

Foraging strategies of wild gelada monkeys (*Theropithecus gelada*) in an Afroalpine grassland at Guassa, Ethiopia

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Dedication

I dedicate this thesis to my childhood hero Thor Heyerdahl. You inspired me to be the adventurer I am today.

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This thesis would not have been possible without the hard work and dedication of many of people.

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Abstract

Studies of the relationship between animal populations and their food supplies are essential for our understanding of their ecology and behavior. Since fitness depends on the ability to acquire food, animals are assumed to have evolved optimal foraging strategies. Optimal foraging theory (OFT) is therefore a useful tool to better our understanding of how animals perceive and utilize their habitats. With the aim of investigating the foraging strategies of the only living graminivorous primate species, a habituated band of gelada monkeys was studied at Guassa, an Afroalpine grassland in the Ethiopian highlands. From August to October 2016, data were collected on their activity budget, diet and patch utilization. The results showed that adult females and juveniles spent more time feeding than adult males, who in turn spent more time resting. All age-sex classes showed selectivity for high-quality food items and consumed a large proportion of mixed short graminoids (the category with the most energy per gram). Adult females and juveniles showed a higher degree of dietary selectivity than adult males and consumed more mixed short graminoids and forbs (the two plant categories of highest nutritional quality) while adult males fed more on mixed tall graminoids (the category of lowest energy per gram). In agreement with the state-dependent theory, the feeding behavior of the geladas was affected by hunger levels at different times of the day. In particular, the geladas were less selective of food items in the morning (when they were assumed to be more hungry) compared to later in the day. Together, these findings show that differences in feeding behavior within the gelada population reflect the differing demands of energy allocation between age-sex classes as well as the food distribution in their habitat. The geladas have two forms of locomotion: walking (used to relocate over longer distances to new feeding sites) and shuffling (a bipedal locomotion used while feeding). Geladas feed sitting down plucking food items with both hands and shuffling allows them to keep feeding while relocating short distances. After establishing basic patterns of gelada feeding ecology, the present study tested predictions of foraging theory in relation to the allocation of time in patches of different quality. To accomplish this, a novel biological definition of patch for geladas was developed by using their distinct foraging behavior (a repetitive sequence of feeding and walking). The

Marginal Value Theorem (MVT) assumes that animals process information about the general quality of their habitat and predicts that an individual will stay longer in patches of higher quality. The results of the present study showed that geladas allocated time in patches according to the quality of the vegetation available in the patch. This provides novel evidence that foraging theory, and the MVT in particular, is a useful framework for characterizing feeding behavior in the only graminivorous primate. It was possible to identify the aspects of the Afroalpine grassland vegetation that were associated with patch residence time decisions. Specifically, time spent in a patch positively correlated with increasing percentages of mixed short and mixed medium graminoid cover and inversely correlated with percentage of mixed tall graminoid cover in the patch. Yet the results showed that the rate of energy available is not the sole factor impacting patch residence decisions, as the geladas spent the longest time in patches of intermediate total energy yield. Time spent in a patch was positively correlated with the diversity of plant categories. Thus, as in herbivores, the geladas showed selectivity for a mixed diet. These findings are consistent with the concept of partial preference and illustrate the limitations of applying foraging theory to geladas using only a single currency (energy) as a variable. The MVT also predicts that travel time between patches should increase with longer patch residence time. However, the results do not support this prediction, suggesting that other ecological and/or social factors dictate the relationship between patch residence time and travel time. The geladas were found to adjust the number of shuffle events according to time spent in patches and quality of the food in the patches. Furthermore, the amount of MSG was shown to be the factor driving the number of shuffle events. The present study contributes to increase our understanding of gelada foraging strategies and adds to the baseline data needed to design conservation actions for this atypical primate living on “the roof of Africa”.

1 Introduction

Since fitness depends on the ability to acquire food, foraging strategies are assumed to have evolved in a way that enables an animal to navigate its environment and choose an optimal strategy for foraging (Schoener 1971). Optimal foraging theory (OFT), established by MacArthur & Pianka (1966), attempts to explain how animals foraging decisions are based on maximizing food intake while minimizing energy and time to search for and consume resources, thus maximizing energy intake per time unit. Two distinct approaches later developed to test the assumptions of OFT (Pyke et al. 1977, Litvaitis 2000).

The first approach focuses on food item selectivity, a branch of OFT called optimal diet (Schoener 1971), and is based on three assumptions. The first assumption is that an animal would benefit from selecting food items of greater biomass yield or caloric value per time unit, and thus it would be optimal to always select for high-quality food items. Different plant species and parts of a single species can vary greatly in nutrient content, which is the basis of determining quality rankings of food items. As such, food items are ranked by their nutritional value (micronutrients) or energy yield (macronutrients), amounts of protein, carbohydrates and fat (Rothman et al. 2012). However, it is important to take into consideration that protein and other nutrients are diluted by the build-up of cell wall components and thus even though taller species offer a higher biomass, they tend to be of lower quality (Westoby 1974). In addition, the level of cell wall components, cellulose and silica a plant contains is a function of its age and diameter (Owen-Smith & Novellie 1982). Taller species therefore are more mechanically challenging to ingest and digest than shorter species (Owen-Smith & Novellie 1982). The second assumption of optimal diet is that a food item is always either taken or not when encountered and thus partial preference does not exist (Schoener 1971). The third assumption is that consumption of a food item is not affected by its own abundance but only by the abundance of higher quality food items (Schoener 1971). Thus, preference for a food item (or plant category) is determined when an animal increases the intake of such item in periods of general food

abundance and lowers the intake of the same item in periods of food scarcity (Leighton 1993, Marshall & Wrangham 2007).

The second approach to testing the assumptions of OFT focuses on food items that are distributed in discrete patches or clumps of food (Schoener 1971, Krebs et al. 1974). Charnov (1976) presented a mathematical model (the Marginal Value Theorem, the MVT) to explain how foragers navigate their environment to maximize energy intake per time unit based on optimal patch residence time and optimal rate of movement between patches. When resources are distributed in discrete patches throughout the habitat, the MVT predicts how long an individual should spend in a patch before moving on to another depending on the rate of food accumulation within the patch (Charnov 1976). As an individual spends time in a patch, food intake rate decreases because resources are depleted until the patch reaches a marginal capture rate, which means that more time spent in the patch will lead to the patch quality dropping below the general quality of the habitat. At this point, it is optimal to leave the patch and find a more productive patch, at the same time minimizing travel time and movement costs (Charnov 1976). The diminishing return rate refers to a decline in the marginal value of food in a patch, which means that after a time spent in a specific patch, even if an individual can maintain a constant foraging effort, less fitness is gained per time unit and consequently further effort will yield smaller benefits (Winterhalder 1981).

Patches with similar characteristics are said to belong to a given “patch type” (Charnov 1976, Winterhalder 1981). It is then reasonable to suppose that different patch types are likely to be characterized by different resources and return rates. The prediction is that given two or more alternatives, the patches with higher average return rates will receive greater allocations of foraging time. This prediction can be derived from the MVT as follows (Winterhalder 1981): the first assumption is that alternative patches are characterized by smoothly decelerating return curves (Figure 1). The second assumption is that none of these curves cross, but instead run roughly parallel to one another. The third assumption is that external constraints (e.g. weather

conditions) are not strongly biased against patch types with higher mean return rates. If these conditions are met, and alternative patch types can be ranked in terms of efficiency (energy yield per time unit foraging time), then the MVT predicts that foraging effort will correlate directly with the efficiency rank order, such that higher ranked patches will receive greater time allocations of foraging time.

