<i>Availability</i>³
2	7.8 (52)	1.5 (49)	5.5 (30)	0.05	1.3
3	4.1 (41)	2.9 (39)	8.4 (18)	0.07	2.1
5	5.5 (38)	1.7 (38)	7.0 (19)	0.06	1.8

¹see Table 3.6 for details of transects

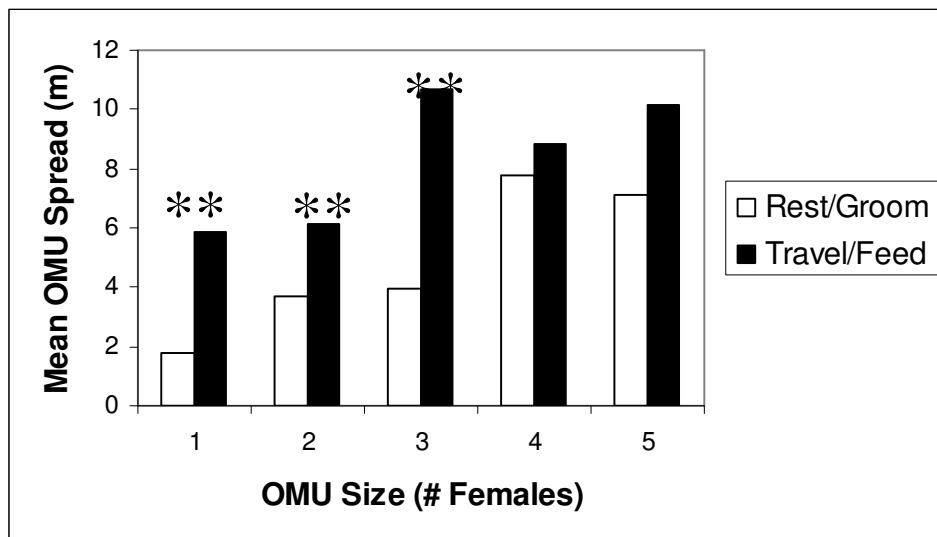
²Density = Number of palm trees per square meter

³Availability = Density X mean DBH

Table 7.5 Clan and band cohesion by activity states and habitat type

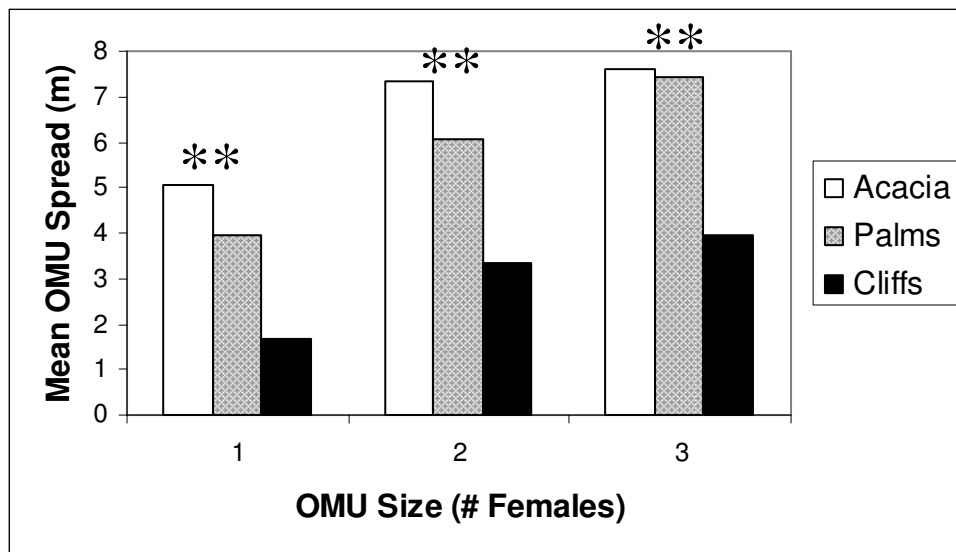
<i>Activity States and Habitat Types</i>	<i>Mean Number of OMUs Within 10 m Radius of Focal Male (N)</i>	<i>Mean Distance Between Nearest Neighbor Leader Males (m)(N)</i>	<i>Band Spread (m) (N)</i>
Rest/Groom	2.3 (821)	6.2 (549)	136.5 (47)
Travel/Feed	1.5 (288)	7.3 (89)	270.7 (88)
<i>Acacia</i> Scrublands	1.5 (527)	6.8 (202)	269.1 (106)
Palm Forests	2.0 (172)	6.5 (101)	161.1 (29)
Cliffs	2.5 (502)	6.2 (358)	158.6 (69)
Swamp Vegetation	1.5 (21)	5.9 (8)	135.0 (4)
Open Grasslands	1.9 (54)	5.4 (34)	144.6 (4)
Rest/Groom			
<i>Acacia</i> Scrublands	1.8 (236)	6.6 (126)	NO DATA
Palm Forests	2.4 (77)	5.7 (55)	
Cliffs	2.5 (456)	6.1 (333)	
Swamps	1.7 (11)	6.3 (6)	
Grasslands	2.1 (41)	5.4 (29)	
Travel/Feed			
<i>Acacia</i> Scrublands	1.3 (201)	7.5 (47)	NO DATA
Palm Forests	1.8 (58)	6.9 (31)	
Cliffs	1.8 (13)	8.4 (8)	
Swamps	1.1 (7)	6.0 (1)	
Grasslands	1.2 (9)	6.0 (2)	

