ADDIS ABABA UNIVERSITY

SCHOOL OF GRADUATE STUDIES

Behavioural ecology of gelada (*Theropithecus gelada*) in the Gich area in the Simien Mountains National Park, Northern Ethiopia

By

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A Thesis presented to the School of Graduate Studies of Addis Ababa University in partial fulfillment of the requirements for the Degree of Doctor of Philosophy in Biology (Ecological and Systematic Zoology)

Addis Ababa, Ethiopia

June 2015

Abstract

Behavioural ecology of gelada (Theropithecus gelada) living in the Simien Mountains National Park, northern Ethiopia

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The main objectives of the present study are to conduct detailed investigations on population status, activity budget, foraging and ranging patterns of geladas living in the Gich area of the Simien Mountains National Park. Population census was conducted from early 2013 to late 2014 using a total-count sampling method. Activity data were collected using focal animal scan sampling method during ten days each month from May 2013 to April 2014. Average population size for two years of census period resulted in 661 individuals. There was a significant difference in the mean percentage of age/sex composition of individuals. Geladas fed on 27 species of plants, but the number of species varied markedly between seasons with dietary diversity being significantly more during the dry season. Festuca spp. formed a major dietary constituent throughout the year, contributing more than 78% of feeding records. Macronutrients had a complex influence on food plant species selection in gelada. Gelada spent on average 56.7% of daylight hours feeding, 14.1% travelling, 10.7% resting, 17.5% socializing and 1.1% in other non-social activities. There was seasonal difference in activity budgets and age/sex classes showed variation in time budgets. Geladas exclusively used cliff-face crevices as sleeping sites at night. The choice of top sleeping sites depended partly on the elevation of cliffs and protection that they provided gelada from natural predators.

Key words: activity budget, cliff, diet, gelada, Gich, population status, SMNP

ACKNOWLEDGEMENTS

My first, sincere gratitude goes to my supervisor, Prof. Afework Bekele for his wholehearted and consistent guidance of my study. I am also grateful to him for the provision of his own research materials and field equipment. I am very lucky to gain his immediate response, encouragement and unreserved genuine support from the very beginning until the completion of the research project in its present form. I have to admit that without his kind support, this Thesis would not have been realized.

My study was funded by the Department of Zoological Sciences of Addis Ababa University and Animal Diversity Thematic Research group. The University of Gondar also provided additional research grant for the completion of the study. I am very grateful to have received financial support from these institutions.

Dr. Abebe Getahun, head of the Department of Zoological Sciences, is highly appreciated for his prompt responses and facilitation of the required logistics for this study.

Permission was granted by the regulatory requirements of the Ethiopian Wildlife Conservation Authority (EWCA). I thank the authority for granting me the permit to conduct the study on geladas in the Simien Mountains National Park.

My field work would not have been possible without the generous logistical support of Mr. Maru Biadglegn, the Chief Warden of the National Park. I would like to thank the staff of the Park for their cooperation.

I would like to extend my gratitude to Dr. Gurja Belay of Addis Ababa University for his words of encouragement and insightful comments on my research methodology and study animals.

Finally, I would like to express my sincere appreciation to my wife, Helen Hailemariam, for her patience and moral support extended to me throughout the course of the study.

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1. INTRODUCTION

Primates constitute one of the 18 orders of mammals and are one of the best studied groups of animals. Conspicuousness and relative ease of identification of different species of primates might have contributed to the intensive investigations of their distribution and behavioural ecology (Chapman, 1995; Douglas, 1996; Fleagle, 1999).

The phylogeny of primates has been an area of broad investigation. A great deal has been already known about the phylogeny and patterns of distribution of many primate clades (Lehman and Fleagle, 2006). Primates are particularly found in the Neotropics, Africa and Asia (Fleagle, 1999). There are no currently extant species of primates on either Antarctica or Australia. There is also no indication which shows that primates had ever inhabited these continents (Reed and Fleagle, 1995; Fleagle, 1999).

Geographically, primates are widespread in most tropical areas. They have the highest diversity in lowland tropical rainforests including mangrove and freshwater swamp forests. Many species have rather restricted distributions, and are threatened by habitat loss and commercial hunting. Conversely, some are abundant and tend to depredate agricultural crops near forest edges (Goodman *et al.,* 2005; Lehman and Fleagle, 2006). Species diversity is highest in the Neotropics, Asia and the island of Madagascar. This is exceptional because the island is considerably smaller in area than any of the other tropical regions (Jolly, 1986; Richard and Dewar, 1991; Godfrey *et al.,* 1999). At higher taxonomic levels, most of the genera are located in Africa whereas most of the families are found in the island of Madagascar and the Neotropics (Fleagle, 1999).

The total number of extant species of primates is not exactly known. Moreover, new species are being discovered or re-described at different times. Reed and Fleagle (1995) estimated the number of genera and extant species to be about 50 and 250, respectively. On the other hand, Lehman and Fleagle (2006) have reported that there are around 348 living species of primates all over the world.

Primates subsist on a variety of diets as there are species that specialize on animals, gums, fruit, leaves and various combinations of these food types. They show diverse patterns of dietary specializations at the continental level. For example, although fruit is utilized by many primate species in each region, this is more easily observed in the Neotropics. On the other hand, while leaves are consumed by many species in many regions, they are exploited by a few species in the Neotropics (Fleagle, 1999). Most primates in the Neotropical region instead exploit gums and tree secretions. Insects and other fauna are commonly exploited by primates in the Neotropics, Africa and Asia. However, these diets are not frequented by primates living in the island of Madagascar. Compared to other regions, Madagascar is dominated by folivorous primate species (Fleagle and Reed, 1996; Godfrey *et al.,* 1997; Lehman and Fleagle, 2006).

Primate populations today are declining mainly as a result of anthropogenic effects. Some of human-induced threats to their survival include habitat loss and fragmentation, deforestation, hunting and transmittable diseases of human origin. About 25 species of primates are already classified as "at risk", ten as "vulnerable" and more than two as "endangered" in Africa. There are 64 species of primates that occur in the African continent (Purves *et al.,* 2000; Chapman *et al.,* 2006; Lehman and Fleagle, 2006).

Primates devote a significant proportion of their time budgets to identify the location of food. The distribution and abundance of food resources may influence the daily travel distance, home-range size and the intensity with which an area within the home range is utilized through time (Milton, 1980; Robinson, 1986; Chapman, 1988). Animals that depend on uniformly distributed food resources are supposed to use their home range relatively evenly. However, when resources are distributed in patchy manner, they are expected to show an irregular pattern of home range use that is focused on shifting of patches (Terborgh, 1983).

Temporal and spatial variation in the availability of resources is one of the many factors that determine primate ranging patterns, and thus has a major influence on home-range size and shape (Watts, 1998; Basabose, 2005; Wallace, 2006). Home-range size of some primate species tends to increase with increasing group size. Similarly, daily travel distance may associate with both group size and habitat quality as larger groups travel farther each day, and travel distances tend to be longer for groups living in poor-quality habitats (Waser, 1977; Dunbar, 1988). In general, these relationships are more remarkable in frugivorous and omnivorous than in folivorous primates (Mace and Harvey, 1983).

Home-range sizes are generally larger in frugivorous than in folivorous primates as fruit tends to be more patchily distributed. Given that there is an abundance and relatively even distribution of leaves in many habitats, folivorous primate species usually spend less time feeding, more time resting and have shorter daily travel distances than frugivorous primates (Richard, 1985; Stanford, 1991; Dasilva, 1992; Milton, 1998). In addition to the availability and distribution of food resources, ranging patterns of primates are influenced by other ecological and behavioural factors including rainfall patterns (Raemaekers, 1980; Isbell, 1983), distribution of drinking water (Altmann and Altmann, 1970), parasite avoidance (Freeland, 1980), reproductive situation (Rasmussen, 1979; Overdorff, 1993), intergroup relationships, sleeping site or resting site location (Rasmussen, 1979; Harrison, 1983) and the need to defend territorial boundaries (Whitten, 1982).

The relationships among primate ranging patterns, habitat quality, group size and diet do not always show a straightforward pattern (Clutton-Brock, 1977; Dunbar, 1988). For example, increased intragroup feeding competition under conditions of resource scarcity may lead animals to increase their individual foraging efforts. This may be reflected in longer daily travel distance, increased time allocation to travelling and larger seasonal home range (Hunter, 2001). On the other hand, animals may respond to food scarcity without changing their ranging pattern considerably by broadening the diet or by spending more time in each feeding patch. In such cases, ranging pattern may be associated with other ecological variables, including climatic conditions (Di Fiore, 2003).

Many factors are known to influence primate activity budgets in natural habitats, most of which are associated with the challenges of gaining food energy. Activity budgets of primates are directly related to energetic requirements and may change with seasonal variations in food availability or in relation to reproductive stage of animals (Coelho, 1986; Halle and Stenseth, 2000). Time budgets are flexible and thus the ways in which animals allocate time to the main activities provide insight into their adaptation strategies. For instance, time spent feeding may be adjusted seasonally in response to changing climate, food availability or both. In this manner, animals may attain an optimal energy balance (Coelho, 1986; Hunter, 2001; Fashing *et al.,* 2014). The major plant parts that primates consume, such as fruit, flowers and leaves, usually show variations in abundance and distribution due to seasonal climatic fluctuations. During a period of food scarcity, some folivorous primates are known to feed more and travel longer distances

(Strier, 1987; Huang *et al.,* 2003), whereas many frugivorous primates tend to feed more but travel less (Terborgh, 1983; Overdorff, 1996). However, the relationships between activity budgets and seasonal variations in food availability do not always show a consistent pattern.

Nutritional factors are known to exert powerful influences on food choice, causing many challenges that primates should overcome. A very few individual plant species contain adequate concentrations of all the major macronutrients, forcing most primates to forage widely for a variety of food from many plants (Richard, 1985; Milton, 1993). Primates should take the level of fibre content into account when selecting food plant species. Food plants with high concentrations of fibrous components such as lignin, cellulose and hemicellulose are difficult to digest (Milton, 1979; Rogers *et al.*, 1990; Yeager *et al.*, 1997). Primates, especially those feeding primarily on leaves or seeds, should also deal with secondary compounds, which intend to deter herbivores from consuming them (Freeland and Janzen, 1974; Glander, 1982).

Primates spend about half of their lives in sleeping sites and thus selection of suitable sleeping site is considered as an important aspect of individual survival (Anderson, 1984; Anderson, 1998). Several factors may determine selection and use of particular sleeping sites, including safety from predators, thermoregulation, and comfort and hygiene (Anderson, 1984; Anderson, 1998; Reichard, 1998).

Predation pressure is one of the primary factors that determine sleeping site selection and use in primates (Cowlishaw, 1994; Anderson, 1998). Primates may select sleeping sites that reduce detection by predators, enhance primates' early detection of predators and that provide difficult access routes for an approaching predators (Anderson, 1998;

Reichard, 1998). Primates under high predation pressure may also employ systematic visits to different sleeping sites on successive days in order to reduce the chance of being detected (Heymann, 1995; Reichard, 1998). On the other hand, reuse of sleeping sites may increase the primates' familiarity with a location, thus improving the chance for escape (Di Bitetti *et al.,* 2000).

Primates may choose to sleep in sites that have warmer microclimates or those that are located at lower elevations protected from wind, in order to maintain a constant body temperature during the night (Anderson, 1984; Liu and Zhao, 2004). Primates may also choose sleeping sites that can facilitate group contact in the early morning. The reuse of limited sleeping sites may facilitate group re-union at dusk if the group had accidentally split up (Chapman, 1989; Anderson, 1998). When primates gather at dusk at the sleeping sites, they usually engage in grooming and other social activities (Kinzey and Wright, 1982).

Gelada (*Theropithecus gelada*) is a large primate, which is endemic to the highlands of Ethiopia (Fig.1) and is the only living species of the genus *Theropithecus*. Member species of *Theropithecus* were widespread during the Pliocene and Pleistocene periods. During the late Pleistocene era, all species became extinct except the living *Theropithecus gelada* (Pickford, 1993; Dunbar, 1998). The *Theropithecus* is one of the best known genera among the primates. However, there is no detailed knowledge about differentiation of the present populations of this genus (Dunbar, 1998; Gippoliti, 2010). *Theropithecus* has currently six known fossil species whose range extends throughout the savannah areas of Africa, Mediterranean coast and India (Jolly, 1972; Delson, 1993; Jablonski, 1993).

Figure 1. Adult male gelada (*Theropithecus gelada*)

Theropithecus gelada is a species of Old World monkeys (Fleagle, 1999). Crook (1966) suggested that gelada "monkey" would be more appropriate name for the species than gelada "baboon" as it is not a close relative of the typical baboons of the genus *Papio*. According to Crook (1966), certain similarities of geladas to baboons in terms of ecological adaptation in morphology and behaviour may be regarded as examples of convergent evolution. However, geladas are often mistakenly called baboons though genetic evidence places them as a sister taxon to *Papio*.

Theropithecus gelada has usually been considered to be composed of two subspecies, namely the *T. gelada gelada* in the northern highlands and *T. gelada obscurus* in the southern part of Ethiopia (Dandelot, 1974). A detailed test with more specimens and modern molecular techniques has not been conducted despite the lack of congruence between biogeographical barriers and the taxonomic arrangement for these subspecies. There may be a possibility of identifying more than two taxa of *Theropithecus*, but only little attention has been paid to it (Gippoliti, 2010).

Geladas are sexually dimorphic in size and appearance as males are taller and heavier than females. Males have a conspicuous brown mane over the neck and a long and heavy cape over the shoulders. Females have shorter pelage than males (Puff and Sileshi Nemomissa, 2005). Both sexes have remarkable red patches of skin on their chests. Chest patch colour in females changes with their reproductive condition (Matthews, 1956; Crook, 1966; Alvarez, 1973). However, in males, it appears to be status-based as there are variations in chest redness among different age groups (Dunbar, 1984; Bergman and Beehner, 2008).

Geladas are almost entirely terrestrial quadrupeds, which inhabit the highlands of central and northwestern Ethiopia. Geladas are ill-adapted to an arboreal way of life. Even where they occur near forested area, they rarely climb up trees (Crook, 1966; Fleagle, 1999). Geladas are habitat specialists and thus their geographic range is narrowly restricted to the high-elevation montane grasslands of Ethiopia (Crook, 1966; Mori and Gurja Belay, 1990). The majority of the population lives in the northern part of the Rift Valley at high altitudinal variation ranging from 2,000 to 4,500 m asl (Crook and Aldrich-Blake, 1968; Gurja Belay and Shotake, 1998).

There is a small isolated population living in the southern part of the Rift Valley, in the Arsi province (Mori and Gurja Belay, 1990). Preliminary research has shown that the Arsi population is quite distinct from other populations. This population may represent a new and still undescribed taxon (Gurja Belay and Mori, 2006; Gippoliti, 2010). From an analysis of blood proteins, Gurja Belay and Shotake (1998) have estimated that the Arsi population may have separated 350,000 years ago from the northern population.

Gelada population of the Arsi province lives in a lower-elevation habitat ranging from 1,800 to 2,300 m asl, and has a rather small population size and restricted geographical range of distribution (Mori and Gurja Belay, 1990). The physical characteristics and behavioural ecology of this population differ from what was previously reported for geladas living in other habitats (Iwamoto *et al.,* 1996; Mori *et al.,* 1997).

Gelada habitats are in general characterized as wet and cool, but they may differ in geographic features, vegetation composition and climatic conditions. The habitats are relatively rich in terms of food availability. At the higher elevation, grasslands stay green for a longer period of time due to high amount of rainfall and low temperatures (Iwamoto and Dunbar, 1983; Iwamoto, 1993; Puff and Sileshi Nemomissa, 2005).

Geladas respond well to temperate climates (Crook, 1966; Dunbar and Dunbar, 1975), which is most likely why they are currently thriving in the Ethiopian highlands regardless of the cold stress they experience during the time of extreme climatic conditions (Dunbar, 1980). Geladas have some adaptations for living in cold climate such as an increased mane density and greater food intake. However, these adaptations may not be enough to completely alleviate them from the cold stress (Beehner and McCann, 2008). A study by Dunbar (1980) has shown that birth within groups was timed in order to decrease the exposure of newborns to the severe climatic conditions.

As ground dwelling primates, geladas have specialized morphological adaptations for feeding and moving on the ground (Dunbar, 1986; Krentz, 1993). They are the only known highly graminivorous primates, with grass forming a major portion of their diet in most habitats (Dunbar and Dunbar, 1974b; Dunbar, 1977). Due to seasonally low precipitation and the subsequent desiccation of the forage, green grass is more patchily distributed during the dry season than in the wet season (Dunbar, 1977; Iwamoto and Dunbar, 1983; Hunter, 2001; Fashing *et al.,* 2014).

Geladas are known to have a relatively small incisors, but large, baboon-like canine teeth. Their molar teeth demonstrate distinct adaptations to resist wear and improve their ability to grind food plants (Crook, 1966; Jolly, 1972). These teeth features reflect why geladas are strictly graminivorous, feeding mainly on grass blades as long as they remain green. However, they prefer to dig for roots and rhizomes once the grasses become desiccated, and less-digestible (Braun, 1973; Dunbar, 1978; Iwamoto and Dunbar, 1983).