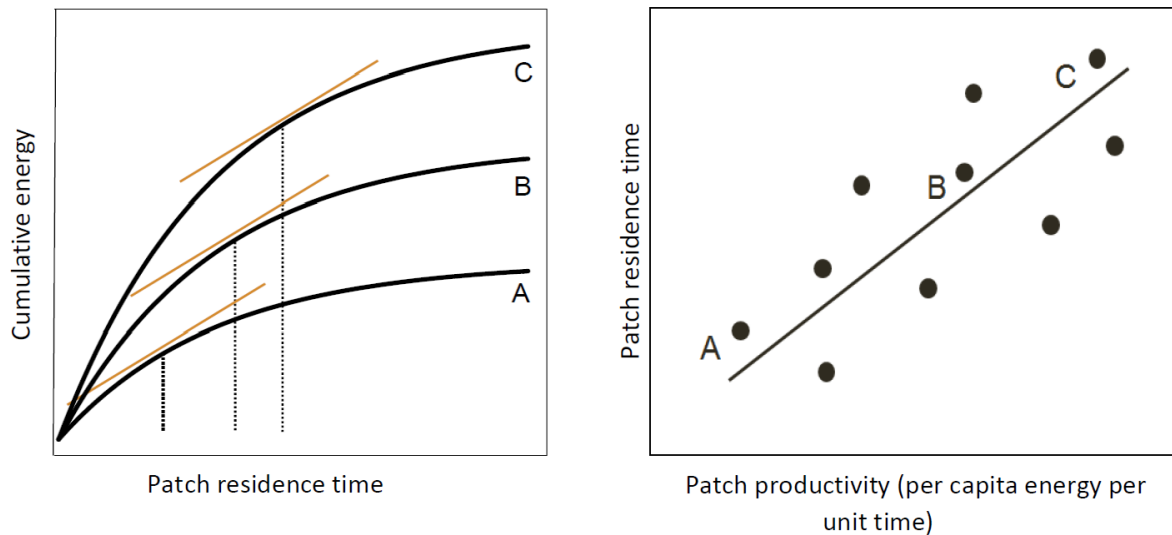


Figure 1. Illustration of an indirect test of the MVT when gain functions cannot be directly measured. A, B and C depict patches with increasing quality from poor to rich.

An initial test should therefore be used to verify that the hypothesized patch gain function actually occurs. If these assumptions are met, the “one-best-patch” rule that foragers base their patch time allocations to stay longer in higher quality patches should be readily testable.

The MVT also predicts that more productive environments should result in longer residence time per patch, and thus lead to higher degrees of mobility, at least as measured in between-patch travelling (Charnov 1976). This is because as environmental productivity rises, the point at which a forager can do better by leaving a partially-depleted patch and move to a new unharvested one fall back earlier on the depletion curve (Winterhalder 1981). The question

therefore is not whether an individual can obtain more energy from a given patch, but rather if the individual can do better by travelling to another resource utilization area. Foragers seeking to maximize overall return rates should, as mentioned above, depart a patch even though abundant resources still remain if even more abundant resources await them in adjacent patches. In all cases, the optimal strategy is to leave a patch before it is totally depleted, as long as there are other patches that will yield a positive return rate. Thus, highly productive environments may be characterized by high degrees of mobility (Winterhalder 1981).

Originally the MVT proposed a solution to test how a forager responds to different numbers of units of food in a patch, suitable for predator-prey situations where food units are equal to whole prey items (Krebs et al. 1974, Charnov 1976). Later studies have added to the MVT by quantifying the total amount of energy yield (carbohydrates and protein) available in the patch and proposed this to be the factor driving patch decisions, instead of simple food abundance alone (Altmann 1988, Grether et al. 1992, Mattson 1980, Plante et al. 2014, Sayers et al. 2010). Energy has been found to be a key limiting factor in female reproduction (Gadgil & Bossert 1970, birds: Drent & Daan 1980, reptiles: Bonnet et al. 1999, mammals: Schneider & Wade 2000). This pattern also holds specifically for female non-human primates, including in chimpanzees (*Pan troglodytes*: Pusey et al. 1997, Wallis 1997, Thompson et al. 2007), Hanuman langurs (*Presbytis entellus*: Koenig et al. 1997), long-tailed macaques (*Maccaca fascicularis*: van Noordwijk & van Schaik 1986) and orangutans (*Pongo pygmaeus*: Knott 1999). Since the two sexes differ in energy requirements for reproduction, they could vary in both activity and diet optimization (van Noordwijk & van Schaik 1986). Differences in food requirements are also affected by body size. As body size increases, energy requirements per unit of body mass decreases (Bell 1971, Jarman 1974), which causes females of sexually dimorphic species and growing juveniles to have a higher requirement of energy and protein per kilogram of body mass (Bell 1971, Jarman 1974, Kleiber 1974, van Noordwijk & van Schaik 1986). Bigger animals, with larger digestive tracts, can also better utilize lower quality and more mechanically challenging (fiber-rich) foods than smaller animals (Bell 1971, Jarman 1974). Due to the above reasons, the amount of energy in a food item or in a patch of food is an important measure for

testing optimal diet and patch decisions, as well as assessing variations in diets and activity between different age-sex groups within a species.

Many studies on primates feeding strategies have been conducted, though there are several significant challenges inherent to study this topic in primates. For example, many primate species feed on the leaves and fruit of trees and therefore forage and move mostly in the canopy (Gebo & Sargis 1994, Gottfried et al. 2016). In forested areas visibility is often a problem and it is difficult to keep individuals within eye-sight for long periods of time and observe all of their activity (Rothman et al. 2012). Most research on wild primates is also non-invasive, which limits the possibilities for more experimental research. Finally, because primates live in groups with high levels of social intricacy, it may be that simple models based in OFT are insufficient to describe the complexity of primate foraging.

Despite these challenges, there is evidence to suggest that the predictions of foraging theory apply to primates. Studies of primate nutritional ecology have demonstrated preference for high-quality food items in many species, including black and white colobus (*Colobus guereza*: Fashing et al. 2007), black colobus (*Colobus satanas*: McKey et al. 1981), black leaf monkeys (*Presbytis johnii*: Oates et al. 1980), mantled howler monkeys (*Alouatta palliata*: Estrada 1984), woolly spider monkeys (*Brachyteles arachnoides*: Milton 1984), free-ranging baboons (*Papio anubis*: Barton & Whitten 1994), lemurs (*Lemuroidea sp.*: Ganzhorn 1995) and mountain gorillas (*Gorilla beringei beringei*: Rothman et al. 2008). Adult females (who must cope with the energetic demands of gestation and lactation) and growing juveniles have been found to feed on higher quality food items than adult males (Gaulin 1979). Juvenile long tailed macaques have a lower food intake rate than adults and feed significantly more on small high protein fruits, avoiding fruits with tough skins or rinds (van Noordwijk & van Schaik 1986). In addition, females and juveniles of some species spend more time feeding and less time inactive than adult males (Gaulin 1979, Rothman et al. 2011).