Figure 7.1 Mean OMU spread by activity state and OMU size



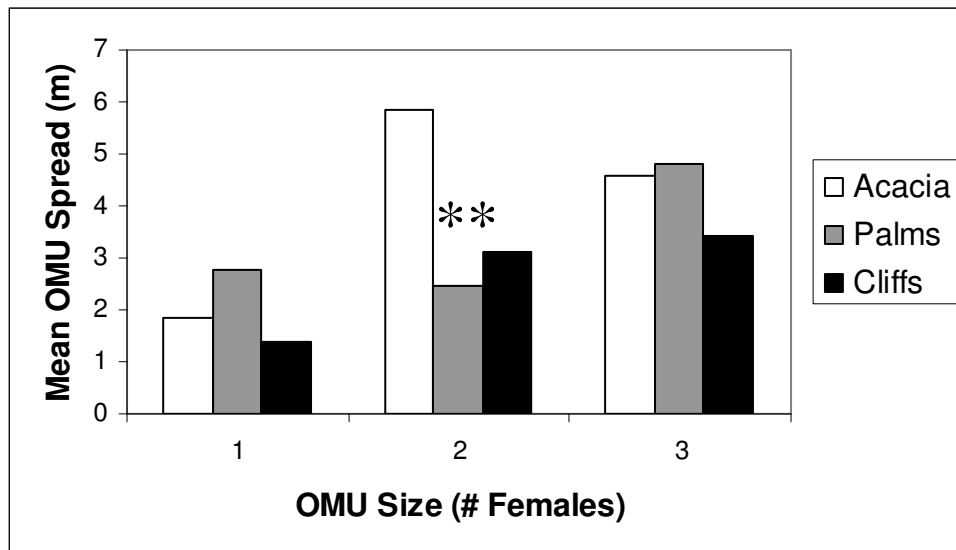
**= significant difference, $p < 0.05$

Figure 7.2 Mean OMU spread by habitat for 1-, 2-, and 3-female OMUs



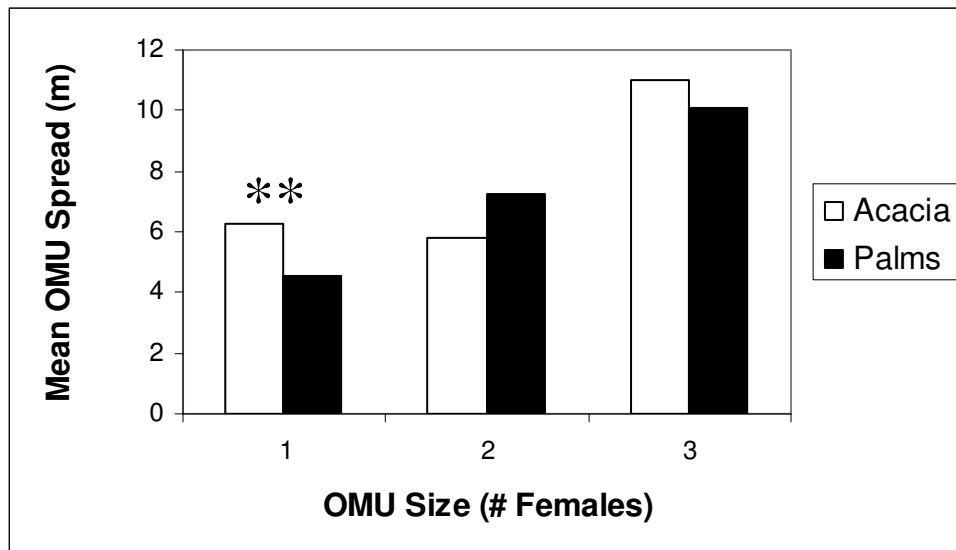
** = significant difference, $p < 0.05$

Figure 7.3 