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

A study by Dunbar and Bose (1991) has shown that geladas break down their food into finer fragments than the omnivorous baboons. Geladas were also found to chew as efficiently as zebras. However, they are less competent than cattle, which are able to reduce particle size more efficiently to increase nutrient availability.

At higher elevation areas, such as the Ethiopian plateau, temperatures are generally lower and thus grasses desiccate at a slower rate. This condition provides the geladas with a better digestibility of grasses for a greater time span during the year. However, at very high elevation habitats, the level of protein content in grasses declines, which makes it hard for them to meet nutritional requirements (Iwamoto and Dunbar, 1983; Dunbar, 1998). Similarly, geladas face difficulty to cope with grasses at lower elevation areas. This is because the digestibility of grass is too low for them to meet dietary needs (Demment and van Soest, 1985).

Geladas show seasonal variation in their food intake. During a period of food scarcity in the dry season, they increase food intake by increasing the time spent feeding. They also change their dietary habits from grasses to herbs and roots (Hunter, 2001). The greater food intake may be due to thermoregulation requirements during the cold dry season. Similarly, geladas that live in higher elevation areas spend more time feeding than those inhabiting the lower elevation habitats due to thermoregulatory needs (Iwamoto and Dunbar, 1983).

Gelada populations living in different habitats appear to differ in their feeding habits. For instance, the diet of the Arsi population in southern Ethiopia comprises considerable amounts of fruit, which have rarely been used as food components by the geladas inhabiting the Simien Mountains National Park (SMNP), where the northern most gelada population is found (Iwamoto and Dunbar, 1983; Iwamoto, 1993).

Geladas are nonseasonal breeders and the period between the birth of one infant and the next conception is relatively long. However, this period may be considerably reduced if a female loses her infant prior to weaning (Dunbar, 1980; Mori and Dunbar, 1985).

Female geladas produce sexual swellings around the time of ovulation (Dunbar and Dunbar, 1974a). This portion of skin noticeably changes colour and becomes outlined in swollen, bead-like vesicles during a period of pre-ovulation. It also undergoes changes in colour during pregnancy and lactation periods (Dunbar and Dunbar, 1974a; McCann, 1995). Furthermore, females have perineal swellings, but they are much smaller in size and less variable in colour than those of other primate species. Females produce sexual swellings only around the time of ovulation though they are known to copulate throughout the year (Dunbar and Dunbar, 1974a).

Mothers may use aggression to physically protect their infants from possible attacks by group members. The deposed leader male or other females in the family unit may form a defensive alliance. Females in particular may demonstrate their alliance to protect their infants (Roberts, 2012).

The adult male may improve his reproductive success by increasing his chance of siring the offspring of a mother and thereby accelerating the onset of the reproductive period. Infants are dependent on their mothers for a long period of time. Therefore, reproductive success for the adult male is affected by its tenure as a unit leader and the size of its family unit because longer tenures and larger units translate into higher reproductive success (Crook, 1966; Dunbar, 1984). A leader male attends closely to its females, but it does not usually attempt to mate with females in other family units. Threats to the reproductive tenure of a leader male may come from young bachelor males, who roam together in all-male groups. Following a successful challenge, a bachelor male takes over the family unit and gain exclusive reproductive access to females (Beehner and Bergman, 2008).

Geladas are known to usually exhibit simple flight as an anti-predator behaviour. However, active anti-predator behaviour was observed in a population of the Arsi province, which showed frequent counter-attacks and severe mobbing at predators.

Sleeping on the cliff-face at night is considered as anti-predator behaviour because the site is too steep for predators to access. A few bands may sometimes aggregate to form large temporary "multi-band herds", which is another anti-predator behaviour that enables the geladas to remain vigilant while travelling in the grassland plains for foraging (Dunbar, 1986; Iwamoto *et al*., 1996).

Geladas are gregarious primates, which live in fairly large groups. The gelada social system consists of multi-tiered hierarchy of social groupings (Crook, 1966; Kawai *et al.,* 1983). The first level of social system is the one-male unit (OMU), which typically consists of a single reproductive leader male, adult females and their dependent offspring, and possibly one or more follower males (Dunbar and Dunbar, 1975). Followers may include either the deposed leader male that remains in the group, or another outside male that enters the unit during its takeover. Follower males may live and socialize within the unit, but they are subordinate to the leader male and therefore rarely mate with females (Dunbar, 1984). The OMU is the smallest grouping within the gelada social system, and provides the context in which most social behaviour and all reproductive activity takes place. It is considered as a reproductive unit in a gelada population. Another first level social group, the all-male group, contains young adult and subadult males that have dispersed from their natal unit (Kawai *et al.,* 1983; Dunbar, 1993; Crook, 1966).

The second level of social system above the OMU is the team. It comprises two or more closely associated units, which are thought to have resulted from unit fission. The team is not an obligatory level of social system and thus most units may not be involved in a given team (Dunbar and Dunbar, 1975; Ohsawa, 1979a; Kawai *et al.,* 1983; Dunbar, 1984).

The third level of social system is the band, which is made up of multiple units and all-male groups. Geladas live in loosely organized bands of 50–280 animals (Dunbar and Dunbar, 1975; Ohsawa, 1979a; Iwamoto and Dunbar, 1983). The bands are formed by the geladas due to the preference of the family units to forage in large groups. For this reason, geladas tend to remain near to those units with whom they can most easily form large aggregations. Though family units may undergo fission from time to time, kinship is an important factor enabling them to live together. Thus, closely related units tend to remain in the same area (Dunbar, 1993). The gelada band is considered to be the fundamental genetic unit as members of a given band are genetically more homologous than members of different bands (Gurja Belay and Shotake, 1998; Gurja Belay and Mori, 2006).

Another social system is the community, which consists of those bands whose ranging areas overlap extensively and who therefore tend to be found in "mixed-band herds" more often than is usually the case (Kawai *et al.,* 1983). The community is sometimes confused with the herd, which is not a stable social system. The herd is a temporary aggregation of reproductive units who do not have particular allegiance or status (Crook, 1966; Dunbar, 1993).

Several important questions remain unanswered concerning gelada taxonomy, distribution, conservation status and priorities for effective conservation actions (Crook, 1966; Hunter, 2001; Roberts, 2012). The geographical distribution of geladas is not thoroughly known at the moment, as the recent discovery of the Arsi population demonstrates (Gippoliti, 2010). The confusion and lack of clarity with regards to the correct taxonomic arrangement of the *Theropithecus* could negatively affect conservation strategies (Gippoliti, 2010). Geladas as a whole are not considered to be threatened at the moment, but they are clearly in need of conservation efforts. They have a limited geographical range and are faced with habitat destruction (Hunter, 2001; Beehner *et al.,* 2007). The distribution of gelada population on the Ethiopian plateau is associated with the availability of easily digested, montane grasses (Crook, 1966; Mori and Gurja Belay, 1990). Consequently, future global warming which may result in the regression of grasslands would raise serious questions over the species' geographical distribution and survival (Dunbar, 1998).

At different times, some researchers have carried out a short to medium-term studies on the population status and behavioural ecology of geladas in the SMNP (e.g., Iwamoto and Dunbar, 1983; Iwamoto, 1993; Hunter, 2001; Beehner *et al.,* 2007). However, there is inadequate data in particular on population distribution, foraging behaviour, activity budget and ranging pattern of the geladas living in the Gich area. To this end, the present study focuses on gathering data on population status and behavioural ecology of gelada inhabiting the Gich area in SMNP.

2. OBJECTIVES OF THE STUDY

2.1. General objective

The main objective of this study was to conduct detailed investigations on population status, and diet and foraging behaviour of gelada living in the Gich area of the SMNP. The study also aims to carry out investigations on activity budget and ranging patterns of gelada.

2.2. Specific objectives

- ✓ Establish current population abundance and distribution of gelada living in the Gich area of the SMNP
- ➢ Determine the demographic structure of the population
- ➢ Examine the degree of flexibility in the foraging strategy of gelada in response to variations in resource availability
- ➢ Analyze nutritional contents of food plant species and the relationship between nutritional variables and plant selection in gelada
- ➢ Examine whether activity budgets of gelada vary with season
- ➢ Elucidate if the age/sex classes differ in activity budgets
- ➢ Identify factors that determine ranging patterns of gelada
- ➢ Identify factors that influence sleeping site selection in gelada

3. THE STUDY AREA AND METHODS

3.1. The Study Area

The Simien Mountains region is best known for its high biodiversity and outstanding scenic beauty (Fig. 2). The Simien Mountains form part of the main escarpment that borders the northern edge of the Ethiopian plateau (Dunbar, 1978; Puff and Sileshi Nemomissa, 2005). It is located in northcentral Ethiopia, North Gondar Zone of the Amhara National Regional State. The Simien Mountains region has the highest peak in Ethiopia at Ras Dejen (4,553 m asl) and is characterized by topographical ruggedness with steep escarpments, rolling hills and flat terraces (Julia, 2005).

Figure. 2. Partial view of the scenic beauty of the Simien Mountains region

The SMNP is part of the Simien Mountains region. The geographic location of the Park extends from 13°06'44.09" to 13°23'07.85" N latitude and from 37°51'26.36" to 38°29'27.59" E longitude (Anonymous, 2009). The National Park is located at approximately 132 km northeast of Gondar town, which in turn is about 741 km away from Addis Ababa. The Park has altitudes ranging from 1,900 to 4,553 m asl (Anonymous, 2009). The SMNP was formally founded in 1966 in an effort to primarily ensure the survival of the highly endangered endemic walia ibex (*Capra ibex walie*) and gazetted in 1969 (Hunter, 2001). Since its establishment, the SMNP has undergone a number of changes in its status, size and management plans. These changes have had effects on the conservation of the Park in terms of habitat degradation and poaching of wildlife. During the time of its establishment, the SMNP was the smallest Park in size in the country, with an area of only 136 km^2 (Hurni and Ludi, 2000). However, an attempt was made at different times to gradually increase its boundaries and thereby include the main habitats of wildlife, especially for walia ibex and the Ethiopian wolf. Thus, at the moment, the Park includes the Limalimo Wildlife Sanctuary, Ras Dejen, and some portions of Telemit and Beyeda (Anonymous, 2009). It now covers a geographical area of about 412 km^2 of the Simien Mountains watershed (Gebremedhin *et al.,* 2009). A remarkable escarpment separates the Park into an approximately equal coverage (Hunter, 2001) of lowlands (1,700 to 2,800 m asl) and highlands (2,800 to 4,070 m asl).

The SMNP has become a World Heritage Site in 1978 due to the presence of endemic wildlife, natural beauty and thus its international significance (Julia, 2005). Unfortunately, the Park was inscribed on the List of World Heritage in Danger in 1996 as a result of population decline in walia ibex and other large mammals, habitat degradation and the impact of road construction (Falch and Keiner, 2000). The field study on which this thesis is based was carried out in the Gich area of the SMNP (Fig. 3). The area represents new study site for a long-term gelada study, which is characterized by a local diversity of distinct vegetation types. The Gich area is reached by travelling approximately 45 km northeast of Debark town. The area ranges in elevation from 3,453 to 3,900 m asl.

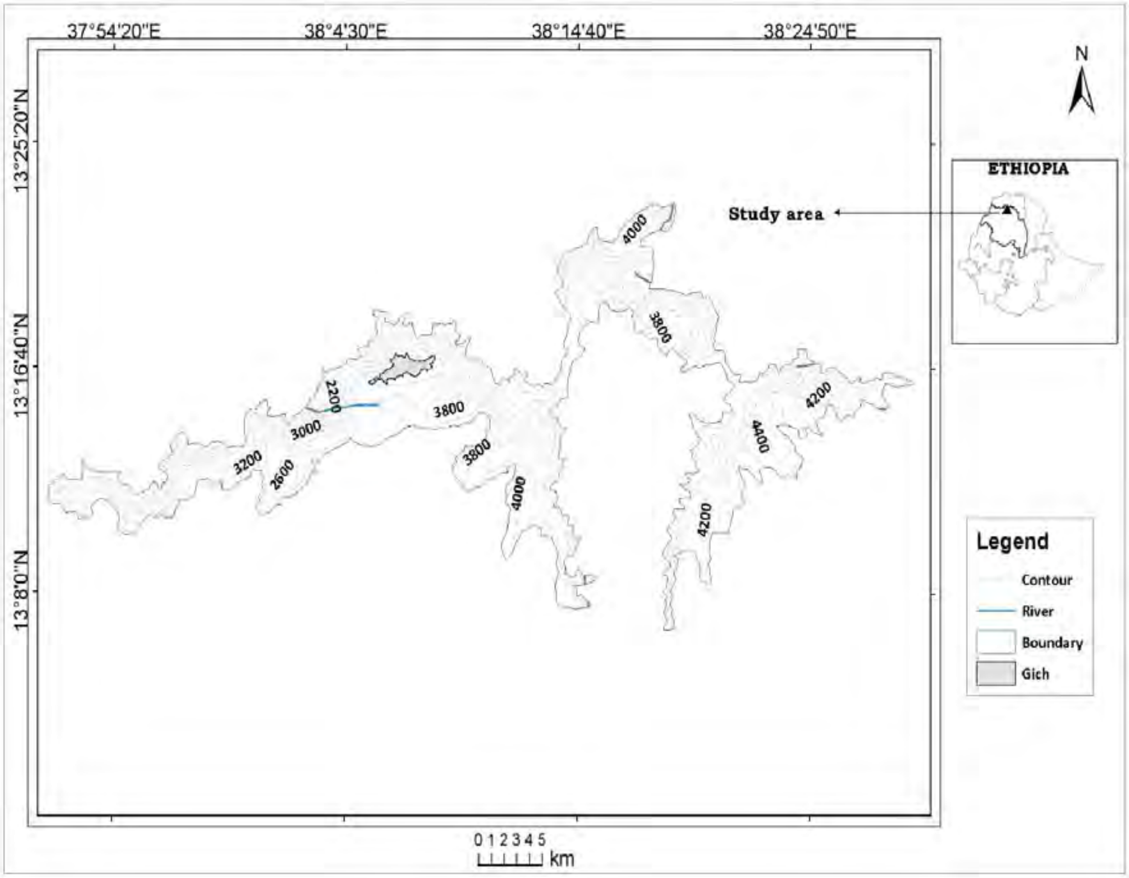

Figure 3. Map of the Simien Mountains National Park showing the study site

The study area exhibits a marked variation in vegetation cover and composition due to differences in topographic features and climatic conditions. Gich consisted of an open plateau of approximately 19 km^2. The area is characterized as cold and wet (Iwamoto and

Dunbar, 1983; Anonymous, 2009) and is dominated by Afroalpine grassland (Fig. 4), which is dotted with the endemic giant lobelia (*Lobelia rhynchopetalum*). The grassland area contains many species of grasses with varying grazing potential for herbivores. The plateau was once described as the best place where an outstanding quality of the natural Afroalpine grassland could be found. Among the three endemic plant species previously identified in the SMNP, *Festuca gilbertiana* is found only in the Gich area (Puff and Sileshi Nemomissa, 1999). *Erica arborea* forest was located in the valleys and inaccessible areas of the escarpment, but the plateau lies above the treeline. The area experiences strong winds, with a dominantly northerly direction (Iwamoto and Dunbar, 1983; Hurni, 1986).

Figure 4. The Afroalpine grassland of the Gich plateau

The Simien Mountains region includes a wide range of altitudes and geographic features, which cause local climatic conditions to be quite variable. In general, detailed climatic data are not completely known for the region. Even those that are already available primarily refer to a few localities in the Park (Puff and Sileshi Nemomissa, 2005).

The Simien Mountains region is characterized by a single main rainy season, which lasts from May to October. There may also be a second wet season, with occasional rains in February and March. The amount of precipitation is quite variable from year to year. The wettest areas receive over 1,500 mm annual precipitation, while the driest areas get about a third of this amount (Puff and Sileshi Nemomissa, 2005).

The climate of the SMNP is temperate (Crook, 1966; Dunbar and Dunbar, 1975), though the Park is known to experience distinct wet and dry seasons. The climate of the area varies with altitudinal gradient and seasonal changes, which can be broadly divided into two categories: upper and lower climatic types. At altitudes between 2,000 and 3,200 m asl (lower climatic type), there is southwest monsoon with trade-winds occurring only during the dry season. The rains are convective type with less frequent hailstorms. Whereas, at altitudinal ranges from 3,200 to 4,500 m asl (upper climatic type), wet season is characterized by a combination of high precipitation, frequent hailstorms and occasional snow (Hurni, 1986; Anonymous, 2009).

Temperature and rainfall patterns for the period June 1, 2013 to May 30, 2014 in the study site were monitored and measured daily using a weather station situated on the area (located at an altitude of 3,650 m asl in the camp site), and these patterns are shown in Figure 5.