Patch use has also been studied in wild primates (Chapman 1988, Whitten 1988, Nakagawa 1989, Nakagawa 1990, Altmann 1998, Grether et al. 1992, Kazahari & Agetsuma 2008, Plante et al. 2014, Sayers et al. 2010, Teichroeb & Aguado 2016). Preference to forage in higher quality patches has been shown in vervet monkeys (*Cercopithecus aethiops*: Whitten 1988, Teichroeb & Aguado 2016), Japanese macaques (*Macaca fuscata*: Agetsuma 1998) and squirrel monkeys (*Saimiri sciureus*: Sloan 2015). Evidence of energy as the currency driving patch use decisions has been found in white-handed gibbons (*Hylobates lar*: Grether et al. 1992), siamangs (*Hylobates syndactylus*: Grether et al. 1992) and langurs (*Semnopithecus entellus*: Sayers et al. 2010). Studies have also shown that primates balance multiple nutrients while foraging (Johnson et al. 2017, Rothman et al. 2011). Both spider monkeys (*Ateles geoffroyi*) and mantled howler monkeys have been shown to increase the time spent in a patch with increasing travel time (Chapman 1988) in accordance to a prediction of the MVT (Charnov 1976).

These considerations show that predictions of OFT as applied to primates seem to be generally valid, despite the absence of direct tests and the near-absence of indirect tests. This suggests that the mechanisms that underlie foraging in primates could be elucidated through further study of OFT in the species that are most amenable to close observation. The gelada monkey (*Theropithecus gelada*) presents an excellent primate species for testing the predictions of OFT because they are known to spend an unusually large percentage of their time feeding and are terrestrial (Fashing et al. 2014, Iwamoto 1979, 1993, Dunbar 1977, Dunbar & Dunbar 1974, Hunter 2001). Their diet makes them unique among primates (Jablonski 1993). Endemic to the alpine grasslands of the Ethiopian Highlands, geladas are the only graminivorous primate and their diet is similar to that of grazing ungulates (Wrangham 1976, Jablonski 1993). Because of the relatively continuous distribution of their food resources (Duncan & Poppi 2008), geladas engage in a repetitive foraging behavior, a sequence that alternates between feeding and walking (Iwamoto 1979). Geladas feed sitting down plucking plant parts from the ground vegetation with both hands (Iwamoto 1979). After 10-20 plucks, they transfer the food items to their mouth (Iwamoto 1993). An elongated thumb and reduced index finger (Venkataraman et al. 2014) allows the geladas to selectively choose food items and pluck green blades from the

vegetation (Iwamoto 1993). While sitting engaged in feeding activity, an individual will often relocate by shuffling (Wrangham 1976). Shuffling is defined as a locomotive behavior where an individual remains on its haunches in squatting position while relocating bipedally over shorter distances (Wrangham 1976). This allows the individual to keep plucking food items while shifting position within a patch. When the geladas want to relocate over longer distances to new feeding patches they get up and walk quadrupedally (Wrangham 1976, Iwamoto 1979, Iwamoto 1993). Therefore, it seems likely that the animal perceives patches in a manner that is reflected by the two forms of locomotion: the individual does not interrupt its feeding activity while shuffling, but it does while walking. Since the geladas follow the two principle components of feeding patterns (feeding and walking) on which the MVT is based, they make a good study species for testing predictions of the model. Geladas also show diminishing marginal returns correlated with time spent in a patch, measured as the number of grass blades plucked per time unit (Venkataraman unpub. data), suggesting that they satisfy assumptions of the MVT. Because of the above, it is possible to use geladas for testing the MVT as well as the “one-best-patch” hypothesis that individuals will stay longer in patches of higher quality.

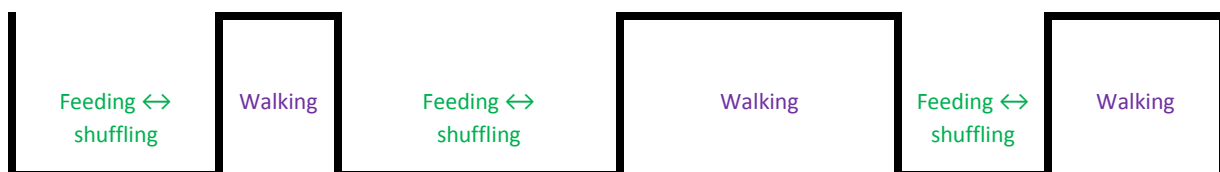


Figure 2. Gelada foraging activity consists mainly of feeding and shuffling within food patches, and walking between food patches.

Geladas exhibit a high degree of sexual dimorphism, with adult males being considerably larger than adult females (19.0-23.0 kg versus 11.7-14.0 kg: Bergman & Beehner 2013). In addition, juveniles weigh a fraction of the adult female weight (1/4-3/4: Bergman & Beehner 2013). Because of differences in body size, geladas are expected to show variations in activity budget and diet between the different age-sex categories. Indeed, small variations in time devoted to

feeding between adult female and adult male geladas were reported by Kawai and Iwamoto (1979: females 81.6% versus males 78.0%) and by Iwamoto (1979: females 67.0% versus males 65.5%). The size of an individual is also known to affect ability to ingest different food items. Dental wear analysis showed a positive correlation between an individual's size and the mechanical toughness of food items in geladas (Venkataraman et al. 2014), with larger bodied individuals ingesting tougher (potentially fiber-rich) graminoid species and younger and smaller individuals feeding more on softer forb and graminoid species (Venkataraman et al. 2014, Fashing et al. 2014).

Since geladas are grazing animals with relatively simple diets and repetitively sequenced foraging patterns, they represent an appropriate model species for investigating how foraging decisions differ between phylogenetically distant animals that have a similar diet (i.e. primates and ungulates). The food resources of grazers offer a low-energy yield per food item, especially due to the high level of fiber, structural indigestible carbohydrates (Searle et al. 2005, Rothman et al. 2012). Therefore, I suggest that geladas exhibit similarities in diet composition and foraging behavior to grazing ungulates due to the utilization of similar food resources and will explore this below.

Graminivores exploit food resources that are fundamentally different from those of most other trophic levels, since graminoids often exist in great abundance and are more or less homogeneously distributed within a habitat (Searle & Shipley 2008). Therefore, for foraging grazing herbivores, spatially subdividing natural environments into units or patches of food as a unit of functional relevance for ecological processes has remained a fundamental challenge in ecological research (McArthur & Pianka 1966, Westoby 1974, Covich 1976, Wiens 1976, Arditi & Dacarogna 1988, Jiang & Hudson 1993, Focardi & Marcellini 1995, Searle & Shipley 2008). In a strict sense, a patch is a well-delimited area where food is uniformly distributed with no other food in the immediate surrounding area (Arditi & Dacarogna 1988). However, the variation in quality between different species of graminoids encourages grazers to make use of small

patches and feeding stations as the basis of their foraging strategies (Searle & Shipley 2008). Therefore, patchiness must be assessed by the perception of the animal and defined operationally by the apparently non-random distribution and activity of the forager, since resource utilization could appear patchy although food abundance varies in a more continuous way (Wiens 1976).