Mean OMU spread when resting and/or grooming across habitat types for 1-, 2-, and 3-female OMUs



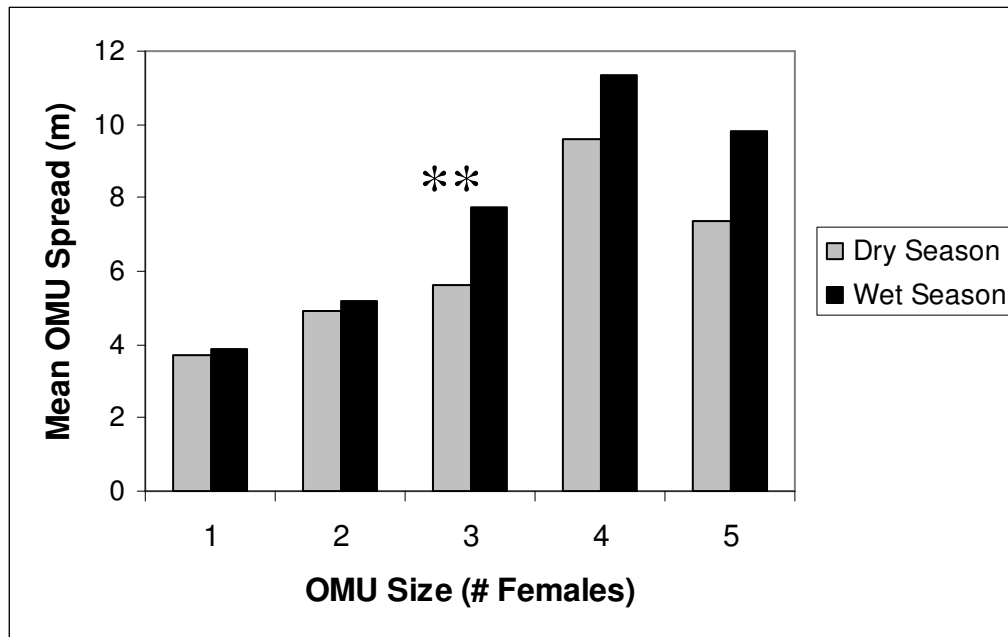
**= significant difference, $p < 0.05$

Figure 7.4 Mean OMU spread when traveling and/or feeding in *Acacia* scrublands and palm forests for 1-, 2-, and 3-female OMUs