The annual precipitation for the study site for the stated period was 1,467 mm. Much of the rainfall came during the wet season, with 84% of annual precipitation received between 1 June and 30 October 2013, which indicates that rainfall was not evenly distributed throughout the year. Average monthly rainfall varied from 29 mm during the dry season to 196 mm in the wet season. Precipitation averaged 122 mm per month (SD=134 mm, range=0–373 mm, n=12 mo). Rainfall varied between a mean monthly minimum of 2 mm in January to a mean monthly maximum of 373 mm in June. Heavy rains occur during the wet season, with three peaks in June (373 mm), July (366 mm) and August (248 mm). The period from November through April, with monthly rainfall of <100 mm, is regarded as a dry season.

There was high diurnal variation in temperature, especially during the dry season (February to April), when daytime temperatures were commonly over 15^{o}C and night-time minima were between 2–4^{o}C. The annual mean maximum temperature was 14.4 ± SD 1.5^{o}C, and the mean minimum temperature was 3.4 ± SD 0.8^{o}C. The mean monthly maximum temperatures varied from 11.8^{o}C in January to 16.7^{o}C in August, while mean monthly minimum temperatures varied from 2.0^{o}C in December to 4.4^{o}C in March. The mean daily temperature for the period June 1, 2013 to May 30, 2014 was 8.9 ± SD 1.2^{o}C.

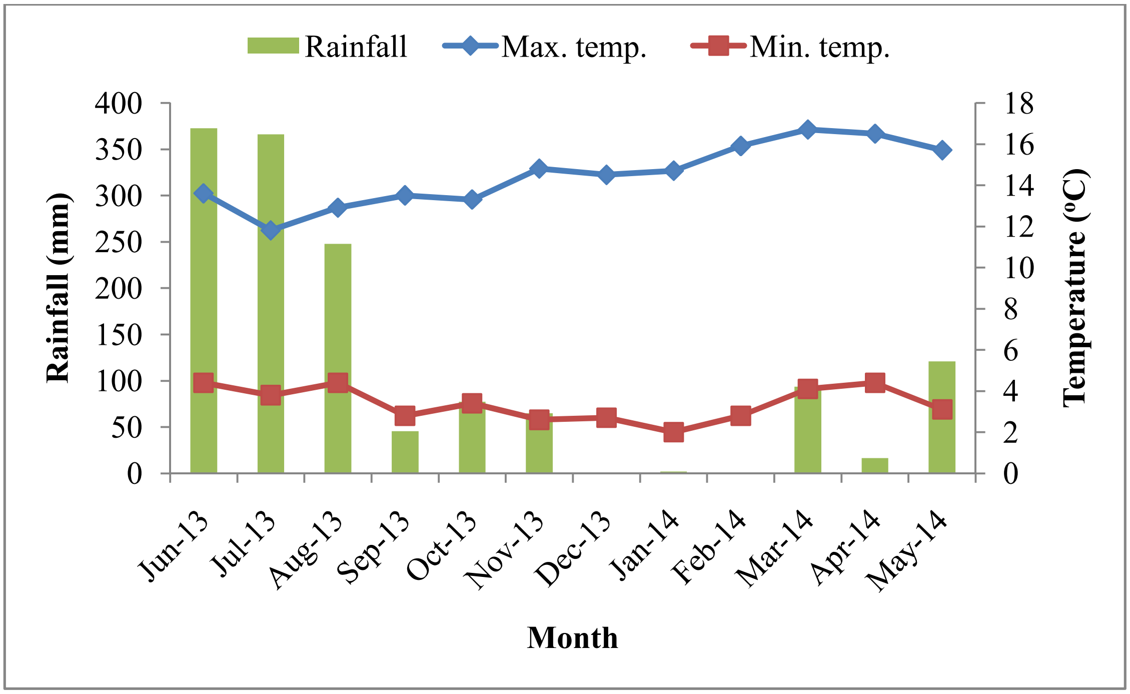

Figure 5. Monthly rainfall (mm), mean minimum and maximum temperatures (^oC)

The Simien Mountains region is characterized by a high, but incompletely quantified level of plant endemism (Puff and Sileshi Nemomissa, 2005). For this reason, it is considered as part of the eastern Afromontane hotspot of plant diversity. Three plant species are endemic to the Simien Mountains: *Festuca gilbertiana*, *Rosularia simensis* and *Dianthus longiglumi* (Anonymous, 2009). The vegetation types of the SMNP are diverse, broadly categorized into three major belts based on altitude and dominant plant species (Puff and Sileshi Nemomissa, 2005; Anonymous, 2009). These include montane forest (1,900-3,000 m), sub-Afroalpine (2,700-3,700 m) and Afroalpine grassland (3,700-4,553 m). This altitudinal variation has resulted in a notable number of species adapted to the diverse habitats and local climatic conditions (Hurni, 1986; Puff and Sileshi Nemomissa, 2005).

The montane forest is located on the less-steep parts of the escarpment. In the area, almost all of the primary forests have been destroyed due to uncontrolled clearing and settlements. However, there are still small remnant patches in gorges and other inaccessible localities, where the original vegetation is maintained more or less intact (Hurni, 1986). The biodiversity in the montane forest is generally much higher than on the highland plateau. Common trees in this forest type include *Juniperus procera*, *Hagenia abyssinica*, *Olea chrysophylla*, *Cordia africana* and *Szygium guineense*. Almost all of these tree species are locally threatened with extinction (Puff and Sileshi Nemomissa, 2005; Anonymous, 2009).

A distinct and extensive range of sub-Afroalpine vegetation occurs between 2,700 and 3,700 m, though this does not correspond to the altitudinal range of similar *Ericaceous* zones on the Mountains of tropical East Africa (Puff and Sileshi Nemomissa, 2005). In the Simien Mountain, it occurs mostly on the escarpment areas, but scattered *Erica* forests are also found on the high plateaus. Tree and shrub forms as well as the remnant forests of *Erica arborea* and *Erica trimera* are widespread, primarily on the cliff areas (Iwamoto and Dunbar, 1983; Anonymous, 2009). The sub-Afroalpine belt is characterized as a transitional zone between the montane forest and the Afroalpine vegetational zone.

The Afroalpine vegetation of the highland plateau is located above 3,700 m. In general, plant diversity is low in this area. It is dominated mainly by grasses and herbs as well as the giant *Lobelia rhynchopetalum*, which is a characteristic feature of the treeless landscape (Iwamoto and Dunbar, 1983). The Afroalpine zone, especially at the highest altitudinal limit, does not have primary vegetation structure (Puff and Sileshi Nemomissa, 1999).

Combinations of remarkable altitudinal variation, unique climate and geographical isolation have given rise to a number of rare and endemic species of animals in the Simien Mountains. Unfortunately, due to their limited distribution, small population size and intense habitat encroachments, many of these species are threatened (Hurni, 1986).

The National Park serves an important role in the conservation of a number of animal species. It harbours 22 large and 13 small mammals, and is also rich in avian diversity. Several species of mammals and birds are either endemic to the Park or the country. Many of the larger mammal species of the Park are rarely seen (Puff and Sileshi Nemomissa, 2005), the exception being the walia ibex (*Capra ibex walie*), gelada (*Theropithecus gelada*), the black-and-white colobus monkeys (*Colobus guereza*), anubis baboon (*Papio anubis*) and hamadryas baboon (*Papio hamadryas*).

In addition to walia and gelada, leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*), klipspringer (*Oreotragus oreotragus*), bushbuck (*Tragelaphus scriptus*), common jackal (*Canis aureus aureus*) and the Ethiopian wolf (*Canis simensis*) are currently sheltered in the Gich area.

When the Park was established in 1966, a number of villages and tracts of land used by the local communities were included within its boundaries. In 1979, seven villages were forcefully evicted from the northern portion, which resulted in tensions between the local communities and Park management (Hurni, 1986; Anonymous, 2009). Despite efforts to resettle inhabitants and boundary re-alignment, a large number of people still live within the Park, mostly in the Gich village. This village is located at about 2.5 km southwest of the camp site of the Gich plateau. A number of other villages, such as Argin and Ambaras, are close to the Park, but lie outside the boundary. The Gich village is quite spread out and it is continuously expanding (Puff and Sileshi Nemomissa, 2005). There are currently about 220 families in the village whose livelihood depends on subsistent farming and animal rearing.

Overexploitation of the Park resources especially *Erica arborea* and *Hypericum revolutum* forest patches at higher altitudinal areas by the local communities is continuing, regardless of the ban imposed by the Park management (Ludi, 2005). The Park is also affected by heavy grazing of livestock up to an altitude of 4,200 m asl. Domestic animals are widespread throughout the Park and represent the main competition for food resources with wild animals (Hunter, 2001). The fragmentation of natural habitats by anthropogenic effects poses serious threat to the rare plants and endemic animals of the SMNP. Intensive exploitation of the Park by the local populations has led to increased run-off and soil erosion, further aggravating land degradation and deterioration of wildlife habitats (Hurni and Ludi, 2000).

The Afroalpine grasslands of the SMNP, particularly those at the higher elevations, have been intensively used as grazing areas. For example, at Gich due to increased encroachment by people and their livestock into the grassland, the plateau has regressed from its natural state (Puff and Sileshi Nemomissa, 1999). There are at present totally eroded and heavily overgrazed areas on the plateau, which indicate that Gich experienced serious overgrazing for a long time (Anonymous, 2009). The most distant areas from the Gich village are in a less disturbed situation though these areas have also been used for livestock grazing.

Data collection in the present study was accomplished using a number of materials. Some of them include two pairs of 10 x 42 Bushnell binoculars, Global Positioning System (GPS, Garmin 72), a digital photographic camera, maps of the study area, stopwatch and compass.

3.2. Methods

A reconnaissance survey was carried out during the second half of October 2012, prior to the actual data collection process. While surveying the area, the main habitats of gelada were located. Further, during this period, all available and relevant literature pertinent to the SMNP and the study animals was gathered from the library of the Park at Debark town. Finally, Gich area was selected as a study site on the basis of topographic features, vegetation composition and habitat type.

During November 2012, population assessment was made to determine the number and size of gelada bands in the Gich area. Four social groups of gelada inhabited various portions of the plateau. The band that ranged into the major area of Gich was the primary focus of the study. The study band varied in size from 183 animals at the start of the study to 205 by the end, due to the birth of individuals. Habituating members of the band to the presence of observers begun in April 2013. The study animals could be followed at a distance of <10 m and many individuals were easily identifiable based on their natural markings.

Different methods were employed to study population status, distribution and behavioural ecology of gelada living in the Gich area of the SMNP. The main methods used were total population census (Beehner *et al.,* 2007), focal animal scan sampling (Altmann,

1974) and home range use analysis using square quadrats (Hunter, 2001; Kaplin, 2001). Each of these methods is discussed in detail in subsequent sections separately.

The entire habitat of gelada in the Gich area was divided into four main census areas. These areas are naturally delineated by topographic features. The following known gelada habitats were used as census sites: Imet Gogo, Kedadit, Saha and Gidir Got. Intensive count of gelada population was carried out in each corresponding census area, first in May and November 2013, and second in April and October 2014. Secondary census data were also collected from literature reviews (Ohsawa, 1979b; Beehner *et al.,* 2007).

Total-count method was employed for determining population status of gelada living in the Gich area. It is the most effective method for determining population status, because geladas range into open habitats that facilitate visibility. They are also readily available along cliff-ledges in the morning, where all individuals can be observed and counted (Beehner *et al.,* 2007).

Two trained local field assistants were deployed to each block to count all geladas observed. Census of gelada was carried out during the wet and dry seasons of each census year. When the geladas were encountered during each counting process, group size, location and time were recorded. Census was conducted only when geladas started moving and no individual remained at the cliff-ledges (Hunter, 2001). To avoid double counting, all surveys were conducted on the same day during morning hours. Repeated surveys were conducted until the best possible estimate had been obtained (Crook, 1966).

Age/sex class was assigned to each individual based on the physical size and development characteristics (Kawai *et al.,* 1983). Accordingly, adult males were identified as males with visible manes and overall body size about twice that of adult females (Ohsawa, 1979a). Subadult males were identified as males similar in size to adult females with the beginning of mane. Adult and subadult females were identified based on body size (Beehner *et al.,* 2007). Similarly, infants and juveniles were identified based on the physical size and other development characteristics.

Data were collected on behavioural ecology of gelada using one focal band. Group size for the study band was recorded by counting the number of individual gelada at hourly intervals throughout the day. This was carried out ten days per month and averaged to provide a mean daily and monthly group size estimate (Hunter, 2001). Demographic changes in the band were also recorded throughout the study period. Morning counts begun when it appeared that no other individual remained on the sleeping cliffs. This normally occurred when a vast majority of band members shifted from social behaviour to feeding activity. Therefore, group size survey did not usually begin before 09: 00 or 10: 00 h. Whenever the study band was observed to undergo internal fission or fusion with other units or bands, the size of departing or merging group was also recorded.

Activity data were collected during ten days between 7: 00 and 18: 00 h following of the study band each month from May 2013 through April 2014. Most of the days in a monthly sample were consecutive. Activity data were recorded using continuous focal animal scan sampling method (Altmann, 1974). Individual gelada was made the focus of follows, beginning 7: 00-8: 00 and ending 17: 00-18: 00 h during different months. Activity data were recorded for different age/sex classes, which were selected opportunistically. Each month, an attempt was made to follow adult male, adult female, subadult male, subadult female and juveniles.

The age/sex class chosen to be sampled was alternatively used on daily basis. While a number of individual members of the study band were easily identifiable, the majority were not. An attempt was made to follow as many different individuals in each age/sex class as possible following Byrne *et al.* (1993).

Activity of the focal individuals was recorded at 30 one-minute sequential scans (Hunter, 2001). Activity recorded for the focal animal in the one-minute point scan was the first activity, which was held for at least 3 seconds once the individual was sighted (Fashing, 1999). Due to the inaccessible and low visibility nature of certain areas, it was not always possible to remain in contact with the focal individual for the duration of the sample period. Furthermore, when juveniles and subadults were approached for scan sampling, they usually became threatened, though it was ameliorated through time. If contact with a focal animal was lost, the data collection process continued with another individual of the same age/sex class. At the end of each scan sample, a new focal animal was chosen from individuals furthest away from the previous focal individual. In this way, it was attempted to collect activity records on as many different animals as possible. An attempt was made to obtain a complete record of each activity period, and thus at the end of each point scan sampling approximately equal number of observations were made.

The activities of focal animals were recorded in categories as: grazing, foraging, digging, travelling, reclining, sitting, self-grooming, standing, allogrooming, aggression, playing and others. Following the common methods for the study of primates, activities were re-grouped. Thus, each focal animal was recorded as performing one of the following four mutually exclusive activities: feeding, travelling, resting and socializing.

Feeding was recorded when the animal was plucking or eating short grasses, plucking or eating above ground food items other than grass and digging or eating underground food. Travelling was recorded when the individual moved at least five or more paces, including walking or running (Hunter, 2001). Resting was recorded when the individual was standing, reclining or sitting, without being engaged in any other activity except for self-grooming. Socializing was recorded when the animal was engaged in interactions with other individuals including grooming another individual or being recipient of grooming by another individual, fighting, chasing, threatening, etc. When the animal was engaged in behaviour that cannot be easily characterized by the above categories, it was recorded as "other".

General dietary profiles were calculated for different age/sex classes using records from focal animal scan sampling. When a focal animal was feeding, the plant part consumed was recorded. The plant parts that the focal individual consumed were categorized as: (1) grass leaves, (2) grass roots, (3) herbs, (4) herb roots, (5) corms/bulbs, (6) seeds, (7) flowers and (8) others.

Different species of plants on which the focal gelada foraged were recorded, collected and identified. Plants that were not easily identified in the field were collected and preserved as specimens for identification in the National Herbarium of Addis Ababa University.

Animal prey was recorded as the food item when it was observed gelada scratching dried *Lobelia rhynchopetalum* bark, turning herbivore dung over or ingesting invertebrates.

Collection of plant species and parts for phytochemical analysis was based on major dietary items used by the study animals. However, in order to determine the role of nutritional composition in food selection, other plant species that were abundant in the study area but were not consumed by the gelada were also included in the analysis. Of the 27 different species of plants observed to be eaten by focal animals during the study period, 9 species were collected in sufficient amounts to be ground and analyzed. Plant samples were collected during the period in which they were consumed. Samples were dried in open air at the camp site and later transported to the Centre for Food and Nutrition Laboratory of Addis Ababa University, where phytochemical analysis of nutritional components of plants was conducted. In the Laboratory, samples were milled into a fine powder consisting of uniform particles and stored them in sealable plastic bags until analysis. Absolute dry matter was measured by drying samples at 100^{o}C. Samples were analyzed for crude protein (CP), crude fat, ash and moisture contents. The total nitrogen content (N) was determined using a macro-Kjeldahl method with a Cu catalyst. Crude content was then determined from nitrogen by the standard formula N x 6.25 (Williams, 1984). Crude fatty acid content was determined using a petroleum ether extraction. To determine the content of inorganic matter (total ash content), samples were burned in a muffle furnace at 500^{o}C for about 5 hours (van Soest *et al.,* 1991).