For ungulate herbivores (hereafter referred to as herbivores), a feeding station is defined as the area where an individual can reach for food items without moving its front legs (Jiang & Hudson 1993, Searle et al. 2005). In this way, a feeding station represents a discrete area that can be operationally defined by the behavior of the grazing animal (Searle et al. 2005). A feeding station can consist of a single species or a mixture of plant species (Searle et al. 2005). However, a persistent problem when studying feeding behavior on the patch level for herbivores is that there is no reliable way to determine the scale at which a herbivore perceives patches. The present study provides a novel biological definition of patch, based on the foraging style of geladas. A feeding patch was defined as the area an individual utilized from the first time it sat down and engaged in feeding activity, until the time it stood up on all fours and moved to the next feeding patch. This patch definition could be considered analogous to a feeding station for grazing herbivores. Due to the distinct and repetitive foraging behavior of feeding and walking, geladas make an excellent species to study patch perception in a grazing animal.

Studies suggest that the behavior of large grazers at the level of feeding stations appears to be consistent with patch use models: an alternating pattern of a series of steps between feeding stations followed by grazing (a series of bites) within each feeding station (Laca et al. 1994). Different species of herbivores have been found to forage following the predictions of the MVT by choosing stations of greater biomass and higher quality (Laca et al. 1993, WallisDeWries et al. 1999, Fortin et al. 2005, Searle et al. 2005), as well as by adjusting the time spent in stations according to travelling time (Laca et al. 1993). However, other studies have failed to support

the MVT (Schaefer & Mesier 1995, Illius et al. 2002, Focardi et al. 1996). Researchers have emphasized the importance of protein as a limiting nutrient for herbivores (Bell 1982, Sinclair 1975). Herbivores actively select food items according to protein content (Albon & Langvatn 1992) and show a preference for specific high-quality plant species (Albon & Langvatn 1992, Parsons et al. 1994, Owen-Smith 1979, Owen-Smith & Novellie 1982). However, it is clear that large herbivore diet always contains a mixture of items to ensure the best mix of nutrients (Parsons et al. 1994, Frair et al. 2005, Mysterud & Austrheim 2016), a strategy of partial preferences. This could be one of the reasons why studies of OFT and the MVT in herbivores have often rejected predictions from the theories. Another factor possibly influencing the rejection of the MVT in herbivores is that the models do not take into consideration an individual's state when the decision is made (McNamara & Houston 1986). One such state is hunger, which can have a high influence on the foraging strategies of diurnal animals (McNamara & Houston 1986, 1996). In a state of hunger, animals are known to take greater risks as well as to be less selective in their food items (McNamara & Houston 1986). The possibility that toxins, tannins and plant secondary metabolites (PSM) could be major factors influencing food selection (Hanley 1982, Glander 1982) must also be taken into consideration. However, since these types of compounds tend to be low in graminoid species (Searle & Shipley 2008) and their impacts are still little understood in primate diets (Rothman et al. 2012) this issue will not be explored further.

If the geladas feed in accordance to the predictions of OFT, it is expected that they focus only on the highest quality food items and patches. In contrast, if the importance of nutrient balancing is a factor affecting gelada foraging strategies, similar to those of grazing ungulates, it might account for divergence from the predictions of OFT.

The present study aimed to investigate the foraging strategies of wild gelada monkeys at the Guassa Plateau in Ethiopia, focusing on plant consumption and patch utilization. Guassa is an ideal site to conduct such study because the basic gelada diet is known (Fashing et al. 2014,

Venkataraman et al. 2014) and the gelada population has been studied continuously for over a decade (Nguyen et al. 2015). Based on predictions from OFT and the MVT, the present study examined two basic principles of foraging models: 1) what plant categories (species) to consume and 2) patch utilization (time allocation). Assuming geladas select for high-quality plants, it is predicted that they will feed more on short graminoid species. Consequently, it is predicted that there will be a positive correlation between the time spent in patches and the amounts of short graminoids in a patch. In contrast, assuming geladas select for a mixed diet, it is predicted that there will be a positive correlation between time spent in patches with a mixture of plant categories (species) in a patch.

Relationships between animal populations and their food supplies are a central problem both in theoretical ecology and for the management of natural and man-modified ecosystems, making OFT a potentially useful tool to better understand the behavioral ecology of organisms. Better understanding of animal foraging strategies through optimization theories will contribute to solving a number of important ecological issues such as the drivers of population dynamics and habitat utilization. At present, with rapid climate change and continuous anthropogenic alteration of natural environments, understanding the foraging and movement strategies of animals is important to facilitating their conservation (Festa-Bianket & Apollini 2003). Thus, the present study aims to increase our understanding of the decisions underlying gelada monkey foraging strategies and offer important insight into their ecology, which in turn will help their future conservation.

The objectives of the present study were: 1) To assess gelada optimal diet strategies, and 2) to test predictions of OFT and the MVT. The following hypotheses were tested:

Hypothesis 1: An individual gelada's foraging decisions are expected to be dependent on its body size (determined by sex and age).

Predictions:

- a) Differences in body size will affect activity budget and diet.
- b) Because of their larger body size, adult male geladas will be less selective when choosing food items than adult females and juveniles and thus feed more on low-nutrition items (e.g. tall graminoids).
- c) Due to their smaller body size than adults, juveniles will spend more time feeding on high-quality food items (e.g., forbs) than adults.

Hypothesis 2a: Gelada foraging decisions, particularly patch residence time, are expected to be based on patch quality and nutritional value of plants (i.e., available energy) in a patch.

Predictions:

- a) An individual gelada will spend longer times per visit in patches with high percentages of short graminoids (more nutritious) than in patches with high percentages of tall graminoids (less nutritious).
- b) An individual gelada will adjust patch residence time according to the total energy yield of each specific patch, and stay longer in patches of higher nutritional value.

Hypothesis 2b: Gelada foraging decisions, particularly patch residence time, are expected to be based on partial preference, and variations of plants in a patch (mix of nutrients available).

Predictions:

- a) An individual gelada will spend longer time in patches as species richness and diversity of plant categories increase.

Hypothesis 3: Gelada relocation (travelling) and locomotion decisions are expected to depend on patch distribution and quality.

Predictions:

- a) Based on predictions of the MVT, an individual gelada will increase travelling time to the next feeding patch with increasing time spent in the previous feeding patch visited.
- b) An individual gelada will engage in a higher number of shuffle events in patches with a high percentage of short graminoids (more nutritious) compared to patches with a high percentage of tall graminoids (less nutritious).

2 Methods

2.1 Study area

Guassa is an Afroalpine tall grass ecosystem located on the Western edge of the Great Rift Valley (10°15' - 10°27'N; 39°45' - 39°49'E), in the Ethiopian Highlands in north-central Ethiopia. It is one of the few remaining large Afroalpine grasslands in Ethiopia and preserves an intact community of large carnivores including leopards, hyenas, Ethiopian wolves, African wolves, servals and caracals (Ashenafi 2001, Rueness et al. 2011, Venkataraman et al. 2015). Guassa is a relatively undisturbed ecosystem due to an indigenous conservation management program, the *Qero* system, which dates back to the 17th century (Ashenafi and Leader-Williams 2005).