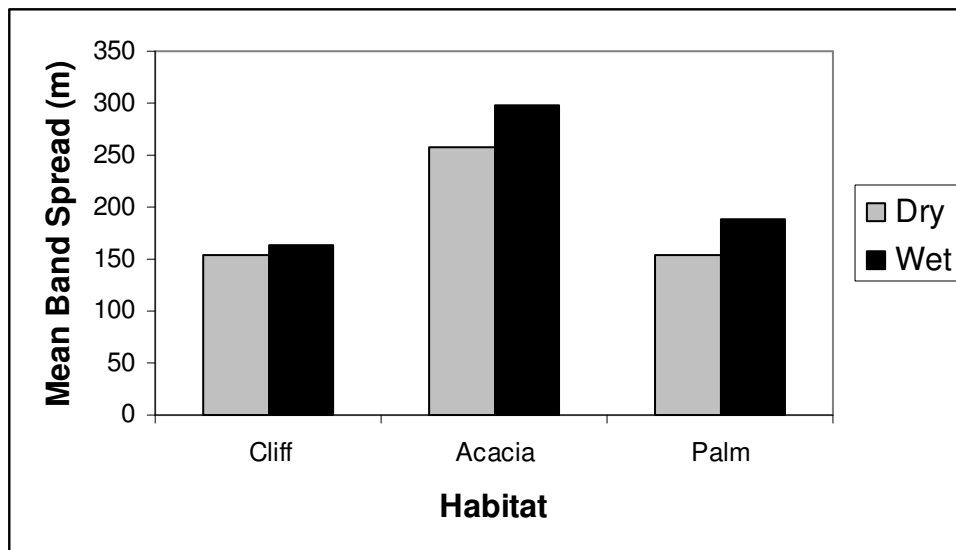
**= significant difference, $p < 0.05$

Figure 7.5 Seasonal variation in OMU cohesion by OMU size



**= significant difference, $p < 0.05$

Figure 7.6 Seasonal variation in band spread by habitat type



CHAPTER 8

CONCLUSIONS AND DISCUSSION

In this study, I quantified the distribution and abundance of resources in the home range of Band 1 of the Filoha hamadryas population, and systematically investigated the relationship between these patterns and changes in Band 1's multilevel social structure, home range use, and travel patterns. In this chapter, I summarize the results presented in Chapters 4 through 7 and discuss them in relation to the evolutionary history of hamadryas baboons. I conclude this dissertation with a discussion of how the results of this study impact current models of the evolution of baboon social organization.

8.1 Summary of Results

8.1.1 Resource Distribution and Abundance

The Filoha region of Awash National Park comprises five habitat types: *Acacia* scrublands, palm forests, open grasslands, swamp vegetation, and cliffs. *Acacia* scrublands, open grasslands, and cliffs are all typical of hamadryas habitat in other parts of their geographic range (Kummer, 1968a; Sigg and Stolba, 1981; Biquand et al., 1992; Al-Safadi, 1994; Zinner et al., 2001a; Swedell, 2006). However, the presence of palm forests and swamp vegetation within hamadryas habitat is uncommon. Overall, during my study period, the availability of food resources was higher in palm forests than in *Acacia* scrublands, and ripe palm fruit was available for seven out of twelve months. Due to the presence of doum palms (*Hyphaene thebaica*) in the Filoha region, preferred food resources are less dispersed than in other parts of hamadryas range. Furthermore, the

Filoha hot springs provide the baboons with a year-round water source. Thus, the Filoha region is a more resource-rich environment than other hamadryas sites.

8.1.2 Feeding Ecology

From March 2005 through February 2006, Band 1 most frequently consumed doum palm fruit and the seeds, leaves, and flowers of several *Acacia* species. The top three plant species – *Acacia senegal*, *H. thebaica*, and *Tribulus cistoides* – comprised more than half of the total feeding records. Each plant's inclusion in the diet, however, varied seasonally. While the baboons' use of *A. senegal* remained consistent across the dry and wet seasons, they fed on *H. thebaica* predominantly during the dry season, and they consumed *T. cistoides* more frequently during the wet season. The baboons' variable consumption of these plant species and their parts corresponded to their abundance in Band 1's home range.

The baboons were selective feeders despite the overall diversity in their feeding behavior. They fed predominantly on *H. thebaica* when its fruit was ripe, and they preferred the dry seeds and fresh flowers of *A. senegal*. The baboons fed on leaves, however, only when fresh leaves were abundant and their preferred foods were not available.

The presence of palms in the Filoha region strongly influenced Band 1's feeding ecology. Doum palm fruit comprised between 20-36% of monthly feeding records during each of the seven months in which ripe fruit was available, and no more than 8% in the remaining five months of the year. Hence, ripe doum palm fruit dominated the baboons' diet when it was available.

Like other baboons, *Acacia* species dominated Band 1's feeding behavior and they preferred their flowers when they were available. Conversely, Band 1 consumed fewer plant species and spent less time feeding than other baboons, and fruit comprised a greater proportion of their feeding records. These differences can be attributed to the presence of *H. thebaica* in the Filoha region and the important role it plays in the baboons' feeding behavior.

8.1.3 Hamadryas Social Structure at Filoha

Overall, the baboons at Filoha displayed the multilevel social structure typical of hamadryas baboons. Several differences, however, emerged among Band 1 at Filoha and other hamadryas populations at the band, one-male unit, and clan levels (Kummer, 1968a; Abegglen, 1984; Biquand et al., 1992; Zinner et al., 2001b).