To study sleeping site selection in gelada, the focal band was followed from the time it left a sleeping site in the morning until it entered a new sleeping site at dusk for 10 days per month from May 2013 through April 2014. A sleeping site is defined as a particular location within the band's home range where most individuals spend the night. Since the geladas sleep on cliff-face, a sleeping site is composed of one or more cliffs where the animals gather to spend the night. At the end of each day, the site to which members of the band retired for the night was recorded. Sleeping time was defined as the time interval between when the entire individual members of the band had settled at night until 50% of individuals had left the sleeping site the following morning. When conditions were permitting, the entry time and behaviour while entering the sleeping site of animals were recorded opportunistically (Altmann, 1974). Detailed notes on all observed predation attempts, including the time, number of predators observed, predator taxa, and behaviours during and after the predation attempt were recorded. To evaluate the influence of low night-time temperature on the selection of sleeping site in gelada, months from November through March were defined as the cold months, when the minimum temperatures was lower than 5^{o}C.

Ranging patterns of the study band was examined by taking the following measurements: (1) daily travel distance, (2) seasonal and annual home-range areas and (3) quadrat use within the home range (Kaplin, 2001).

Geographic coordinates were collected on the centre-of-mass of the study band at 30-min intervals throughout the day using Garmin GPS 72 handheld unit (Altmann and Altmann, 1970; Waser and Floody, 1974; Hunter, 2001).

The size of monthly home range and the percentage of the total home range used by the band per month were recorded. Using the number of times each quadrat was entered, the usage frequency of individual quadrat within the home range was calculated. To determine temporal patterns of home range use, each quadrat entered in a month was classified as: (1) new (not previously entered), or (2) previously entered (Kaplin, 2001).

4. ANALYSES OF DATA

All statistical analyses were performed using SPSS statistical software (version 16.0) for windows. All data were assessed to determine whether they were normally distributed following Shah (2003). Non-parametric tests were used for data that were not normally distributed. All correlations were non-parametric Spearman's rank correlations. All statistical tests were 2-tailed with a level of rejection set at $p=0.05$ (Hill, 1999).

Population density of gelada was calculated by the extent of area and expressed as the number of individuals per km^2 (Bocian, 1997). To obtain the value, the number of groups per km^2 was multiplied by mean group size. Mean group size was estimated from the best available data for each census area (Shah, 2003).

Percent contribution of the various activity categories to each scan was calculated. The daily activity budget was calculated by averaging the values from all scans within a day. Monthly activity budgets were computed by averaging daily values within each ten-day follows. Annual activity budgets represented a grand mean of the monthly budgets (Shah, 2003).

The daily mean of feeding time on food categories and number of food plant species eaten were used to calculate the monthly mean. Monthly mean was used to calculate the seasonal mean. Annual diet composition is reported by plant species, part or type as the proportion of total feeding observations.

To examine dietary diversity over the study period, the Shannon-Weaver index of diversity (H') was calculated for each month of the study (Krebs, 1989). Dietary evenness was also computed on a monthly basis using the evenness index, J (Krebs, 1989). J

provides a measure of how evenly the different food plant species were represented in the diets of gelada each month. Potential scores range from '0' (most even) to '1' (least even).

The formula for computing dietary diversity was:

$$H' = -\sum_{i=1}^{s} \mathrm{pilnpi}$$

where, H' is Shannon-Weaver index of diversity, s is the number of species and pi is the proportion of the total number of individuals represented by the ith species.

Dietary evenness is calculated by using the evenness index formula:

J=H'/H maximum

where, H' is Shannon-Weaver index of diversity and H maximum is maximum diversity index.

Home-range size was calculated using two different methods. First, ranging patterns were analyzed by superimposing a grid of 200 x 200 m quadrats on the maps of daily spatial locations. Home range area was calculated by summing the total number of different quadrats entered during the study period and multiplying by the area of each quadrat (40,000 m^2). Second, home range was calculated using the minimum convex polygon method (Hunter, 2001; Kaplin, 2001; Hill, 1999).

Distances between centres-of-mass for consecutive half hourly intervals were measured along the route taken by the majority of band members. The length of the daily travel distance was calculated by summing the distances between the location points each day.

5. RESULTS

5.1. Population status

The survey of gelada population covered four different areas of the Gich plateau. Geographic distribution of the geladas extended from Gidir Got in the southernmost portion of the plateau to the northern end at the Imet Gogo (Fig. 6). Four social groups with varying population size were recorded in the study area. The gelada groups were sighted at altitudes ranging from 3,453 to 3,900 m asl. A single group was observed living in a census area in 2013. The same number of group in each area was also recorded in 2014.

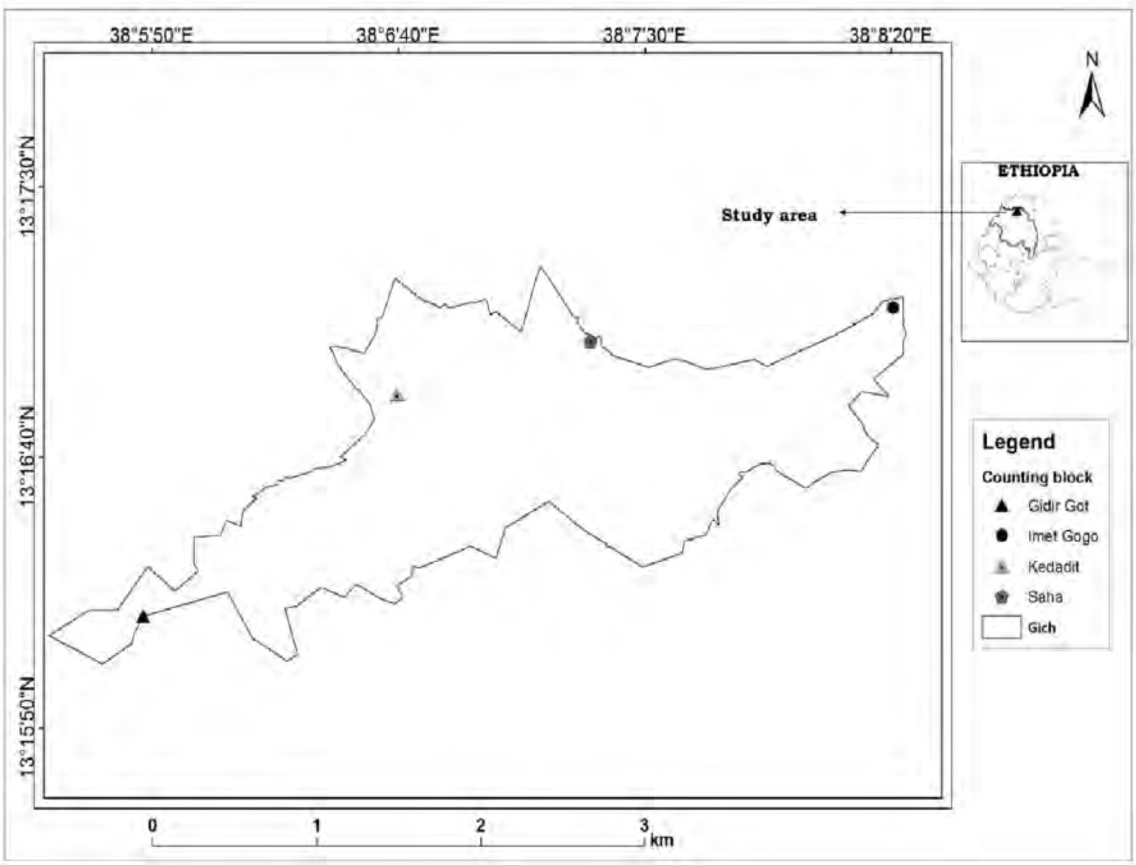

Figure 6. Counting sites for gelada population on the Gich plateau

During the wet season census of 2013, groups ranged in size from 104 to 186 individuals, with a mean of 154.5 ± SD 38.5 individuals. During the dry season, there was a slight increase to the mean group size (158.0 ± SD 38.3), with a range of 114–193 individuals per group. Group size for 2014 ranged from 119 to 217 and 126 to 218 individuals during the wet and dry seasons, respectively (Table 1). The overall mean group size for the study period was 165.4 ± SD 38.0 individuals and there was a significant difference in the size of groups from different census areas (ANOVA: $F_{[3,12]}=49.677$, $p<0.001$).

During the two continuous census years, the lowest population count of gelada was recorded during the wet season of 2013 (104 individuals) from the Gidir Got area and the highest count was recorded during the dry season of 2014 (218 individuals) from Saha. The population of the whole study area during the wet season of 2013 was 618 individuals and for the dry season of 2014 there were 705 animals.

Table 1. Individual count in the census areas during the wet and dry seasons of each year

No.	Census area name	2013 count		2014 count	
		Wet	Dry	Wet	Dry
1	Gidir Got	104	114	119	126
2	Imet Gogo	183	187	200	205
3	Kedadit	145	138	155	156
4	Saha	186	193	217	218
	Total	618	632	691	705

The mean population sizes of gelada for the census years of 2013 and 2014 were 625.0 ± SD 9.9 and 698.0 ± SD 9.8 individuals, respectively. The overall mean population size for the two census years resulted in 661.5 ± SD 51.6 animals. There was no significant difference in individual count of gelada between the wet and dry seasons for either census year (2013: χ^2=0.156, df=1; p>0.01; 2014: χ^2=0.07, df=1; p>0.01). However, there was a significant difference in population census results between 2013 and 2014 (χ^2=4.025, df=1; p<0.01).

During the 2013 census year, females in general comprised 48.0% (n=300 individuals) of the total population, out of which adult females accounted for 34.1% (n=213). Males represented 20.5% (n=128) and adult males alone consisted 11.4% (n=71.5, Table 2).

Table 2. Census data for the age/sex classes during the wet and dry seasons of 2013

Season	Adult		Subadult		Juveniles	Infants	Total
	Males	females	males	females			
Wet	71	212	61	86	132	56	618
Dry	72	214	52	88	134	72	632
Average	71.5	213.0	56.5	87.0	133.0	64.0	625.0

During the count of 2014, the population consisted 238 adult females and 80 adult males (Table 3). There was a significant difference in the percentage of age/sex composition of the population for each census year (2013: χ^2=172.29, df=5; p<0.01; 2014: χ^2=196.56, df=5; p<0.01). Except for infants, individual count in the age/sex classes between the wet and dry seasons of the years did not show a significant difference (infants 2013: χ^2=1.99, df=1; p<0.05; 2014: χ^2=0.186, df=1; p<0.05).

Table 3. Census data for the age/sex classes during the wet and dry seasons of 2014

Season	Adult		Subadult		Juveniles	Infants	Total
	Males	females	males	females			
Wet	79	237	58	98	152	67	691
Dry	81	239	63	101	149	72	705
Average	80.0	238.0	60.5	99.5	150.5	69.5	698.0

The ratio of adult female-to-adult male was 3:1 in the population, which indicates that the population was female biased and the difference was statistically significant ($\chi^2=74.503$, df=1; $p<0.001$).

Individuals of the all-male groups contributed 7.3% of the total population and had a mean size of 8 ± SD 2.1 (range=6-12, n=8 all-male groups). The most common group size comprised 8 individuals. However, 92.7% of the population was recorded in the one-male unit social system. One-male units were of typical composition, which comprised 1–2 adult males, 3–5 reproductive age females, subadults of both sexes, 2–4 juveniles and 2–3 infants. The most common one-male unit size consisted 12 individuals.

The population density of gelada at the Gich area in 2013 was 32.9 individuals per km^2. There was small increase in density in 2014 with 36.7 ind/km^2, but it was not statistically significant ($\chi^2=151.84$, df=1; $p>0.05$). The mean density for the two census years resulted in 34.8 ind/km^2.

5.2. Feeding behaviour

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

Table 4. Proportions of the diet made up by each plant species during the study period (B=Bud, C=Corm, F=Flower, L=Leaf, N=Nectar, R=Root, P=Pith, S=Stem)

Family	Plant species	Habit	Items eaten	Percentage
Poaceae	*Festuca* spp.	Grass	L, S, R	78.9
Colchiaceae	*Merendera abyssinica*	Herb	C	6.6
Lobeliaceae	*Lobelia rhynchopetalum*	Herb	B, L	2.9
Rosaceae	*Alchemilla pedata*	Herb	L	1.8
Rosaceae	*Alchemilla abyssinica*	Herb	L	1.5
Crassulaceae	*Rosularia simiensis*	Herb	L	1.5
Lamiaceae	*Thymus schimperi*	Herb	R	1.0
Asteraceae	*Carduus schimperi*	Herb	F	1.0
Asteraceae	*Haplocarpha schimperi*	Herb	L, R	0.9
Asteraceae	*Dianthoseris sehimperi*	Herb	S	0.8
Asteraceae	*Bidens macroptera*	Herb	L	0.05
Asteraceae	*Bidens pachyloma*	Herb	L	0.1

Asteraceae	*Bidens carinata*	Herb	L	0.1
Rubiaceae	*Galium simense*	Herb	L	0.3
Asteraceae	*Launaea rueppelii*	Herb	L	0.2
Apiaceae	*Pimpinella pimpinelloides*	Herb	L	0.1
Asteraceae	*Helichrysum citrispinum*	Shrub	F	0.1
Asteraceae	*Carduus macracanthus*	Herb	L	0.1
Asteraceae	*Carduus nyassanus*	Herb	F, L	0.1
Asphodelaceae	*Kniphofia foliosa*	Herb	F, N, P	0.05
Asphodelaceae	*Kniphofia uvaria*	Herb	L	0.1
Crassulaceae	*Aeonium leucoblepharum*	Shrub	L	0.05
Ericaceae	*Erica aerbora*	Shrub	P	0.04
Malvaceae	*Malva verticillata*	Herb	L	0.03
Ranunculaceae	*Ranunculus multifidus*	Herb	L	0.05
Asteraceae	*Sonchus oleraceus*	Herb	L	0.05
Rosaceae	*Rubus apetalus*	Shrub	L	0.04

Inclusion of the top 10 plant species that contributed more than 0.5% to the annual feeding budget was variable on monthly basis (Table 5). Of the 3 most frequently consumed plant species, *Festuca* spp. contributed at least 62% to the feeding records each month. *Merendera abyssinica* made up at least 1.6% of the feeding records during 10 months. During August, the peak of the wet season, *Festuca* spp. contributed more than 90% to the feeding records. This is a significantly higher percentage than any other plant species accounted for gelada feeding. Some of the species did not consistently provide edible parts throughout the year and their inclusion in the diet on a month-by-month basis was highly variable. Only *Festuca* spp., *Merendera abyssinica* and *Lobelia rhynchopetalum* were consumed during every month of the study period. One-way ANOVA demonstrated that there were significant differences between months in the number of species of plants consumed by geladas ($F_{[2,32]}=0.06$, $p<0.05$).

Table 5. Contribution (%) of the top 10 plant species to monthly feeding records (0.0=Species not consumed)

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

When diets were considered in terms of the types of food that were utilized, there was an overall preference primarily for leaves (mostly of grasses) monthly and annually (Table 6).

Grass blades accounted for 74.3 ± SD 12.9% (range=54–90%, n=12 mo) of the annual diet of gelada. Underground items were the second most dominant food, which contributed to 18.3 ± SD 11.6% (range=3.5–36.5%) of the overall diet. Herb leaves made the third largest contribution to the diet at 2.8 ± SD 1.8% (range=0.7–6.3%). When underground food items were analyzed separately, grass roots made the largest contribution to the diet at 7.6 ± SD 4.7% (range=0.9–15.5%). Corms/bulbs made the second largest contribution to the underground diet at 6.7 ± SD 5.6% (range=1.1–18.3%). Herb roots accounted for 3.9 ± SD 2.9% (range=1–12%) of the diet. Geladas also consumed other food items, such as flowers, 2.4 ± SD 2.2% (range=0–5%) and seeds, 0.6 ± SD 1.0% (range=0–3%), which made a very small contribution to the annual diet.

Table 6. Monthly and annual diets as percentage of feeding records spent on each food type (*=underground food)

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

Animal prey was a less important sources of food of geladas, which accounted for <0.05% of the foraging time. On few occasions, they were observed turning herbivore dung over or scattering dried *Lobelia rhynchopetalum* bark around, in search of insects, whilst feeding on plant food items.

There were significant differences in the average consumption of each food type between the wet and dry seasons. The proportion of the consumption of different food types by the geladas varied with season, except for herb roots and seeds as presented in Table 7. The diet depended mainly on the availability of plant types, with some plants clearly being preferred over others.