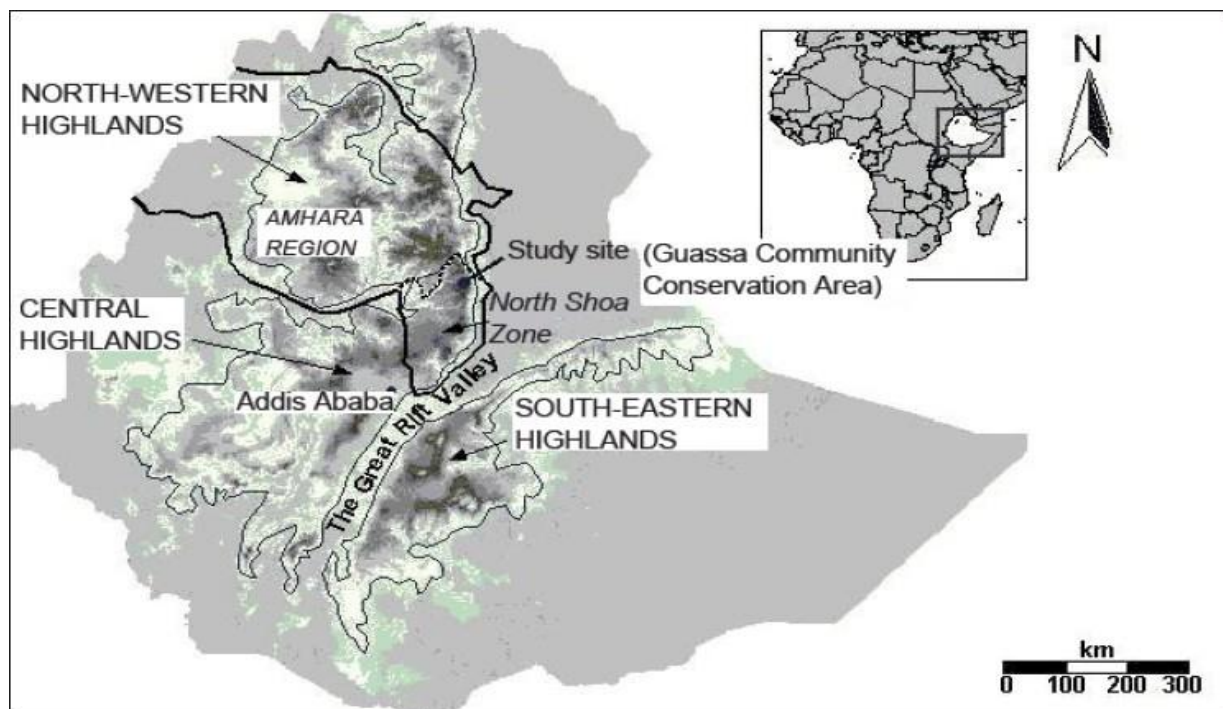


Figure 3. Map of study area, Guassa Community Conservation area.

The study area covers 111km², with elevation ranging from 3,200 to 3,600 m.a.s.l. (Ashenafi 2001, Fashing et al. 2014). The Guassa Gelada Research Project's camp is located at 3,438

m.a.s.l. Average annual temperature at Gelada Camp is 11.0°C (Fashing et al. 2014). Mean highest monthly temperature is reached in June at 19.6°C and mean lowest monthly temperature occurs in December at 1.8°C (Figure 4.). Rainfall averages 1650 mm per year and is strongly seasonal, with a unimodal peak during July and August when more than half of the annual rain falls (Fashing et al. 2014). Following Venkataraman et al. (2014), for the present study, I used <400 mm of three-month cumulative rainfall as the cutoff to classify months into the “dry season” (November–June) whereas those months with >400 mm were classified into the “wet season” (July–October).

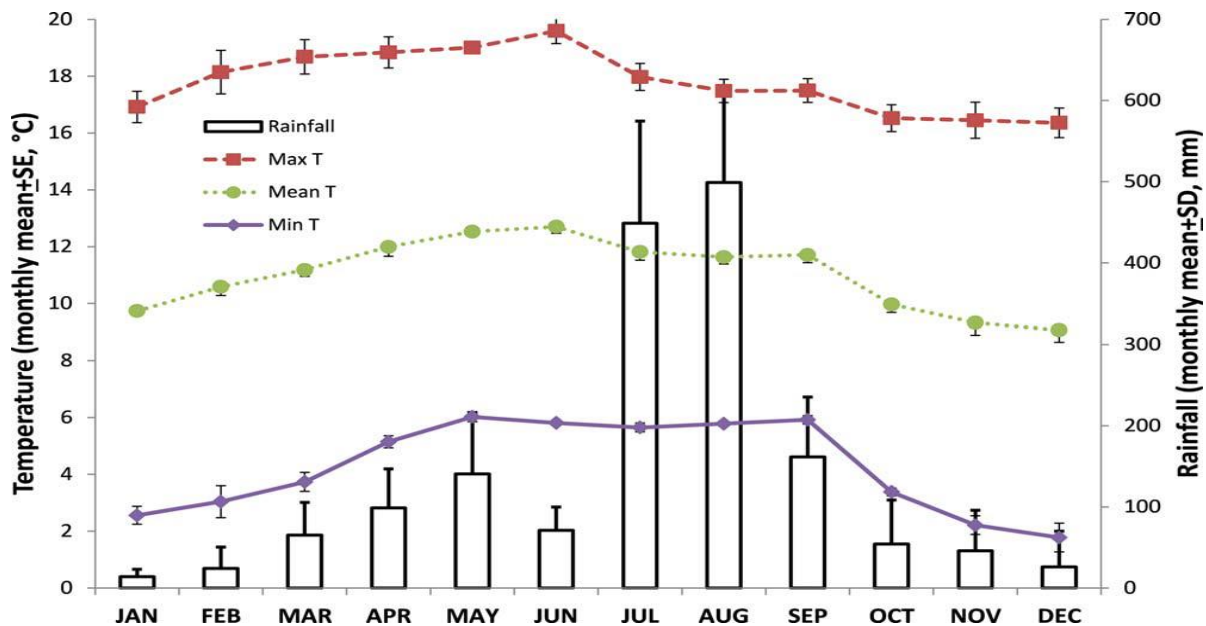


Figure 4. Rainfall and temperature at the Gelada Research Camp in Guassa, Ethiopia, from 2007-2012 (taken from Fashing et al. 2014).

The study area is an Afroalpine grassland where the ground cover consists of 34.5% forbs, 24.4% tall graminoids, 11.9% shrubs, 9.4% bare soil, 5.5% short graminoids, 3.6% rocks, 0.4% lichens, 0.1% ferns and 10.2% unidentified vegetation (Fashing et al. 2014). Thus, tall graminoids account for four-times more ground cover than short graminoids at Guassa. Rainfall appears to drive temporal variation in green graminoid availability at Guassa; the best predictor

of monthly green graminoid availability was cumulative rainfall from the previous three months (Fashing et al. 2014).

The study site at Guassa can be divided into two distinct topographies delineated by the upper plateau and lower cliff edges (Erskine 2016). The lower cliff edges drop into steep slopes dominated with tall graminoids and shrubs before they drop into vertical cliff edges. The upper plateau is relatively flat with a higher variation of graminoid species, forbs and shrubs.



Figure 5. Left: geladas on top of a sleeping cliff (lower level). Geladas sleep on small ledges in the vertical cliffs to avoid predators (Wrangham 1976). Center and right: examples of vegetation on the plateau (upper level).