Consistent with previous research at Filoha (Swedell, 2002b, 2006), the band sizes from March 2005 through February 2006 were larger than those described elsewhere, and this is attributable to the high abundance and availability of food resources relative to other hamadryas sites. The size and composition of OMUs in Band 1 over the study period were similar but less consistent over time compared to other known Ethiopian hamadryas populations. Females transferred in or out of almost half of the OMUs in Band 1 during this time. The majority of these changes were due to immigration and emigration to and from other bands, while three transfers occurred among OMUs within Band 1.

Prior to this study, clans had been described in only one wild hamadryas population at Erer Gota, Ethiopia (Abegglen, 1984). Cluster analyses based on spatial association among leader males revealed that during the study period, Band 1 at Filoha

consisted of two large clans with 13 and nine OMUs, respectively. The clan sizes at Filoha were larger than those at Erer Gota (Abegglen, 1984). Similar to the clans at Erer Gota, however, OMUs within each clan at Filoha rested near one another on sleeping cliffs, foraged together during daily travel, and sometimes traveled independently from the rest of the band (i.e., the other clan). Furthermore, band fissions, takeovers, and extra-OMU interactions occurred along clan lines.

The evolution of this flexible, multilevel social structure unique to hamadryas is likely related to the wide dispersion and low availability of resources in their habitats (Kummer 1968a,b, 1971, 1990, 1995; Dunbar, 1988), enabling the baboons to split up into individual OMUs when resource density and abundance is lowest. Kummer (1968a,b, 1995) suggested that the size and spatial cohesion of hamadryas groupings are related to resource density and distribution: both total band cohesion and individual OMU cohesion would be greatest in areas with high resource density and lowest in less dense locales. Prior to this study, however, the ecological and spatial cohesion data needed to test Kummer's postulated association were not available.

Overall, spatial cohesion at each level of hamadryas social structure (i.e., one-male unit, clan, and band) was highest when the baboons were resting and grooming on cliffs. There were no clear relationships, however, between spatial cohesion and the distribution and abundance of food and water resources. Cohesion was greater in palm forests than in *Acacia* scrublands only at the clan level of hamadryas society; that is, clans were more internally cohesive – i.e., OMUs within clans were closer together – in palm forests than *Acacia* scrublands. Furthermore, cohesion did not vary within either *Acacia* scrublands or palm forest patches according to the density of *A. senegal* and *H. thebaica*, respectively. Finally, there was a pattern of increased spatial cohesion during the dry

season across levels of social structure, despite the higher abundance and availability of *Acacia* spp. flowers, leaves, and seeds during the wet season.

This observed seasonal pattern is likely due to the different ways that the baboons spread out while foraging in *Acacia* scrublands. When foraging on *Acacia* species, the band tended to separate into smaller parties with each OMU going to a different shrub, corresponding to these shrubs' clumped distribution. In contrast, *T. cistoides* is more uniformly distributed, and consequently, the baboons were able to spread out more evenly when foraging on this species. During the wet season, therefore, when the baboons concentrated their feeding on *T. cistoides* flowers, they were able to spread out while eating them, instead of increasing their cohesion in relation to the abundance of *A. senegal* leaves and flowers. The differences in cohesion *within* the wet season confirm that the baboons displayed different patterns of dispersion in *Acacia* scrublands depending on which species they foraged. While *T. cistoides* flowers dominated Band 1's wet season feeding records, they were not available until August, the second month of the season. In July, the baboons fed predominantly on the fresh flowers of *A. senegal*. Both OMU and clan cohesion was higher in July than in August. In other words, OMU members remained closer to one another when foraging in *Acacia* shrubs and spread out more when feeding on *T. cistoides* flowers. Clans also spread out more in August than in July, reflecting the widespread, uniform distribution of *T. cistoides* flowers.