Table 7. Seasonal contribution of different food types to the diet

Food type	Wet season (%)	Dry season (%)	$F_{[1,58]}$	*P*
Grass leaves	84.0	64.5	17.90	0.001
Grass roots	3.6	11.6	5.162	0.027
Herbs	1.2	4.3	25.639	0.001
Herb roots	2.1	5.8	2.753	0.102
Corms/bulbs	3.2	10.3	9.523	0.003
Seeds	0.7	0.6	1.354	0.249
Flowers	3.7	1.2	11.70	0.001
Others	1.3	1.5	10.83	0.002

The mean monthly Shannon-Weaver' index for plant species diversity in the annual diet was 0.45 ± SD 0.1 (range=0.26–0.67, n=12 month; Table 8). Dietary diversity was high during December and November and low in May. The diet of gelada showed variation in diversity over the study period. The mean monthly dietary evenness index (*J*) was low at 0.67 ± SD 0.2, ranging from 0.39 in May to 0.84 in November. Geladas used a mean of 12 ± SD 3.0 plant species per month as sources of food (range=7–15 species, n=12 month).

Table 8. Monthly food plant species diversity and evenness indices during the study period

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

Spearman's rank correlations demonstrated that across months, the consumption of grass leaves decreased as the consumption of grass roots, herbs, herb roots and corms/bulbs increased and these relationships were statistically significant (Table 9). However, there was a significantly positive correlation between the consumption of grass roots and herbs. Similarly, there were positive correlations between the consumption of grass roots and herb roots, and between herbs and herb roots. There was no significant correlation between the consumption of other food types.

Table 9. Spearman rank correlation coefficients for different food types

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

Nutrient composition of the main food plant species of gelada in the Gich area is presented in Table 10. *Alchemilla pedata* has the highest level of crude protein content and *Dianthoseris schimperi* has the lowest. *Alchemilla pedata* and *Lobelia rhynchopetalum* contain the highest and lowest crude fat concentrations, respectively. The level of ash content is highest in *Rosularia simiensis* and lowest in *Alchemilla pedata.* Moisture content is highest in *Lobelia rhynchopetalum* and lowest in *Haplocarpha schimperi*.

Table 10. Nutrient composition of the main food plant species of gelada

Plant species	Nutrient content (% dry mass)			
	Protein	Fat	Moisture	Ash
Rosularia simiensis	13.63	3.54	4.77	16.73
Alchemilla pedata	20.81	4.35	5.2	2.40
Alchemilla abyssinica	18.49	3.63	4.97	2.53
Lobelia rhynchopetalum	19.00	0.84	8.30	12.80
Thymus schimperi	12.88	0.85	4.78	5.60
Carduus schimperi	12.91	0.94	4.82	6.22
Haplocarpha schimperi	13.31	0.90	4.37	16.00
Festuca spp.	14.00	1.65	4.38	14.34
Dianthoseris schimperi	12.13	3.69	4.59	2.41

Samples of plants that were abundant in the study area, but were not eaten by the gelada were also analyzed for nutrient composition (Table 11). Plants eaten and uneaten were significantly different in crude protein content (paired samples t test, $t=2.72$, $p<0.05$), but there was no significant difference in crude fat ($t=0.43$, $p>0.01$), moisture ($t=0.76$, $p>0.05$) or ash contents ($t=0.91$, $p>0.05$).

Table 11. Average nutrient composition of eaten and uneaten plants by the gelada

Plants	Nutrient content (% dry mass)			
	Protein	Fat	Moisture	Ash
Eaten	14.20	2.41	4.63	10.18
Uneaten	13.41	2.31	4.51	9.90

5.3. Activity budget

Geladas are very active animals, allocating more than 70% of their active time feeding and travelling activities. Based on pooled data from all age/sex class scans, the overall activity budget was dominated by feeding (Fig. 7), which contributed to 56.6% (grazing 44.7%, foraging 3.5%, digging 8.4%) of the time gelada spent on the four main activities recorded. Feeding occurred at a rate of 34.0 minutes per focal hour of observation. Socializing was the next most common activity, accounting for 17.5% (allogrooming 14.9%, aggression 0.9%, playing 1.7%) of the time (10.5 min/focal h). Travelling contributed to 14.1% of the time (8.5 min/focal h) recorded. Resting was the least common activity, accounting for 10.7% of the time (6.4 min/focal h). Other non-social activities contributed to 1.1% of the time.

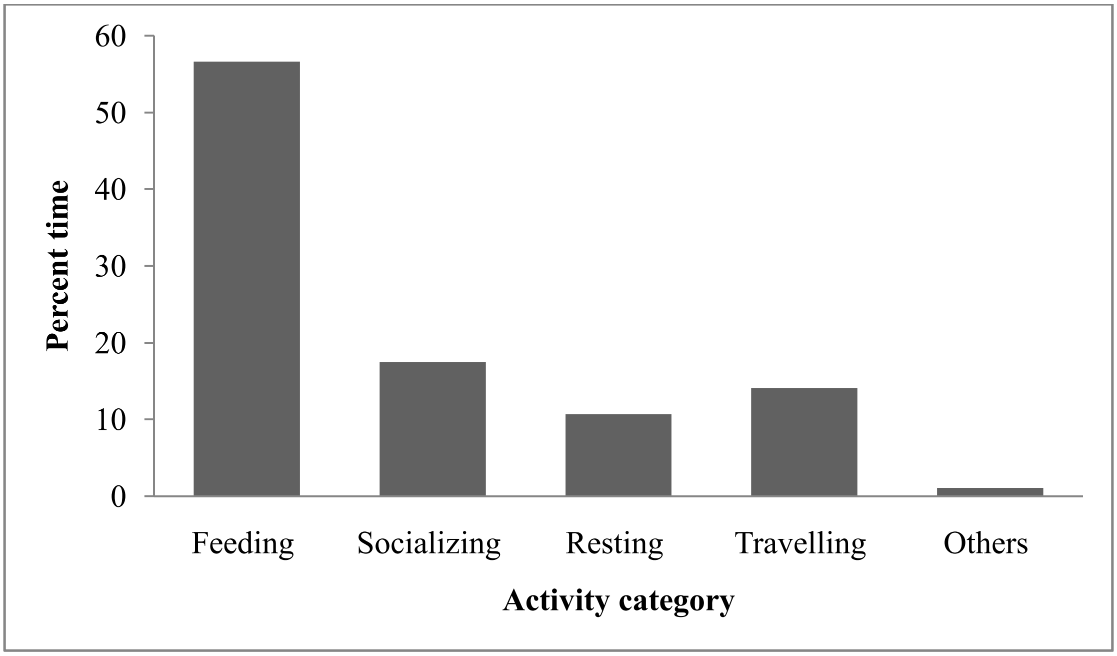

Figure 7. Percentage of time budget of geladas for different activities

Analysis of the daily activity patterns of gelada revealed many active peaks (Fig. 8). Feeding activity indicated an increase during the early afternoon (13:00–14:00 h) and towards the end of the early afternoon (15:00–16:00 h). Gelada travelled the longest distance during the late morning between 10:00 and 11:00 h, travelling at an average speed of 343 metres per hour. Between 16:00 and 17:00 h, travel speed decreased to an average of 205.2 m/h, but after 17:00 h, distance travelled increased again as the animals headed for the sleeping site. Gelada usually had a long resting period from 8:00-10:00 h and 12:00–13:00 h. Social activities peaked from 8:00–9:00 h. Similarly, other non-social activities peaked from 13:00–14:00 h. In general, resting and socializing were predominant activities during the early morning and late afternoon hours.

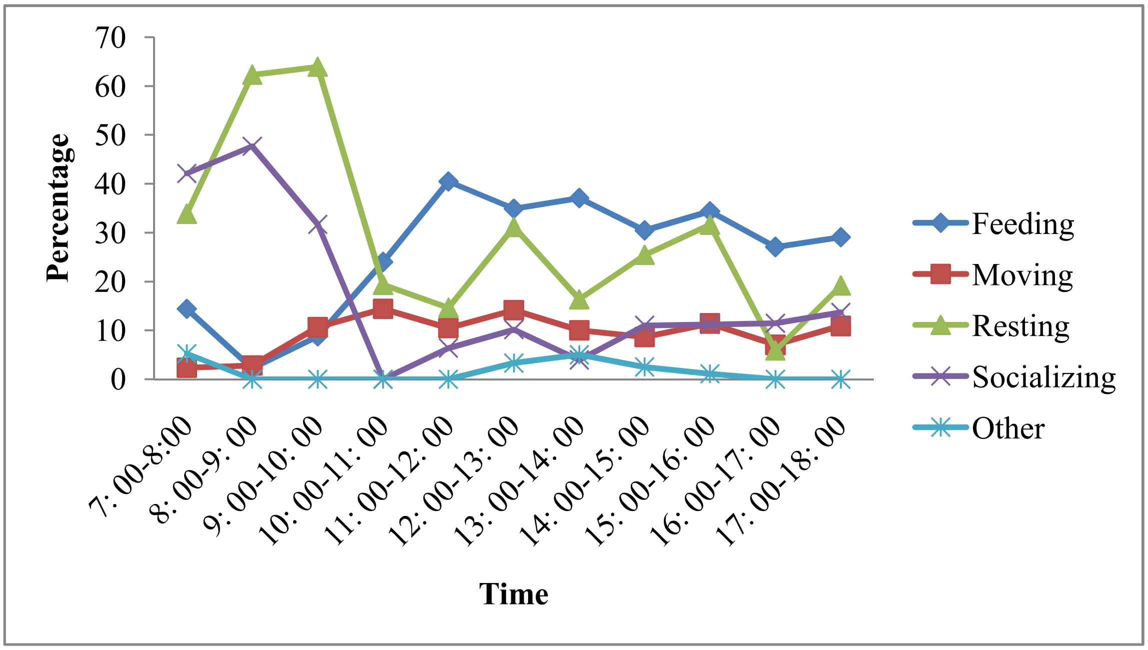

Figure 8. Daily activity patterns of geladas during the study period

Adults of both sexes were observed leading group progressions, but males led more often than females. Group movements were usually initiated by an adult male of the all-male groups, although this individual did not necessarily stay as the head of the group. As group movements were not cohesive, various subgroups followed different pathways, with the entire group aggregating at the end of movement.

There were monthly differences in the activity budgets of gelada (Table 12). The proportion of time spent feeding ranged from 50.2% during the peak of the wet season (August) to 62.8% during the dry season (April). The time spent travelling also showed variations. It was at its lowest level during the wet season (August, 10.5%) and peaked during the dry season (April, 17.4%). Socializing time was lowest during the dry season (March, 15.1%) and peaked in December (21.0%). Resting time peaked in June during the wet season (13.7%) and was the lowest in February (8.3%) during the dry season.

Table 12. Monthly time budgets as the percentage of time spent in each activity category

Month	Time budgets (%)				
	Feeding	Travelling	Resting	Socializing	Others
May	57.0	14.6	11.1	16.4	0.9
Jun	52.1	16.6	13.2	17.0	0.9
Jul	50.6	16.8	13.7	17.9	1.1
Aug	50.2	10.5	12.1	18.9	1.5
Sep	54.2	17.2	10.2	17.3	1.1
Oct	54.5	15.4	12.1	16.4	1.4
Nov	57.3	12.2	10.1	19.5	0.9
Dec	57.7	10.8	9.9	21.0	0.7
Jan	59.0	15.1	8.7	16.6	0.8
Feb	60.8	11.6	8.3	17.8	1.8
Mar	62.7	11.2	9.6	15.1	1.5
Apr	62.8	17.4	9.5	16.5	0.9
Mean ± SD	56.6 ± 4.3	14.1 ± 2.7	10.7 ± 1.7	17.5 ± 1.6	1.1 ± 0.3

Pair-wise comparisons of the main activity categories for the wet season through LSD multiple comparisons demonstrated that feeding and socializing had significantly ($p<0.05$) more time allocation compared to travelling and resting. Feeding and socializing time budgets were significantly different ($p<0.05$). Travelling time budget was significantly more than the resting time budget ($p<0.05$). During the dry season, geladas allocated time for the main activities in the same trend like during the wet season.

There were seasonal differences in the activity budgets of gelada. The proportion of time allocated for different activity categories by the geladas varied with season, except for socializing and other non-social activities as presented in Table 13.

Table 13. Mean (± SD) proportion of time (%) spent on the activity categories of gelada

	Proportion of time spent (%)			
Activity category	Wet season	Dry season	$F_{[1,58]}$	*P*
Feeding	53.1 ± 4.7	60.1 ± 4.7	32.843	0.001
Travelling	16.3 ± 4.0	11.9 ± 3.2	22.326	0.001
Resting	12.1 ± 3.6	9.3 ± 3.2	9.675	0.030
Socializing	17.3 ± 3.4	17.8 ± 3.9	0.242	0.625
Others	1.2 ± 0.6	1.1 ± 0.7	0.069	0.794

Time budget for different activity categories of the age/sex classes were analyzed. One way ANOVA demonstrated that the age/sex classes differed in all activity budgets, except socializing ($F_{[4,55]}=1.124$, $p>0.05$).

Adult females spent significantly more time feeding compared to adult males, whereas adult males spent more time resting (paired-samples t test, feeding: t=-3.561, $p<0.01$; resting: t=2.72, $p=0.05$; n=12 month). The two sexes were alike in the proportion of time allocated to travelling, socializing and non-social activities (travelling: t=-1.043, $p=0.319$; socializing: t=0.177, $p=0.863$; others: t=1.262, $p=0.233$). Adults spent significantly more time in travelling and other non-social activities than subadults (travelling: t=2.774, *p*<0.05; others: t=2.639, *p*=0.05). There was no significant difference in all activity budgets between the sexes of subadult individuals. Juveniles were significantly different from adults and subadults in time budgets for many of the activity categories. Adults spent significantly more time in feeding and other non-social activities than juveniles (feeding: t=12.956, *p*<0.001; others: t=3.913, *p*<0.01), but they spent significantly less time resting (resting: t=-3.403, *p*<0.01). Similarly, subadults spent significantly more time in feeding than juveniles (feeding: t=11.836, *p*<0.001), but they spent significantly less time resting and travelling (resting: t=-3.403, *p*<0.01; travelling: t=-3.897, *p*=0.01). The annual time budget for different activity categories of the age/sex classes are presented in Table 14.

Age/sex variations in some of the socializing activities were apparent. Specifically, females groomed more than males. Most of the grooming activities involving adult females were engaged in by lactating females. The greater amount of time spent engaged in play behaviour is attributed to the juveniles. Juveniles were recorded as playing approximately 10% of their active periods.

Table 14. Mean (± SD) proportion of time (%) spent on the activity categories based on age/sex classes

Activity category	Adult		Subadult		Juveniles
	males	females	males	females	
Feeding	55.8 ± 4.4	58.9 ± 6.2	57.0 ± 3.3	61.0 ± 4.4	50.3 ± 4.7
Travelling	14.5 ± 4.2	15.4 ± 4.1	11.8 ± 3.1	11.6 ± 3.3	17.3 ± 4.0
Resting	10.8 ± 3.7	7.6 ± 1.9	10.9 ± 3.6	10.0 ± 2.3	14.2 ± 3.2
Socializing	17.3 ± 3.3	17.0 ± 3.1	19.4 ± 3.5	16.5 ± 4.1	17.5 ± 3.8
Others	1.7 ± 0.7	1.4 ± 0.5	1.0 ± 0.6	0.8 ± 0.5	0.8 ± 0.7

Spearman's rank correlations demonstrated that the proportion of time spent in feeding was significantly negatively correlated with travelling and resting times (Table 15). Similarly, the proportion of time spent in travelling was negatively correlated with time spent in socializing. Resting and socializing times were inversely related to each other. However, there was no significant correlation between the other activity categories.

Table 15. Spearman rank correlation coefficients for different activity categories

Activity category		Travelling	Resting	Socializing	Others
Feeding	r_s	-0.698	-0.584	-0.049	0.025
	p	0.001	0.001	0.709	0.851
Travelling	r_s		0.273	-0.387	-0.046
	p		0.073	0.002	0.727
Resting	r_s			-0.34	-0.244
	p			0.008	0.06
Socializing	r_s				0.01
	p				0.937

5.4. Ranging patterns

Group spread of the main body of the study band ranged commonly from 70 to 100 m. The range did not include isolated all-male groups that were 150 m or more away from other members of the band. The group spread distance varied with the types of activities individual members of the band were engaged in. It was minimal when most of the individuals were resting or involved in socializing activities and maximal when they were engaged in feeding activity.

The mean daily travel distance of the focal band over the entire course of the study was 3006.5 ± SD 468.7 m (Table 16). The minimum and maximum distances travelled per day by the band were 2,102 m (September) and 4,900 m (December), respectively. Monthly mean of daily travel distances ranged from 2,252.6 to 3,568.4 m (n=12 month).