2.2 Study subjects

The gelada monkey is endemic to the alpine grasslands of the Ethiopian Highlands. The gelada is the only living representative of a once widespread genus (Jablonski 1993) and is thought to have been pushed up into the Ethiopian highlands by a combination of climate change, hunting, and interspecific competition with baboons (*Papio*) (Dunbar 1998). Today, the gelada distribution occurs only between 1,800 and 4,400 m.a.s.l. (Fashing & Nguyen 2016).

Geladas live in a multi-level social system consisting of multiple one-male units (OMU's) with a fluid social organization (Snyder-Mackler et al. 2012). An OMU consists of a single dominant reproductive male with his respective females (1-12), their dependent offspring and sometimes a follower male (Crook 1966, Dunbar & Dunbar 1975). The OMU has a considerable degree of temporal stability (Kawai et al. 1983). Multiple OMU's form aggregations that fission and fuse throughout the day and the year (Snyder-Mackler et al. 2012). A cluster of OMU's that share a common area is defined as a band (Kawai et al. 1983). Temporary aggregations of OMUs, such as OMU's travelling together on a specific day, is defined as a herd (Kawai et al. 1983). A herd has a mean size of 160 individuals, but can contain up to 1000 individuals (Snyder-Mackler et al. 2012).

Approximately 800 geladas inhabit Guassa (Fashing and Nguyen, unpub. data). More than 220 habituated, individually-recognized wild gelada monkeys, composing a single band (the Steelers band) have been monitored at Guassa on a near daily basis since January 2007 (Nguyen et al. 2015). All individuals were habituated to the presence of researchers within a distance of two meters.

Between 2007 and 2013 geladas at Guassa were found to consume 56 plant species from 22 families, with leaves being the most common plant part eaten. Gelada teeth are highly adapted for a graminoid diet (Jablonski 1993, Venkataraman et al. 2014), and the largest proportion of the gelada's diet wherever they have been studied is graminoids (Fashing et al. 2014, Iwamoto 1979, 1993, Dunbar 1977, Dunbar & Dunbar 1974, Hunter 2001). For example, the annual diet of Guassa geladas consisted of 56.8% of graminoid parts (Fashing et al. 2014).

This study complies with the American Society of Primatologists requirements for Ethical Treatment of Nonhuman Primates and with the legal requirements of the Ethiopian Government.

2.3 Data collection and analyses

My fieldwork was conducted entirely during the rainy season (from August 7th to October 23rd, 2016) adding a total of 45 days of data collection. On these days, data were collected from 8:00 (when the geladas typically emerge from their sleeping cliffs) to 17:30 (when they usually begin to move towards their sleeping cliffs for the night). All data were collected by myself.

2.3.1 Activity budget

Behavioral activity data were recorded using instantaneous scan sampling (Altmann 1974) at 30-minute intervals. The day was divided into five time periods (following Bernstein 1975), each consisting of three behavioral scans at 30-min intervals: 1) early morning (EM) 08:00-09:30, 2) late morning (LM) 10:00-11:30, 3) early afternoon (EA) 12:00-13:30, 4) late afternoon (LA) 14:00-15:30, and 5) evening hours before sunset (S) 16:00-17:30.

Data were collected for the five nearest individuals in sight, recording the first activity that lasted ≥ 5 seconds. The herd was scanned from left to right to avoid biasing observations toward eye-catching activities such as aggressive or sexual behaviors (Fashing 2001). Individuals were recorded as adult male, adult female, subadult male or juvenile. Infant behavior was not recorded. For activity scan samples, individual identity was not recorded. Comparisons of activity budgets for the present study were made between adult females, adult males and juveniles. Data on subadult males were excluded due to low sample size.

The following behavioral activities were recorded: feeding, resting, walking, grooming, playing, drinking, aggression and other activity. Feeding was recorded when an individual engaged in plucking, pulling towards the mouth, or chewing food items. For the purpose of diet composition analyses, the plant category (see below) was recorded for each feeding scan.

Resting was recorded when an individual was inactive or stationary, either sitting or lying down. Walking was recorded when an individual changed spatial position by using upright quadrupedal movement (i.e., taking a step). Grooming was recorded when an individual used its hands to clean the fur and body of another monkey. Playing was recorded when an individual engaged in entertaining interaction with other individuals or with an object. Aggression was recorded when an individual showed any agonistic behavior directed towards another individual, including chasing, pulling or grabbing, displacing or making threatening gestures (such as lifting the eyebrows, showing the teeth, pulling vegetation) or emitting agonistic vocalizations. Any behavioral activity that did not fit into these categories was noted as other activity, such as drinking (ingesting water), sexual activity, giving birth, or chasing predators.

Activity budget was calculated from the behavioral records of the band. The proportions of time spent on different activities were computed dividing the number of scans recorded for each behavioral category by the total number of scans during the whole study period.

2.3.2 Diet: Plant category consumption

It is reasonable to assume that short graminoid species are of higher quality (higher level of protein and lower amount of fiber) in relation to biomass than tall graminoid species (Westoby 1974, Owen-Smith 1982, Adler et al. 2004). Graminoids were therefore divided into the following categories, based on height when fully grown: 1) mixed short graminoids (MSG): < 10 cm, 2) mixed medium graminoids (MMG): 10 – 15 cm, and 3) mixed tall graminoids (MTG): > 15 cm. In addition to graminoids, the following categories were included: 4) Forbs (F): included non-graminoid herbs, and 5) Other (O) included all plants not eaten by the geladas such as *Alchemilla* (a genus of herbaceous plants that is dominant at Guassa) and several shrubs. In addition, foraging for underground storage organs (USOs) from graminoids and forbs (Fashing et al. 2014), feeding on graminoid seeds, or invertebrates were recorded during the scan

samples and additionally these behaviors were recorded as events during focal sampling (see below).

The nutrient currency chosen for this study is kcal/g (energy) because it is the most readily analyzed proxy for nutritional quality of the species included in the study, and because of the importance of energy to primate fitness (Thompson & Wrangham 2008, Rothman et al. 2012). Nutrition data generated in Jessica Rothman’s lab at Hunter College, City University of New York for plants collected at Guassa (Fashing et al. unpub. data) were used to establish the nutrition values of MSG, MMG, MTG and forbs based on kcal/100g of fresh samples (Table 1). Nutrition data from one species of MSG, one species of MMG, two species of MTG, and six forbs were used for the present study. While these do not reflect the full diversity of graminoids found at Guassa, I assume they are reasonable representatives and were used for the estimates in the present study. Energy includes protein, carbohydrates and fat. Besides energy, the quality of a food item also takes into account the amount of fiber.

Table 1. Energy scores of the four plant categories.

Plant category	Species	Family	Kcal/100g	Energy score
MSG	<i>Pennisetum humile</i>	Poaceae	121.28	0.5
MMG	<i>Agrostis quinqueseta</i>	Poaceae	105.5	0.4
MTG	<i>Festuca macrophylla</i>	Poaceae	53.0	0.2
	<i>Festuca abyssinica</i>	Poaceae		
Forbs	<i>Ranunculus</i> sp.	Ranunculaceae	263.0	1
	<i>Trifolium</i> sp.	Fabaceae		
	<i>Haplosciadium abyssinicum</i>	Apiaceae		
	<i>Agrocharis melanatha</i>	Apiaceae		
	<i>Cotula cryptocephala</i>	Asteraceae		
	<i>Galium simense</i>	Rubiaceae		

Plant species not eaten by geladas were sat at energy score = 0.
(Fashing, Nguyen, Venkataraman & Rothman (unpub. data)).