Another reason for the lack of a clear relationship between spatial cohesion and the distribution and abundance of resources may be due to the limited data available to test this association. There were only five *Acacia* scrublands patches for which I had enough data to compare measures of spatial cohesion, and sample sizes were small. While I conducted 23 vegetation transects in *Acacia* scrublands in Band 1's home range, I

only used spatial cohesion measures in these analyses when I was certain that the baboons were located in the patch represented by the transect. Similarly, there were only three palm patches for which I had enough data to compare spatial cohesion measures. In one of these patches, the baboons spent the majority of their time resting and grooming, and the other two patches were very similar in density and availability of palms. These patches, therefore, did not provide a useful basis for comparisons of spatial cohesion while foraging in palm forests. This study would have benefited from additional spatial cohesion data in patches in which the baboons most frequently foraged as well as more extensive sampling of the vegetation in these locations.

Furthermore, more systematic phenological sampling of palm fruit and *A. senegal* would have improved this study. While I had originally intended to sample the abundance of these species bi-monthly in each vegetative transect, this was not possible due principally to the prohibitively large size of Band 1's home range. The baboons extended their range over a wider area by the end of the study compared to when I began collecting data, and while I was able to complete additional vegetative transects as the baboons exploited new areas, these regions were not monitored consistently over the study period.

Despite the limitations of this study and the fact that no clear discernible relationship emerged between spatial cohesion measures and the distribution and abundance of important resources in Band 1's home range, the presence of doum palms in the Filoha region does appear to influence aspects of the baboons' social structure. Namely, the large band and clan sizes at Filoha compared with those at other hamadryas sites likely reflect the high abundance and availability of doum palm fruit.

Although Band 1 at Filoha was more than twice as large as the bands at Erer Gota (Kummer 1968a), results from this study suggest that the baboons did not spread out as far during daily travel as did their counterparts at Erer Gota (Kummer, 1968a). Furthermore, bands at other sites separated into OMUs and clans after departing from the sleeping cliff in the morning and often reunited only at water holes and as they approached the evening sleeping site (Kummer, 1968a; Sigg and Stolba, 1981; Abegglen, 1984; Stambach, 1987). While Band 1 members associated along OMU and clan lines during daily travel, the band remained as a cohesive unit over the course of the day for the majority of the study period, and Swedell (2002b, 2006) found this to be the case as well. The relatively resource-rich environment at Filoha, therefore, appears to allow the baboons to forage as a cohesive band for most of the year. When limited availability of palm fruit and fresh *A. senegal* leaves, flowers, and seeds necessitated separating into independent clans, cohesion within and between OMUs remained the same. This suggests that the availability of resources does not influence whether the baboons break into individual OMUs. Rather, the distribution of palm trees allows the baboons to forage as clans rather than OMUs during periods of both high and low availability of palm fruit. Clans, therefore, appear to be more important than OMUs as foraging units at Filoha.

8.1.4 Hamadryas Habitat Use and Travel Patterns at Filoha

Band 1's home range size from March 2005 through February 2006 was at least 38.6 km². The band probably ranged over a much larger area, however, as there were periods of time in which I could not locate the baboons at either the Filoha or Wasaro sleeping cliffs. The baboons did not use their home range evenly, spending less time than expected in *Acacia* scrublands, and more time than expected on cliffs and in palm forests.

This uneven use of their home range corresponds with the large proportion of time that the baboons spent resting and grooming on sleeping cliffs and the clumped distribution of doum palm fruit.

The baboons' mean daily path length was 8.3 km. Despite the presence of both a permanent water source and doum palm fruit in proximity to the Filoha cliff sleeping site, Band 1's home range size was not smaller and daily path lengths were not shorter than those at other hamadryas sites. Although they were not constrained by food and water resources, the baboons still traveled up to 14.2 km each day.

Furthermore, Band 1's long daily paths do not appear to be a consequence of its large band size. The mean daily path length when clans traveled independently was larger than when Band 1 traveled as a cohesive band, despite the fact that clans consisted of only half the number of individuals as the entire band. Additionally, Band 3's mean daily path length was shorter than that of Band 1 even though it comprised twice as many baboons than did Band 1. Finally, Band 1's mean daily path length was comparable to those reported at Erer Gota, despite the larger band sizes at Filoha.

Seasonal patterns in Band 1's ranging behavior were evident. The baboons spent more time away from Filoha during the wet season than the dry season. Presumably, it was not necessary to stay near Filoha due to the availability of standing water throughout their home range during the wet season. Furthermore, the mean daily path length was significantly shorter in the dry season than the wet season, likely a reflection of the baboons' need to remain in proximity to the permanent water sources at Filoha.