Table 16. Monthly mean of daily travel distances (m) for the study band

Month	Mean distance travelled	Range
May	3,503.2 ± SD 413.6	3,125–4,150
Jun	2,940.0 ± SD 292.1	2,626–3,315
Jul	2,590.4 ± SD 315.8	2,180–2,900
Aug	2,585.6 ± SD 316.6	2,121–2,990
Sep	2,336.0 ± SD 195.3	2,102–2,616
Oct	2,252.6 ± SD 158.2	2,120–2,500
Nov	2,968.2 ± SD 871.0	2,130–4,410
Dec	3,268.2 ± SD 765.0	2,120–4,900
Jan	3,180.4 ± SD 408.4	2,800–3,707
Feb	3,423.8 ± SD 372.6	2,910–3,719
Mar	3,568.4 ± SD 200.4	3,351–3,737
Apr	3,461.6 ± SD 691.3	2,800–4,613
Mean ± SD	3,006.5 ± SD 468.7	2,102–4,900

The most frequently recorded daily travel distances were between 2,600 and 3,100 m (23%). The second most frequent were between 2,000 and 2,500 m (16%) and the least frequent were between 3,800 and 4,300 m (5%). The percentage of days during which the band travelled various distances is shown in Figure 9.

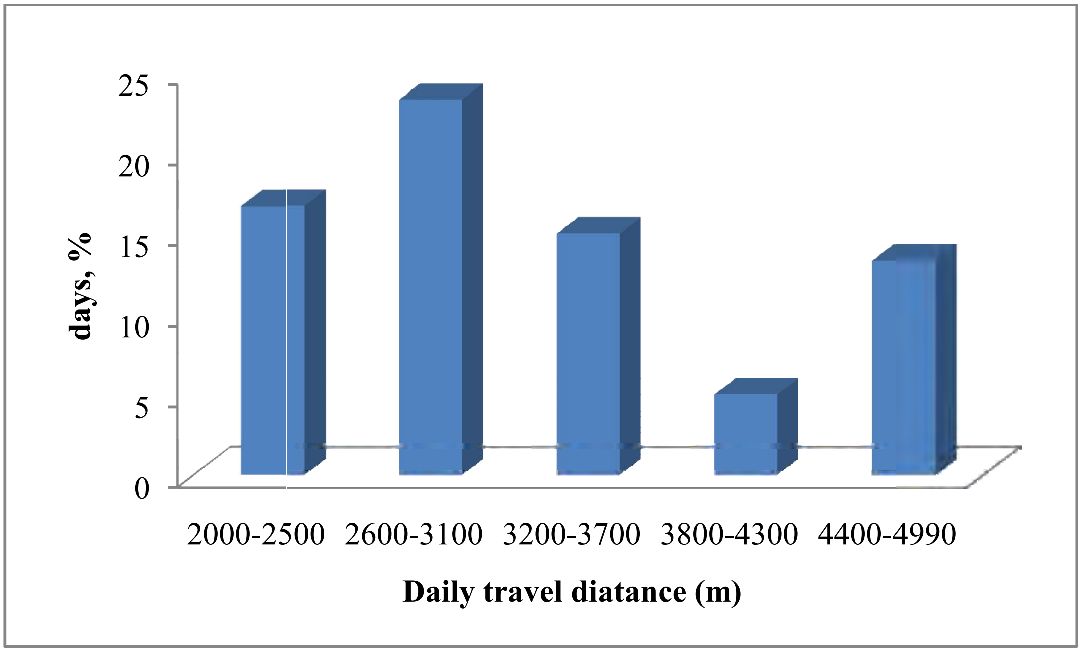

Figure 9. Frequency distribution of daily travel distances of the study band

Analysis of the average daily travelled distances showed significant monthly variations (ANOVA: $F_{[10,48]}=9.987$, $p<0.001$). Similarly, there was a seasonal variation in daily travel distance. The mean daily travel distance for the band during the wet season was 3,321.7 ± SD 26.9 m (n=6 month) and 3,636.5 ± SD 38.5 m during the dry season (n=6 month). The seasonal difference in daily travel distance was statistically significant (independent-samples t test, t=0.43, df=10; $p<0.03$).

Human disturbance was observed to have influence on daily travel distance of the band, especially during the dry months. Geladas were changing their direction of movement and travelled longer distances due to the presence of shepherds, who were herding livestock in the study area. Spearman's rank correlation test revealed a positive correlation between daily travel distance of the band and human and livestock presence in the area ($r_s=0.693$, $p<0.01$).

Monthly averages of daily travel distances were tested for correlations with group size and activity budgets. There was a significantly positive correlation between daily travel distance and group size for the study band (r_s=0.769, p<0.01). There was also a significantly positive correlation between daily travel distance and the percentage of time the band spent in travelling (r_s=0.455, p<0.05), but negative correlation with time spent in resting (r_s=-0.35, p<0.05) and socializing activities (r_s=-0.742, p<0.05).

The study band used a total of 157 quadrats (each 200 m x 200 m) during the study period. The annual home-range size of the band using the Grid Cell Analysis (GCA) method was therefore calculated to be 6.3 km^2. Enclosed quadrats that were not entered by the band during the study period accounted for 3.8% of the home range. However, the annual home-range size of the band using the Minimum Convex Polygon (MCP) method was computed to be 6.9 km^2 (Fig. 10). The difference in home-range size estimate using the GCA and that derived from MCP method was statistically significant (paired-samples t test, t=-25.50, p<0.05).

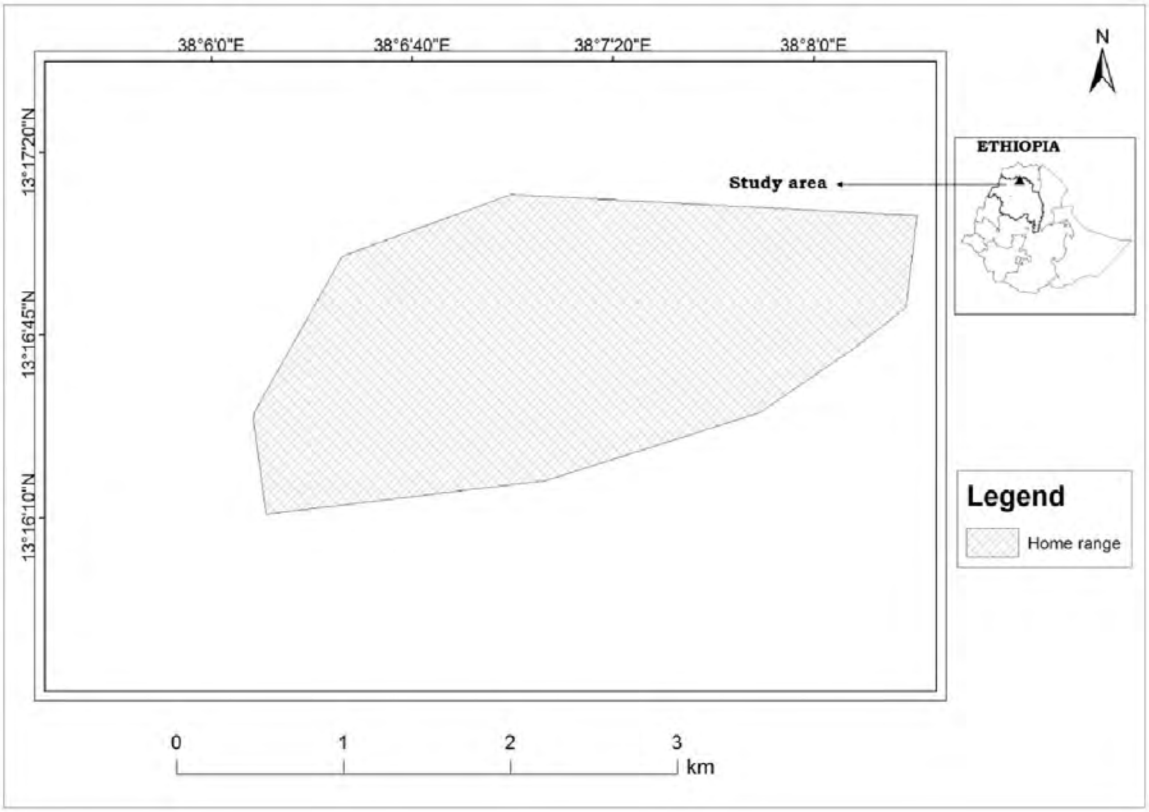

Figure 10. Depiction of the 100% MCP annual home range of the study band

The mean number of 1 quadrat used per day was 12.5 SD ± 2.4 (range=8–19 quadrats, n=120 days), on average about 1 quadrat per hour. These values were equivalent to 1.6% of the annual home range area of the band. The mean monthly quadrats used by the band was 62.4 SD ± 8.7 (range=49–76 quadrats).

During the dry season, the band ranged widely, using 116 quadrats and occupying 54% of the annual home range, while during the wet season the band used 104 quadrats, occupying 46% of the home range. The home-range size of the band was significantly larger during the dry season (paired-samples t test, t=19.00, $p<0.05$; Figs. 11). The degree of overlap between wet and dry seasons ranges was 73.9% (the area of overlap was 5.1 km^2).

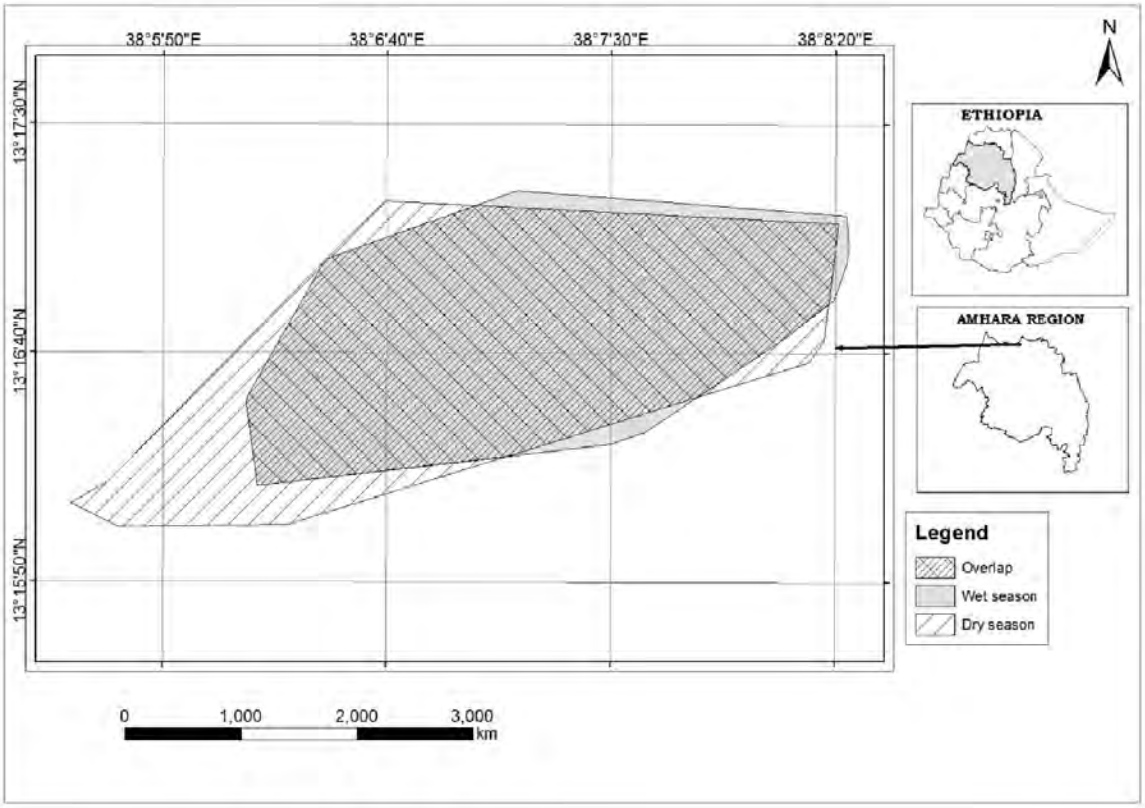

Figure 11. Home range of the study band during wet and dry seasons

One way ANOVA demonstrated a significant difference in the size of monthly area used by the band ($F_{[2,11]}=1.40$, $p=0.01$). The mean monthly area used by the band was 1.3 ± SD 0.2 km^2 during the wet season (n=6 mo) and 1.7 ± SD 0.7 km^2 during the dry season (n=6 mo). The smallest monthly range area during the wet season was about 1.1 km^2 and the largest was approximately 1.5 km^2. Similarly, the smallest monthly range area during the dry season was 1.7 km^2 and the largest was about 2.0 km^2. There was an overlap between ranges in different seasons.

The pattern of range use of the focal band was measured using quadrat use. During the study period, the overall mean reuse frequency of quadrats was 1.4 ± SD 0.8 (range 1-5 quadrats). Reuse frequency of quadrats was higher during the dry season (mean=2.4 ± SD

0.8 quadrats, range 2-5) than in the wet season (mean=2.0 ± SD 0.2 quadrats, range 2-3). The band had a serious of contiguous quadrats within the home range which they entered frequently. The band did not utilize the home range evenly, but rather tended to concentrate on an area of abundant resource supply. Frequently used area accounted for 23 quadrats or 0.9 km^2. This area constituted 21% of all quadrat entries and about 15% of the annual home range.

There was differential use of the home range throughout the year. Some months showed a diverse, widespread use of the home range (e.g., December and February) and some a more concentrated use (July and August), which corresponds to seasonal variations in resource availability. The study band's core area was entered sometimes by a neighbouring band, indicating that it was not an area of exclusive use. However, based on opportunistic observations, the area did not appear to be part of the core area of the neighbouring band.

There were noticeable variations in the ranging patterns of the study band in relation to the availability of drinking water. There were only two permanent sources of surface water in the home range of the band. Water sources were located in the streambed and the focal band was sharing them with other bands and domestic livestock. Direct meetings of two bands at water source sometimes resulted in increased aggressiveness. Fighting did not occur, but adult males were observed herding their own family units and chasing other males away from females. The availability of drinking water was thought to be limiting on the plateau in general and in the home range of the study band in particular.

The frequency of visit to water source by the study band varied seasonally. Individual members of the band drank little from them during the wet season, but as often as 1–2 times per day during the dry season. After the first precipitation during the onset of the rainy season in May, they drank from seasonal streams in the home range area and contained water for about 3–4 months.

Influence of drinking water scarcity on the ranging patterns of the band was observed during the dry season. For instance, the size of seasonal home range was influenced by the extent and characteristics of the band's movements. The band ranged repeatedly into areas where water sources were located. The band usually returned to the core area of the home range within some hours after drinking, but they switched their ranging center to areas that were close to water sources during a period of critical water scarcity.

During the study period, the focal band exclusively used cliff-face crevices as sleeping sites at night during all the observations and at all times of the year. Geladas were also observed using cliffs as refugia when they were threatened by predators or humans during the day time. The band slept only on six different sleeping cliffs (Fig. 12), some of which were located at the periphery of the home range.

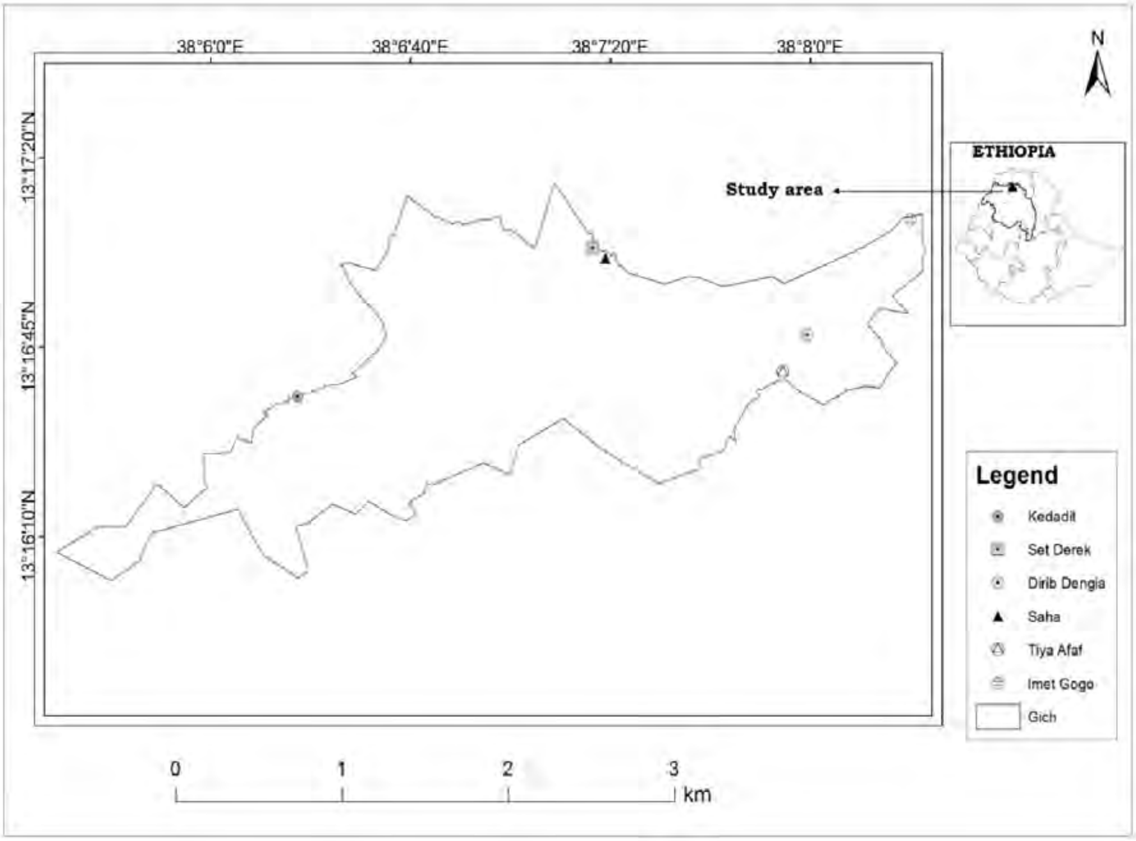

Figure 12. Map of the study area showing sleeping cliffs of the band

Chi-square tests were performed to test whether the band used sleeping cliffs at random, which means that the band used all sleeping cliffs in the same proportion. The analysis in Table 17 revealed that geladas were not using the sleeping cliffs randomly (χ^2=5.09, df=5; p<0.05).