The proportions of plant categories consumed by the different age-sex classes were calculated dividing the number of feeding scans recording each plant category by the total number of feeding scans per age-sex class. The proportions of plant categories consumed in the different time periods of the day were calculated dividing the number of feeding scans recording each plant category by the total number of feeding scans per time period.

2.3.3 Patch utilization, travelling and locomotion

Because of the relative homogeneity of the Afroalpine grassland habitat (Kidane et al. 2012), it is not intuitively clear how to define patches. In the present study, a behavioral patch definition was used since a patch definition using discrete vegetation areas was difficult to operationalize. Therefore, the action of an individual entering a feeding patch was recorded once the individual sat down and began engaging in feeding activity. A feeding patch was defined as the area (m^2) an individual utilized from the first time it sat down and engaged in feeding activity, until the time the individual stood up on all fours to move to the next feeding patch. While staying in the patch the individual would engage in feeding and shuffling. Due to shuffling, the shape of the patch could take different shapes: circular, oval or linear. The middle section of a patch was estimated by visualization and the center of a patch was defined as the approximate middle point of middle section utilized by the individual. When an individual moved out of a feeding patch, the center of the patch was marked by placing a stick in the ground. To estimate the size of an area an individual could utilize for feeding while in a sitting position (foraging width), measurements were obtained from the point where the back of the right hip of an individual had contact with the vegetation to the furthest point an individual plucked a food item from the vegetation while reaching forward (Figure 6, center). Measurements on foraging width were obtained using marks in the vegetation (e.g. flowers, a blade of graminoid, rocks).

The time spent in a patch by a focal individual was measured to the nearest second. At the start of each focal sample, the first patch utilized by an individual was marked using a GPS location.

Travelling to the next feeding patch was recorded when an individual relocated by quadrupedal walking, a state consisting of a number of individual steps. One step was defined as the distance from where the right back heel was lifted from the ground to where the right back heel made contact with the ground while walking (Figure 6, left). In order to calculate the average time it took an individual to travel one step, the time it took an individual to travel a series of ten steps was measured to the nearest second. As a proxy for energy spent relocating (cost), the number of steps were counted as a focal individual travelled between patches. Measurements of step length were obtained using marks in the vegetation.

The distance relocated bipedally by shuffling was defined as the length an individual's hip relocated with one shuffle movement and each of these movements was defined as a shuffle event (Figure 6, right). While a focal individual engaged in feeding activity in a patch, the number of shuffling events was recorded. Measurements of shuffle length were obtained using marks in the vegetation. All measurements were obtained using a measuring tape and noted to the nearest centimeter.



Figure 6. Adult male gelada walking (left), plucking food items in a patch (center) and shuffling (right).

To avoid pseudo replication, a total of 24 individuals (19 adult females and five adult males) from eight existing study groups (A, B, D, K, L, R, T, S) were chosen based on morphological traits, obvious marks such as scars, cuts or parasitic swellings (these last caused by tapeworm larvae *Taenia serialis*: Nguyen et al. 2015). Each day, the sequence to study OMU's was determined at random. The sequence of focal animals within an OMU was sampled at random until all individuals of an OMU had been included before moving to the next OMU. Each focal consisted of an individual gelada feeding in and travelling between three patches. Data were collected on: 1) patch residence time, 2) patch vegetation (to estimate quality), 3) travelling between patches and shuffling within patches.

2.2.4 Patch vegetation assessments

Patches were not homogenous, but instead consisted of many species from different plant categories. Therefore, after collecting data on a focal individual, all three patches marked with a stick were revisited to collect vegetation data using the plant categories defined earlier. With the aim of distinguishing rich and poor-quality patches as well as calculating the total energy yield of a feeding patch, the following data were collected:



In a radius of 50 cm from the patch center (based on measurements of foraging width), the percentage of ground cover occupied by each plant category (MSG, MMG, MTG and forbs) were visually estimated to the nearest 10%. Ground cover occupied by plants not eaten by geladas and the presence of rocks, dirt roads or water in the category O (other) were also recorded.

Figure 7. Method used to estimate ground cover in a patch.



Figure 8. Geladas foraging in patches dominated by MSG (right) and MTG (left).

None of the patches assessed during the study period contained both MSG and MTG plant categories. In contrast, MMG and forbs could be found in patches with both MSG and MTG. Therefore, for initial estimations rich-quality patches were defined as patches where ≥ 40 -100% of the vegetation cover was composed of MSG and poor-quality patches were defined as patches where ≥ 40 -100% of vegetation cover was composed of MTG.

In addition to these initial definitions, total energy yield available in a patch was calculated using the energy scores and percentage of ground cover accounted for by the different plant categories using the following formula:

$$\text{MSG\%/100*s} + \text{MMG\%/100*m} + \text{MTG\%/100*t} + \text{F\%/100*f}$$

Where s is the energy score for MSG, m is the energy score for MMG, t is the energy score for MTG and f is the energy score for forbs. Each patch could score a value between 0-1.

A measure of plant category richness and plant category diversity in a patch was calculated for each patch using the Simpson's diversity index:

Simpson's Index (D):

$$D = \frac{\sum n(n-1)}{N(N-1)}$$

n = the total percentage of organisms of a particular plant category.

N = the total percentage of organisms for all plant categories (eaten by geladas).

Simpson's index measures the probability that two individuals randomly selected from a sample will belong to the same plant category.

Simpson's Diversity Index = 1 – D

By subtracting the Simpson's diversity index from 1, a measure is also obtained on plant category diversity.

2.3.5 Statistical analyses

All statistical tests were done using R version 3.3.3, with significance level set at $p < 0.05$. Data were tested for normality using qq-plot in R. Correlations between activity budget, diet and age-sex classes as well as plant category consumption and time periods were tested using the G-test. Significant differences between age-sex classes were tested using the pairwise G-test. Linear regressions were used to assess correlations between patch residence time and patch vegetation, patch residence time and total patch energy and patch residence time and inter-patch travelling time. Data on patch residence time and time travelled between patches were log transformed to ensure normal distribution. Linear regressions were used to assess correlations between number of shuffle events and patch vegetation. Correlations between shuffle events, patch vegetation and patch residence time were tested using Poisson regression.

3 Results

3.1 Activity budget

The geladas devoted 46.1% of their time to feeding, 26.5% to walking, 13.6% to grooming, 10.4% to resting, 3.0% to other social activities (aggression, playing, or sexual activity), and 1.3% to other activities (n = 2645 scans on 29 days). Graminoid parts accounted for 73.8% of feeding scans (33.1% MSG, 28.0% MMG, 9.7% MTG, and 3.0% seeds). Forb leaves accounted for an additional 16.8% of scans. The geladas also dug for underground storage organs (USOs) from graminoids or forbs during 9.2% of feeding scans and the remaining 0.2% of scans were of feeding on invertebrates.

Table 2. Proportion of time spent on different activities by different age-sex classes of geladas at Guassa.