These seasonal patterns, however, are not as clear-cut as they seem. The baboons employed two disparate ranging strategies during the wet season. In July, when water and fresh leaves were available throughout the Filoha region, the baboons ranged widely

and increased their feeding breadth, taking advantage of the widespread resources. In August, however, when water and *T. cistoides* flowers were available, the baboons ranged over a smaller area that they were unable to utilize as intensively during the rest of the year. Band 1 remained in the Wasaro vicinity for all of August, despite the fact that these flowers were available throughout their home range, including surrounding the Filoha cliff. The baboons seem to have taken advantage of the small window of opportunity in which both water and a preferred food resource were available in order to decrease their foraging effort.

Contrary to expectations, daily path lengths did not decrease as the proportion of doum palm fruit in the baboons' diet increased. During periods of peak consumption of palm fruit the baboons started their day on one cliff and traveled to the other more frequently than in months when palm consumption was low; daily paths were significantly longer when they traveled from one cliff to the other than when they started and ended their travel route on the same cliff (section 5.4.1). The baboons' reliance on palms, however, did appear to influence their travel patterns. The band's use of its home range was tied to where the baboons fed on palm fruit; the baboons utilized the northern part of their home range when they foraged in the Hot Springs and Alibete palm forests, and they used the southern portion of their home range when they fed from the palm clumps southeast of Filoha. Furthermore, the farthest point from the evening sleeping site was located in palms in over two-thirds of the complete travel routes in which the baboons were observed eating palm fruit.

8.2 Socioecology, Evolutionary History and Baboon Social Organization

8.2.1 *Hamadryas Baboons, Socioecology, and Evolutionary History*

The behavior and social systems of non-human primates have generally been described and explained within the context of socioecology, the study of how environmental conditions influence observed patterns of behavior and social structure (e.g., Crook and Gartlan, 1966; Clutton-Brock and Harvey, 1977; Wrangham, 1980; Terborgh and Janson, 1986; van Schaik, 1989; Isbell, 1991; Sterck et al., 1997). The primary objective of the current study was, in fact, to investigate how environmental conditions – namely the distribution and abundance of resources – influence the feeding and ranging behavior and social structure of wild hamadryas baboons at Filoha.

Results indicate that Band 1 at Filoha had a large home range and traveled long distances each day, despite both the high availability of doum palm fruit and the presence of a permanent water source in close proximity to the Filoha cliff, a pattern also found by Swedell (2002b, 2006). The baboons still traveled up to 14 km a day even though ample food and water resources were available within 0.5 km of the Filoha sleeping site. I did not observe the baboons feeding on any food species away from Filoha that were not also available in the Filoha region, suggesting that the baboons did not need to range over such a large area or travel such long distances to obtain critical resources. The baboons at Filoha also still displayed the multilevel social structure typical of hamadryas even though resource distribution did not necessitate the breaking up into smaller units in order to obtain sufficient food during most of the year.

These results suggest that Band 1's ranging behavior and social structure cannot be explained solely through the lens of socioecology. Furthermore, various lines of evidence, including a comparison of the daily path lengths of individual clans with those

of the entire band, show that the large band sizes at Filoha are also not responsible for their large home range and long travel routes.

Primatologists have, in fact, long been aware that phylogenetic history likely plays a role in explaining aspects of primate behavior and ecology (e.g., Struhsaker, 1969; Clutton-Brock, 1974; Dunbar, 1988; Di Fiore and Rendall, 1994; Rendall and DiFiore, 1995; Henzi and Barrett, 2003, 2005). Phylogenetic approaches view present-day populations from a historical perspective. Each species brings with it a different phylogenetic history into a particular ecological situation, and this heritage may outweigh the influence of ecology as the limiting factor determining social structure and behavior due to its resistance to change or yield (Di Fiore and Rendall, 1994; Rendall and Di Fiore, 1995). For example, in a phylogenetic analysis of the social systems of 37 primate genera, Di Fiore and Rendall (1994) found that nine of the 10 cercopithecine species clustered together as a derived group, displaying very similar social structures that are quite different from those of other primates. They suggest that this pattern of divergence shows that the social organization of Old World monkeys is highly influenced by their evolutionary history.