Table 17. Number of entries into each sleeping cliff compared to expected values

Sleeping cliff name	No. of entries		χ^2	*P*
	Observed	Expected		
Kedadit	40	20	2.13	$p<0.05$
Set Derek	23	20	0.40	$p<0.05$
Dirib Dengia	7	20	0.83	$p<0.05$
Saha	27	20	0.05	$p<0.05$
Tiya Afaf	5	20	1.63	$p<0.05$
Imet Gogo	18	20	0.03	$p<0.05$

All members of the study band were observed on a single sleeping cliff, with only 19 recorded instances of splitting up the band and individuals sleeping on different cliffs. Individual members of the band slept on different cliffs, with a mean of 1.5 ± SD 0.1 cliffs used per night (range=2–3 cliffs, n=19 nights).

During the times of opportunistic observation, mother-infant dyads usually entered the sleeping cliffs before other age/sex classes (χ^2=0.21, df=3; $p<0.05$). Adult and subadult members of the all-male groups (n=3 groups) were usually the last to enter the sleeping sites. However, the sequence of departure from sleeping sites was different from the entering sequence, with adult males commonly observed leaving the site first. It took a mean of 32.3 ± SD 3.4 min (range=28-49 min) for the whole group to leave the sleeping site. Different individuals entered the sleeping sites from different directions and the entrance time lasted a mean of 23 ± SD 9.5 min (range=27-35 min). Geladas' time staying on the sleeping site was longer during the dry season (paired-samples t test, $t=2.99$, $p<0.01$).

The choice of top sleeping sites depended partly on the elevations of the cliffs. As such, the band favoured large, low-elevation sleeping cliffs. The most frequently used sleeping site was located at the Kedadit cliff, where the band slept for 40 (33.3%) nights (Table 18). The overall use of each cliff as a sleeping site correlated negatively with elevation (Spearman's rank correlation, $r_s=-0.951$, $p<0.01$).

Some of the sleeping sites of the study band were shared with that of other bands. Fifty percent of the sleeping cliffs were located in the home range of the band's exclusive use and the band spent more nights on these cliffs than expected based on availability ($\chi^2=21.82$, df=5; $p<0.01$). The band slept on these cliffs 83.3% of the nights.

Table 18. Proportion of the six cliffs used as sleeping sites by the band

Rank	Sleeping cliff	Elevation (m)	% use of all sleeping cliffs
1	Kedadit	3,674	33.3
2	Saha	3,761	22.5
3	Set Derek	3,780	19.2
4	Dirib Dengia	3,782	15.0
5	Tiya Afaf	3,842	5.8
6	Imet Gogo	3,903	4.2

When the sleeping sites were analyzed in terms of their geographic location, the band slept more frequently in the western part of the home range ($\chi^2=21.83$, df=2; $p<0.01$), at lower-elevation cliffs during the dry season than in the wet season (Table 19).

Table 19. Nights spent at the sleeping cliffs by the band during each season

Sleeping cliff	Nights observed	
	Dry season	Wet season
Kedadit	25	15
Saha	18	11
Set Derek	9	14
Dirib Dengia	4	2
Tiya Afaf	3	15
Imet Gogo	1	3
Total	60	60

There were two distinct classes of cliffs that the band used as sleeping sites: those repeatedly used cliffs and cliffs used only rarely (Table 20). During a monthly 10 days of recording sleeping sites, the band re-used sleeping cliffs consecutively on 43.3% of the nights. These cliffs were recorded being used between 2 and 8 times. The focal band used a specific sleeping cliff on average for 4.3 consecutive nights before selecting a new sleeping site.

Table 20. Consecutive nights at the sleeping cliffs by the band during each season

Sleeping cliff	Number of consecutive nights	
	Dry season	Wet season
Kedadit	16	3
Saha	9	4
Set Derek	1	3
Dirib Dengia	1	3
Tiya Afaf	1	7
Imet Gogo	1	3
Total	29	29

6. DISCUSSION

Four gelada groups with varying population sizes were recorded in total on the plateau. The average group size was 165 individuals and there was a significant variation in the size of groups from different census blocks. Such differences in group size may have resulted from differences in the level of human and livestock disturbances as well as habitat quality in each of the local areas.

There was a significant difference in the percentage of age/sex composition of the population. The adult female-to-adult male ratio was 3:1, indicating that the population was female biased. The proportion of mature females that can give birth influences birth rate and effect population growth. Many of the reproductive females had an infant, which shows that there was high rate of recruitment in the population.

Over the past 7 years (2007–2014), the population of gelada in the Gich area has shown significant increase. In 2007, there were 327 individuals inhabiting the plateau (Beehner *et al.,* 2007). The population increased to 698 individuals in 2014. Thus, on average, 53 individuals per year were added to the population. However, the population estimate of 2007 was based on one day census result, which probably has missed some individuals uncounted. Ohsawa (1979b) has reported a population size of 325 individuals on the plateau, which is almost identical to that documented by Beehner *et al.* (2007). Geladas in the Gich area and other localities of the SMNP are increasing in number, and thus underestimation of the population size by Beehner *et al.* (2007) appears to be a reason for the similarity of their census result to that of Ohsawa (1979b).

One of the many possible reasons for the apparently high growth of the gelada population may be the presence of low mortality and high natality. Geladas are in general nonseasonal breeders, and thus they copulate throughout the year (Dunbar and Dunbar, 1974a). However, females in the same reproductive groups may experience close reproductive synchrony, due to environmental as well as social factors (Dunbar, 1980).

Detailed accounts on the rate of gelada predation in the study area are not available in literature, but possible predators include large carnivores such as the leopard (*Panthera pardus*), spotted hyaena (*Crocuta crocuta*) and common jackal (*Canis aureus aureus*) (Kawai, 1979; Jablonski, 1993; Iwamoto *et al.,* 1996). However, actual predation on gelada by any of these predators was not observed in the field during the course of the study. The absence of any recorded predation in the area may indicate that natural predators are found at low densities. The presumably low density of predators at Gich resulted in higher survival rate of geladas.

Geladas respond well to cool, temperate climates (Crook, 1966; Dunbar and Dunbar, 1975), which may be another reason why they are at present flourishing in the study area regardless of the cold stress they experience during a period of extreme weather (Dunbar, 1980). Furthermore, geladas were not hunted by humans (for food or pet trade) in the study area. Ban on killing of gelada and their adaptability to humans and livestock-modified environments might have contributed to the growth of the population (Hunter, 2001).

There were availability of additional food resources from adjacent farms (Puff and Sileshi Nemomissa, 2005; Mesele *et al.,* 2008). Anecdotal evidence has shown that crop raiding behaviour of geladas may have become an alternative mechanism to cope with the increased population pressure, especially when food availability is constrained during the dry season. Wild animals may tend to raid crops because it provides them with increased availability of alternative food resources. Cultivated plants are also commonly rich in energy and are found clumped, therefore they provide increased foraging efficiency and greater digestibility than natural food items (Hill, 1997; Loudon *et al.,* 2006).

High growth of gelada population in a rather restricted area may cause various problems in the future, including competition to the scarce resources, loss of fitness and transmission of diseases. Furthermore, high growth of the population may not necessarily be positive because in areas where the geladas are in contact with humans, they tend to raid crops (Mesele *et al.,* 2008). Crop raiding may sometimes lead to decreased tolerance of the animals by the local community. Increasing human population and intensified agricultural practices in the Gich village is likely to increase the conflict between man and gelada. Conflict between humans and wildlife is in general a major conservation concern in many areas. Sometimes, the conflict can be a major cause of wildlife mortality as farmers may attempt to protect their crops against raiding by killing wild animals (Marker *et al.,* 2003; Andren *et al.,* 2006). The growth in gelada population has come at a serious economic cost for the local community due to crop raiding, which is likely to be exacerbated in the future if the government does not relocate the community by providing proper incentive.

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

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

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

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

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

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

Nutritional factors exert powerful influences on plant selection in primates. Most species of plants do not contain sufficient concentrations of all the required nutrients, forcing animals to feed on a variety of plants (Richard, 1985; Milton, 1993). In the present study, macronutrients had influence on food plant selection in gelada. For instance, among the eaten plants, *Alchemilla pedata* and *Lobelia rhynchopetalum* were the first and second in terms of crude protein content. However, the most dominant diet, *Festuca* spp., are fourth in the rank. This indicates that the level of protein content in plants alone may not be the determinant factor for plant selection. It appears that plant choice in gelada may also be strongly influenced by factors other than macronutrient contents.

The average crude protein content of consumed plants is about 15.24% dry mass, with some plants containing protein levels above this average. This indicates a high nutritional quality of food plants as good quality forage is generally supposed to have protein content to the level of >9% of the dry matter (AOAC, 2000 as cited in Eshetu Moges and Balakrishnan, 2014). Furthermore, average protein content of consumed plants is comparable with recommendations for non-human primates (NRC, 1978), and therefore, it appears that protein may not be a limiting macronutrient of geladas at Gich.

The level of protein content was probably one of the factors that determined whether the geladas consumed specific plant species, as there was a significant difference in the averages of protein contents between eaten and uneaten plants. In general, the overall crude protein content profiles of gelada food plants at Gich are similar to those of conspecifics (e.g., Eshetu Moges and Balakrishnan, 2014), suggesting that dietary quality may not have been compromised.

Protein-to-fibre ratio of leaves is an important factor influencing leaf selection in primates, whereby leaves with higher protein and low fibre ratios are chosen (Milton, 1979). It is known that young leaves contain more protein, have lower fibre content, and are more digestible than mature leaves (Milton, 1979; Baranga, 1986; Chapman *et al.,* 2002). Similarly, Braun (1973) stated that the digestibility of grass blades is reduced by 50% when they mature. Young leaves are also good sources of minerals and have low tannin and toxin levels (Altmann, 1998). The higher digestibility and probably low level of secondary compound content may explain why the geladas preferred fresh grass blades over other food types at Gich.

Most plants are generally poor in fat content, with the exception of some fruits and seeds (Rothman *et al.,* 2011). Similarly, most food plants of gelada have lower level of crude fat content. Relatively, higher fat contents are found in *Alchemilla abyssinica* (3.63% dry matter) and *Alchemilla pedata* (4.35% dry matter). Rothman *et al*. (2011) have reported 5.3% dry mass of fat in forage leaves of primates, which is much higher than the average level of fat content in the food plants of gelada (2.27% dry mass). This shows that the foraged plants by geladas are in general low in fat content.

The average level of ash content in food plants of geladas at Gich is 8.78% dry mass, which is much lower than what was reported in other studies (Eshetu Moges and Balakrishnan, 2014). Mineral content tends to exert an influence on plant selection in gelada, even though foliage available to primates is in general thought to be high in most minerals relative to recommended dietary requirements (Milton, 2003). However, Gaynor

(1994) suggests that some plant species of low nutritive value may be selected on the basis of mineral content.

Geladas at Gich ignored the foliage of several common plant species. They were feeding instead on a limited subset of the available plants. Selection of food in many animals is constrained by secondary compounds that plants produce as chemical defense against herbivory (Coley, 1983; Bryant *et al.,* 1992). Primates, especially those feeding considerably on leaves, should overcome the influence of secondary compounds (Freeland and Janzen, 1974; Glander, 1982). It is suggested that both nutritive and defensive compounds may be important factors in influencing food selection in primates. Unfortunately, the role of secondary plant metabolites in foraging behaviour of gelada was not addressed in the phytochemical analysis of the present study.

Many factors are known to influence the activity budgets of primates, most of which are associated with the challenges of acquiring sufficient food energy (Coelho, 1986). The present study has shown that the activity budgets of gelada derived from focal animal scans generally resemble those of geladas studied at other sites (Iwamoto and Dunbar, 1983; Hunter, 2001). Geladas are markedly active animals that dedicate more than half (56.6%) of their time to feeding over other activity categories. The apparent prioritization of time allocation for feeding is in accordance with the results of other gelada studies (e.g., Iwamoto and Dunbar, 1983; Hunter, 2001). The reason for such high proportion of time devoted to the feeding activity may be due to the geladas' high degree of dietary specialization on grasses, which may have lower nutritional quality (Dunbar and Bose, 1991). The bulk feeding strategy of gelada requires a very large proportion of their time to be dedicated to feeding over other activities. According to Dunbar (1992), the availability of food and its energy content are critical factors that determine activity budgets in animals; therefore factors that affect food availability have a strong influence on time allocation decisions.

Travelling as an activity contributed to 14.1% of the time recorded. More time spent traveling may reflect the overall low density of food, as the encounter rate with potential food resources at Gich may be lower than in less-disturbed habitats. Geladas consistently spent more time in the travelling activity than resting due to high level of human presence in the study area, extensive habitat degradation and thus lower food availability (Crook, 1966; Dunbar and Bose, 1991; Fashing *et al.,* 2014). The study area had unusually high level of livestock presence and geladas were often disturbed by the close proximity of livestock. The disturbed condition of the environment coupled with large group size may have forced the geladas to spend more time travelling to fulfill their collective dietary requirements. In general, group size and habitat quality have great influences on activity budgets of primates. The result of this study is consistent with observations made on other primates that have shown larger groups to spend more time travelling than smaller groups (Stacey, 1986; Barton *et al.,* 1992; Isbell and Young, 1993; Menon and Poirier, 1996). Furthermore, low level of food availability may force primates to spend more time in travelling and feeding activities to meet their dietary needs (Onderdonk and Chapman, 2000; Gillespie and Chapman, 2001). On the other hand, Iwamoto and Dunbar (1983) have stated that better habitat quality is associated with decreased feeding and increased resting among gelada groups.

Socializing time was maintained consistently higher than resting time, which shows that geladas could spare more time for social activities than they did for resting. Dunbar

(1992) suggested that many social primates require time to establish and maintain relationships that affect their access to resources or mates (Dunbar and Dunbar, 1988). This may explain why geladas, which are gregarious primates, allocate more time to social activities and thereby reinforce their social bonds than they did for resting.

Resting was the least common activity of gelada, accounting for 10.7% of the time recorded, partly due to the habitat at Gich being resource constrained. The nutritional stress associated with resource scarcity in the area may have resulted in reduced resting time. However, the small amount of time they allocated for resting is common for some primates, because resting needs relatively less time compared to other activities (Dunbar, 1992). Indeed, resting time is considered to be a reserve of uncommitted time that animals can solicit from when they are in need of allocating more time to any of the other activities (Dunbar and Sharman, 1984; Dunbar, 1992). For instance, previous studies have shown that additional feeding time is taken first from resting time until this reaches a minimum threshold level (Dunbar and Sharman, 1984; Dunbar and Dunbar, 1988). It is suggested that time allocation to various activities by some primates is typically determined by considering the time left over after feeding (Dunbar, 1992; Brownikowski and Altmann, 1996). Geladas at Gich increased feeding, but decreased resting times during a period of food scarcity. Similarly, Dunbar (1992) stated that primates may reduce resting time for increased feeding time requirement under poor ecological conditions.

Geladas have shown significant monthly variations in their activity budgets. For instance, time spent feeding was highest during the months of January to April. Similarly, significant monthly differences were found in time spent resting and other activity categories, but these were not concentrated at any time of the year. There were also significant seasonal variations in the proportion of time allocated to the main activities. Geladas spent significantly more time feeding during the dry season than the wet season. This could be related to the difference in the nutritive quality of certain food resources, dropping during the dry season (Braun, 1973), forcing them to feed more to meet their daily energy requirements. It has been presumed that the dry season imposes conditions of nutritional stress (Crook, 1966; Dunbar, 1977; Iwamoto, 1979). During the dry season, geladas are faced with shortage of food, as the most preferable grass blades become desiccate and thus less-digestible (Crook, 1966; Braun, 1973; Hunter, 2001). Therefore, the significant increase in feeding time during the dry season is due to the paucity of the green grass blades (Crook, 1966; Iwamoto and Dunbar, 1983; Dunbar and Bose, 1991), which forced the geladas to partly shift their diet to herb leaves and underground food items that demand increased processing time and energy (Hill, 1999; Hunter, 2001).

More time was spent resting during the wet season than the dry season, which could be attributable to resources being more readily available. This may not have pushed the geladas to travel longer distances to meet their daily energetic requirements.