Several aspects of hamadryas behavior have been shown to be invariable over an assortment of environmental conditions, including ranging behavior (Lackman-Ancrenaz, 1994) and aspects of male social behavior (Kummer and Kurt, 1965; Colmenares, 1990). With current ecology and group size ruled out as determining factors of Band 1's large home range, long travel routes, and multilevel social system, it seems likely that their evolutionary history may also be responsible for their ranging behavior and social structure.

8.2.2 *Hamadryas Baboons and the Evolution of Baboon Social Organization*

The results of this study impact current models of the evolution of baboon social organization (e.g., Bercovitch, 1990; Kummer, 1995; Henzi & Barrett, 2003, 2005; Jolly, 2007). The social structure of most *Papio* species consists of multi-male, female-bonded groups in which females are philopatric and males disperse. The place of hamadryas baboons within the genus – with their flexible social structure, cohesive one-male units, philopatric males, and the majority of social interactions taking place between males and females – has long been a puzzle in primate socioecology.

The multi-male, female-bonded social groups of most baboon species were viewed as adaptations to environments consisting of defensible clumped resources (Wrangham, 1980; Dunbar, 1988) while hamadryas' multilevel social structure made sense as adaptations to an arid environment with dispersed food resources. Populations of other *Papio* species, however, inhabit mountains and deserts – areas with low density and scattered distribution of food resources (Jolly, 2007). Furthermore, genetic evidence does not place hamadryas baboons as the sister taxon to the rest of the baboons; rather, anubis and yellow baboons are more closely related to hamadryas baboons than either are to chacmas (Newman et al., 2004; Wildman et al., 2004). The neat ecological scenario for the evolution of baboon social structures, therefore, has not held up and phylogenetic history must play a role in reconstructions of the evolution of baboon social organization (Henzi and Barrett, 2003, 2005 and Jolly, 2007).

As discussed above, results of this study, in which Band 1 at Filoha traveled long distances each day and split up into clans and OMUs during daily travel despite the relatively resource-rich environment in which they live, suggest that ecology cannot be the sole factor influencing social structure and behavior. Results also show that the large

band sizes at Filoha are not responsible for their large home range and long daily paths. It follows, then, that evolutionary history plays a large role in shaping hamadryas behavior. This point is further made by the facts that hamadryas and anubis baboons live in the same area in the Awash region yet retain the social structures characteristic of their own species (e.g., Nagel, 1971, 1973). In contrast, while chacma baboons living in extreme montane environments sometimes live in one-male groups (Byrne et al., 1987), they do not exhibit the multilevel social structure typical of hamadryas baboons.

Furthermore, Guinea baboons – the *Papio* species about which we know the least – share an assortment of traits with hamadryas baboons even though they live in a variety of habitats in western Africa, including savannas, woodlands, and forests (Galat-Luong et al., 2006). Despite this range of habitat types, Guinea baboons appear to have a multilevel social structure similar to that of hamadryas baboons. They live in large troops of up to several hundred baboons that tend to congregate at sleeping sites (Sharman, 1981; Anderson and McGrew, 1984). Within these large aggregations, clear one-male units exist and, like hamadryas OMUs, they consist of a leader male, one or more females, their dependent offspring, and sometimes a follower male (Dunbar and Nathan, 1972; Sharman, 1981; Boese, 1975). Guinea baboons display an additional level of social structure between that of the OMU and troop, which appears to be similar to hamadryas clans in size, composition, and the affiliative relationships among males (Galat-Luong et al., 2006), and this clan-like level appears to be the main foraging unit. Further research is necessary to determine whether males are philopatric, if females enter OMUs as a result of aggressive takeovers by males, and if mating occurs exclusively within the OMU, as in hamadryas baboons. In addition to these similarities in social structure,

Guinea baboons share several physical characteristics with hamadryas such as a distinct mane in adult males (Jolly, 1993, 2007).

The fact that hamadryas share a similar social structure with Guinea baboons, despite the clear differences in their habitats, lends support to Jolly's (1993, 2007) claims that Guinea and hamadryas baboons are sister taxa. Future studies are needed to investigate whether Guinea baboons are more likely to forage as clans in marginal areas of their range and in periods of low food availability, as seems to be the case for hamadryas, and if their travel patterns vary according to the distribution of resources in their various habitats, which does not appear to occur in hamadryas baboons.

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