The energetic requirement for thermoregulation is an important factor that may influence the time budget decisions of primates (Oates, 1977; Marsh, 1981; Iwamoto and Dunbar, 1983). Thermoregulatory mechanisms have a strong influence on a number of activities, particularly during the colder dry season months. More time and energy is required for feeding in order to maintain homeostasis. Thermoregulation is also a factor worth considering in relation to seasonal activity budgets of geladas in the study area. During the dry season, especially in the months of November to March, Gich experiences nearfreezing night-time temperatures due to its high elevation. Therefore, additional nutritional requirements for thermoregulation may be one of the reasons for the increased feeding time during the dry season. Similarly, Iwamoto and Dunbar (1983) have suggested that geladas allocate more time to feeding over other activity categories as elevation increases due to the increased energetic needs, resulting from lower temperatures as well as a decrease in resource quality.

Age/sex classes of gelada demonstrated significant variations in activity budgets. Age/sex classes differed in all time allocations, except for social activities. Comparisons of male and female activity budgets for the study period indicate that there were significant differences in time allocated to various activities. It was expected that males feed more than females due to the relative size difference between the sexes, but such was not the case. Even though adult females are about half of the body size of adult males (Ohsawa, 1979a), they spent significantly more time in feeding than adult males, whereas adult males spent more time in resting. Earlier studies on baboon activity budgets have also shown that females spend more time feeding than males (Cowlishaw, 1993; Gaynor, 1994; Weingrill, 1998). Many of the focal adult females were either pregnant or had dependent offspring during the study period. The increased feeding time in adult females may be due to the extra energetic requirements of pregnancy, lactation and maternal care (Teichroeb *et al.,* 2003). Shanee and Shanee (2011) have reported similar results in the study of free-ranging yellow-tailed woolly monkeys (*Oreonax flavicauda*). Pregnant and lactating females have high energetic burdens imposed by reproduction (Hanwell and Peaker, 1977). Female geladas with dependent infants spent the least time resting of all age classes. Adults of both sexes spent significantly more time in travelling and other activity categories than subadults. This may not be surprising as adults and subadults may not have the same activity budgets due to variations in metabolic requirements resulting from different physical size.

Analysis of daily activity patterns of gelada demonstrated many active peaks. For instance, feeding activity increased during the late morning and towards the end of the early afternoon. Similarly, travelling activity peaked during the late morning and late afternoon, when the geladas headed for a sleeping site. Socializing and resting activities peaked during the early morning and late afternoon hours, probably due to the presence of animals around sleeping cliffs. Variations in the timing of daily activity patterns are characteristics of primates (Clutton-Brock and Harvey, 1977). Feeding activity may be peaked at the beginning of the day, and resting and social activities over the midday hours (Chapman and Chapman, 1991; Barrett, 1995). Daily activity patterns of most primates are dependent on habitat type, availability of food resources and water accessibility (Adeyemo, 1997).

Monthly average of the study band's daily travel distances over the entire period of the study was more than 3 km, which indicates that geladas range relatively long distances. However, human disturbance was observed influencing daily travel distance. Geladas were changing their direction of movement and travel longer distances due to the presence of shepherds, who were herding grazing livestock in the study area (Fig. 13). In general, foraging effort and daily travel distance of some primates may vary depending on group size because larger groups need to forage more and travel longer distances than smaller groups (Collins, 1984).

Figure 13. A shepherd herding livestock in the study area

Monthly average of daily travel distance of the study band is higher than what was reported for gelada of similar group size in other study sites (e.g., Sankaber area: Hunter, 2001). Longer daily travel distance of the band may reflect increased foraging effort, due to disturbed condition of the area and thus low resource availability. Isbell (1991) suggests that travel distance is more sensitive to patterns of food abundance and distribution.

There was seasonal variation in average daily travel distance of the band, indicating a significant increase during the dry season (Crook, 1966). This may be due to the patchy distribution of food resources during the dry season compared to the wet season. Reduction in seasonal resource availability may have forced the band to travel significantly longer distances in order to meet their daily dietary requirements. In accordance with this result, Garber (1993) and Poulsen *et al.* (1998) have reported that during the dry season when food availability is low, daily travel distance of some primates increased. However, during the wet season, when food availability is high, travel distance decreased. Similarly, Byrne *et al.* (1993) have reported that mountain chacma baboons (*Papio hamadryas ursinus*) travelled more distances when food availability was at its lowest towards the end of the dry season.

The present study has shown a significant positive correlation between the band's monthly mean daily travel distance and group size. Daily travel distance may directly correlate to group size, as larger groups tend to travel longer distances each day (Waser, 1977; Dunbar, 1988). During a period of food scarcity, intragroup feeding competition may force members of larger groups to increase their individual foraging efforts, which may be reflected in longer daily travel distances, increased time allocation to travelling and larger seasonal home ranges (Fashing, 1999; Hunter, 2001; Di Fiore, 2003).

Seasonal and annual home-range size estimates for the study band were calculated using the minimum convex polygon method, which is widely used for studying the ranging patterns in animals (Aebischer *et al.,* 1993). Home-range size was also computed using the grid cell analysis method (Fashing, 1999; Hunter, 2001; Kaplin, 2001). Both methods produced significantly different home-range size estimates for the band. The minimum convex polygon method overestimated the home-range size, because it may have included some areas that were not actually occupied by the band in the calculation. Different methods of estimating home-range size can produce a marked variation in the results obtained (Kaplin, 2001).

There was a significant variation in the size of the monthly area used by the band, indicating differential use of the home range. During some months a widespread use of the home range was observed, whereas during other months a more concentrated use. During the dry season, the band ranged widely occupying more than half of the size of the annual home range. The larger home-range size of the band during the dry season was primarily related to the overall low availability of green grass and other resources in the study area. The change in foraging strategy to less-desirable diets was apparent during the dry season, forcing the band to travel long distances and expand the seasonal home range. In general, home ranges are expected to expand and contract seasonally in response to variations in resource availability. As such, home ranges are expected to be larger during a period of resource scarcity during the dry season and smaller when resources are abundant during the wet season (Phillips *et al.,* 1998; Chapman and Chapman, 2000; Moyer *et al.,* 2007). However, home-range size is also dependent on other factors, including energy requirements of animals (Kelt and van Vuren, 1999) and intragroup interactions (Grant *et al.,* 1992). Furthermore, home-range size is influenced by habitat diversity in that animals inhabiting relatively homogeneous habitats have larger home ranges than those living in an area of greater diversity (Moyer *et al.,* 2007). This explanation gives support to the present study result as the habitat was relatively homogeneous Afroalpine grassland and the focal band had a larger annual home-range size.

There was a significantly positive correlation between monthly averages of group size and the size of monthly home range. Similarly, previous studies on baboons have shown home-range size to be directly related to group size (Stacey, 1986; Barton *et al.,* 1992).

As group size increases, the amount of food needed collectively by members of a group also increases and thus home range size should increase accordingly (Clutton-Brock and Harvey, 1981; Chapman and Chapman, 2000). A larger group size provides individuals with increased vigilance against predators and improved knowledge of resource availability (Altmann, 1998; Galef and Giraldeau, 2001). The disadvantage of foraging in large groups is increased intragroup competition for food (Shopland, 1987).

The band used the home range in a heterogeneous way, with some quadrats being more intensely used than others. Several studies have shown that primates utilize areas with higher food concentrations within their home ranges in order to maximize food intake relative to energy expenditure (Barton *et al.,* 1992; Nakagawa, 1999). Pattern of home range use is affected by the species diet, feeding behaviour and nutritional quality of food (Dunbar, 1988). However, the most important factor influencing primate ranging patterns and habitat use is the distribution of food, spatially and temporally (Davidge, 1978; Anderson, 1981; Dunbar, 1988). Reuse frequency of quadrats was higher during the dry season than the wet season, indicating more intensive use of certain quadrats. Pattern of food availability as well as other factors, such as access to suitable sleeping site and drinking water, may have caused much of the variation in habitat use. Earlier studies on baboons have also shown that habitat use may be influenced by factors such as energy requirements, distribution of food in a habitat, availability of cover from predators, places to rest and access to drinking water (Mckenna, 1982; Barton *et al.,* 1992; Morris, 1992; Cowlishaw, 1999). The distribution and abundance of resources may influence home-range size and the intensity with which an area within the home range is used through time (Milton, 1980; Robinson, 1986; Chapman, 1988).

There were marked variations in the ranging patterns of the study band in relation to the availability of drinking water. There were only two permanent water sources in the home range of the band, which were being shared with other bands and livestock. The presence of a permanent water source within the home range was an important factor affecting ranging patterns. The frequency of visit to water source by the band varied seasonally. Individual members of the band drank little from them during the wet season, but as often as 1–2 times per day during the dry season. This corresponds to observations on other primate species that also drank water on an almost daily basis (Nakagawa, 1999).

Effects of water scarcity on the ranging patterns of the band were apparent during the dry season as the home-range size was influenced by the extent and characteristics of the band's movement. During the dry season, the band ranged repeatedly into the areas where water sources were located. However, during the wet season longer periods of time were spent away from the permanent water sources as there was abundant supply of water throughout the home range, particularly after the first precipitation during the onset of the wet season in May. In general, availability of surface water is considered to be a key factor in determining ranging patterns of primates (Barton *et al.,* 1992; Hill *et al.,* 2003).

Primates spend about half of their lives within sleeping sites and therefore choice of suitable sleeping sites is considered to be an important aspect of their survival (Anderson, 1984; Anderson, 1998). Geladas are not adapted to arboreal life, and thus they rarely climb up trees (Crook, 1966; Fleagle, 1999). In the present study, the focal band exclusively used cliff-face crevices as sleeping sites at night during all observations of the year. Sleeping sites were located on the side of a limestone cliff that vertically drops precipitously into the lowland areas. Similar to the geladas, hamadryas baboons (*Papio hamadryas*) that live in the highlands of Ethiopia sleep on sheer cliff-faces (Kummer, 1968). The study band slept on six different cliffs, two of which were located in the periphery of the home range. Three of the sleeping cliffs of the focal band were also shared by other bands, while the rest were located in the home range of the band's exclusive use. Various factors, including safety from predators, thermoregulation and comfort, may determine selection and use of particular sleeping sites in primates (Anderson, 1984; Anderson, 1998; Reichard, 1998).

Given the presence of known gelada predators in and around the study area, including large carnivores such as leopard, spotted hyaena and common jackal (Kawai, 1979; Jablonski, 1993; Hunter, 2001), sleeping on cliff-face at night is regarded as anti-predator behaviour (Iwamoto *et al*., 1996). However, geladas were not using night-time sleeping cliffs at random. Instead, they use cliff-ledges as sleeping sites that were located at middle levels of cliffs, which may have provided them with effective physical barriers to natural predators. Indeed, the sleeping cliffs selected by the band had steepness that reduces the number of access routes to predators. Predation pressure is in general considered as one of the primary factors influencing sleeping site selection and use in primates (Cowlishaw, 1994; Anderson, 1998; Reichard, 1998).

Predators pose a major survival threat to primates, especially during night. For instance, baboons suffer from night-time predation by leopards and therefore trees and mainly cliffs are used as sleeping sites (Altmann and Altmann, 1970; Hamilton, 1982; Cowlishaw, 1994). An important natural predator of the gelada around the study area is leopard, although anecdotal evidence has shown that its density may be low. There are records of predation attempts by leopards in other localities of the SMNP. Similarly, spotted hyaena and common jackal have been identified as likely predators of gelada, especially on subadults and juveniles (Hunter, 2001). Overall, geladas in the study area were faced with low predation pressure, as only two instances of predation attempts by leopards were recorded during the study period. In general, the rate of predation on large-bodied primates is low compared to small-bodied species (Cheney and Wrangham, 1987; Kierulff *et al.,* 2002). Furthermore, large-bodied primates that live in human-modified habitats may face low predation pressure (Stanford, 2002). The present observations of the band shifting sleeping cliffs after encounters with predators suggest that predation pressure may be one of the determinant factors influencing selection of sleeping site in gelada.

Living in temperate environments, such as the Gich plateau (Crook, 1966; Dunbar and Dunbar, 1975) may have forced the geladas to cope with seasonal cold climate. Climatic factors are thought to be of particular importance for gelada ranging patterns in the study area (Iwamoto and Dunbar, 1983), which is known to experience extremely cold nights. Average monthly minimum temperatures as low as 2^{o}C have been recorded for the Gich area during the dry season months. The band predominantly slept on low-elevation cliffs during the dry season, which may be related to the more favourable climatic conditions as areas that lie at lower elevations have higher temperatures than those at high elevations. Furthermore, geladas chose sleeping sites that were located at the middle levels of the cliffs and in the shadow of ridges, which might have provided them with protection from strong winds. Thermoregulation thus could be achieved by the selection of optimally insulated sleeping sites. Similar to the geladas, many primates need to cope with cold temperatures (Anderson, 1984). One way of maintaining thermoregulation is to choose warm microclimates within their home ranges. Indeed, because of the harsh environment, some temperate primates may adopt altitude migration to buffer seasonal climatic stress (Bishop, 1979; Wada and Ichiki, 1980). Primates may choose to sleep in sites that are located at lower elevations, in order to thermoregulate during the night (Anderson, 1984; Liu and Zhao, 2004). Barrett *et al.* (2004) have suggested improved thermoregulation as an important factor that determines the use of caves by chacma baboons (*Papio hamadryas ursinus*).

The physical structure of the cliff appears to be an important factor influencing the choice of sleeping site in gelada. In general, the band favoured large sleeping cliffs as this would enable group cohesion to be maintained at night. Large cliffs may allow all group members to sleep in the same site and therefore facilitate social interaction and communication. Most species of primates are highly social and therefore prefer to stay in physical or visual contact at sleeping sites (Dunbar, 1992; Anderson, 1998; Di Bitetti *et al.,* 2000). All individual members of the band were observed in a single sleeping site, with some recorded instances of splitting up and sleeping in different sites. Geladas usually slept in compact huddles of varying sizes, with family unit members having a tendency to spend the night in the same area. Huddling of animals may serve to increase warmth or to conserve body heat (Gaulin and Gaulin, 1982).

The study band used six cliffs as sleeping sites, probably due to the limited availability of suitable sleeping sites within the home range. Baboons are also known to use a few sleeping sites in their large home ranges (e.g., Sigg and Stolba, 1981), because appropriate sleeping sites are rare in savanna habitats. There were two classes of cliffs that the band used as sleeping sites: those repeatedly used cliffs and cliffs used only rarely. Two out of the six sleeping cliffs were used more frequently than others, together comprising two-thirds of the sleeping nights. The reuse of few sleeping sites may facilitate group re-union at dusk if the group had accidentally split up (Chapman, 1989; Anderson, 1998). When primates gather at the sleeping sites, they usually engage in grooming and other social activities (Kinzey and Wright, 1982). The reuse of sleeping sites may increase the primates' familiarity with a location, thus improving the chance for escape from predators (Di Bitetti *et al.,* 2000). Repeated uses of sleeping sites in response to harsh climatic conditions have also been found for some primate species (Zhao, 1999; Liu and Zhao, 2004; Wang *et al.,* 2011).

In general, predation avoidance, thermoregulation and comfort may not be mutually exclusive factors that determine selection of sleeping sites in gelada. Other factors as well may have shaped the pattern in sleeping site use. For instance, seasonal availability of resources acting on the ranging patterns of the band might have indirectly affected the choice of sleeping sites.

7. CONCLUSION AND RECOMMENDATIONS

The gelada population living in the Gich area has shown a significant growth over the years. Population growth of geladas has come at a serious economic cost for the local community due to crop raiding. The availability of additional food from adjacent farms may have become an alternative mechanism of coping with increased gelada population pressure. The conflict between humans and gelada will likely be exacerbated in the future if the government does not relocate the community by providing proper incentive.

The Afroalpine grassland of the Gich area has been intensively used for livestock grazing. There were domestic animals throughout the plateau and represent the main competition for food and other resources with wild animals. The encroachment of natural habitats by humans and their livestock poses serious threat to the endemic wildlife.

Baseline data on gelada population status in the Gich area is documented, and thus it is important to regularly monitor trends of the population in the future. Detecting changes in the population through time is of high priority in order to take effective conservation measures.

Based on the results of this study, the following recommendations are made:

- ✓ The extensive human disturbance and livestock grazing on the plateau need to be reduced to conserve the area as a sanctuary for the endemic wildlife.
- ✓ Future surveys of gelada populations should be carried out in other localities of the SMNP and surrounding areas to get a better representation of their geographic distribution.
- ✓ Geladas should serve as an umbrella species for conservation of the SMNP as maintaining habitat for geladas would also conserve habitat for other wild animals

- ✓ The most important plant species in the gelada diet should be monitored to get an understanding of food availability in the area.
- ✓ Nutritional analyses focusing on micronutrients and secondary compounds contained in plants eaten and avoided by geladas should be conducted to better understand the foraging strategies of geladas in SMNP.

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