Age- Sex	N ^a	Activity						
		Feeding	Walking	Grooming	Resting	Aggression	Playing	Other
Adult female	1530	49.0	26.7	14.6	9.2	0.3	0	0.1
Adult male	414	39.7	24.6	15.3	19.3	0.9	0	0.2
Juvenile	534	46.0	24.9	10.9	7.5	0.2	10.5	0

^a= Number of records.

Activity budget was found to be strongly correlated with sex and age ($p = 1.904e^{-05}$). Adult females and juveniles spent significantly more time feeding than adult males (adult females: $p = 0.064e^{-02}$, juveniles: $p = 0.049$; Table 2). Adult males spent significantly more time resting than adult females and juveniles (adult females: $p = 4.3e^{-08}$, juveniles: $p = 5.3e^{-08}$). Adult females and adult males did not differ significantly in time spent grooming ($p = 0.077$), but juveniles spent significantly less time grooming than adult females and adult males (adult females: $p = 0.024$,

adult males: $p = 0.046$). The different age-sex classes did not significantly differ in proportion of time spent walking (AF-AM: $p = 0.388$, AM-JU: $p = 0.937$, AF-JU: $p = 0.395$).

3.2 Diet: Plant category consumption

3.2.1 Age-sex classes

Table 3. Proportion of plant category consumption by different age-sex classes of geladas at Guassa.

Age-Sex	N ^a	Graminoid leaves			<u>Graminoid seeds</u>	<u>Forb leaves</u>	<u>USOs^b</u>	<u>Other</u>
		MSG	MMG	MTG				
Adult female	750	29.5	30.0	9.4	1.7	20.4	8.0	1.0
Adult male	164	26.8	32.9	16.5	1.7	14.0	7.9	4.9
Juvenile	246	40.2	14.2	2.4	4.4	28.0	8.8	2.0

^a= Number of records.

^b= Obtained by excavating and include USOs from both graminoids and forbs.

Plant category consumption was found to be strongly correlated with age-sex class ($p = 3.974e^{-08}$, $n = 1160$ feeding scans over 29 days; Table 3). Adult females selected significantly more for high-quality food items (MSG, MMG and forbs) than males ($p = 0.033$). In addition, juveniles fed significantly more on MSG ($p = 0.0073$), and forbs ($p = 3.9e^{-07}$) than adult females. Adult males fed significantly more on low-quality graminoids (MTG) than females ($p = 0.033$) and juveniles ($p = 3.3e^{-05}$).

3.2.2 State dependent foraging decisions

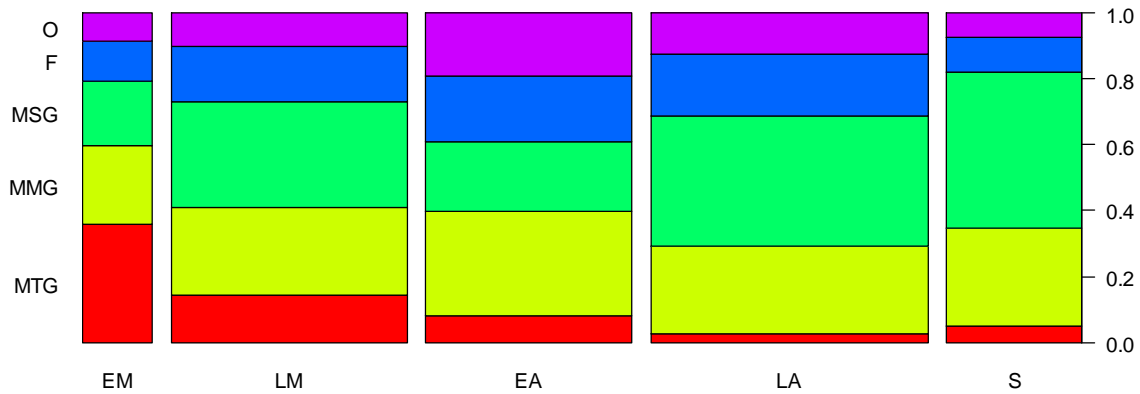


Figure 9. Proportion of plant category consumption by geladas organized by time period (EM: 08:00-09:30 = early morning, LM: 10:00-11:30 = late morning, EA: 12:00-13:30 = early afternoon, LA: 14:00-15:30 = late afternoon, S: 16:00-17:30 = evening hours before sunset). Mixed short graminoids (MSG = green), mixed medium graminoids (MMG = yellow), mixed tall graminoids (MTG = red), forbs (F = blue) or other plant or food items (O = purple). The different width of bars illustrates the number of feeding scans recorded for each time period.

Table 4. Proportion of plant category consumption by geladas at Guassa organized by time period.

Time of day	N ^a	Graminoid leaves			Graminoid seeds	Forb leaves	USOs ^b	Other
		MSG	MMG	MTG				
EM	66	19.6	24.0	35.9	6.5	11.9	2.1	0
LM	256	32.2	26.7	14.1	0.3	16.7	10.0	0
EA	196	21.3	31.0	8.1	8.1	19.9	10.7	0.3
LA	273	39.3	26.5	2.7	1.1	18.9	11.2	0.2
S	125	47.1	29.8	5.1	1.7	10.7	5.6	0

^a= Number of records.

^b= Obtained by excavating and include USOs from both graminoids and forbs.

Plant category consumption was strongly correlated with time of day ($p = 1.904e^{-05}$, $n = 1160$ feeding scans over 29 days; Figure 9; Table 4). Forb consumption stayed more or less stable

(15.6 ± 4.3 S.D.) during the whole duration of the day, as did consumption of MMG (graminoids with medium energy score), with an average of 27.6 ± 4.4 S.D. MSG (graminoids with highest energy score) had a mean frequency 31.9 ± 12.3 S.D., ranging from 19.6 to 47.1 from early morning (EM) to evening hours before sunset (S), respectively. In contrast, MTG (graminoids with lowest energy score) had a mean frequency 13.2 ± 22.7 S.D., ranging from 35.9 in early morning (EM) to the lowest frequency of 2.7 in late afternoon (LA). At the sleeping cliffs (Figure 5), the plant category availability is less diverse than on the plateau (Figure 5), which could drive the decrease in selectivity in early morning (EM). However, plant category consumption was also correlated with time of day starting from 10:00 (late morning: LM) to 17:30 (evening hours before sunset: S) ($p = 2.02e^{-05}$). Plant category consumption was found to be significantly different between early morning and evening hours before sunset ($p = 0.032$).

3.3 Patch utilization, travelling and locomotion

Table 5. Patch residence time and number of shuffle events in patches of different nutritional quality.

	a) Patch residence time in seconds				b) Shuffle events			
		Mean values ± S.D.				Mean values ± S.D.		
Age-Sex	N ^a	Per feeding patch	Rich-quality patches ^b	Poor-quality patches ^c	Per minute	Per feeding patch	Rich-quality patches ^b	Poor-quality patches ^c
Adult female	1280	59.5±84.3	174.9±174.0	28.9±33.7	1.4±1.8	1.4±2.5	4.9±4.2	0.47±1.0
Adult male	86	76.2±114.7	305.8±267.1	31.4±30.6	1.4±2.1	1.9±3.5	6.0±6.0	0.35±0.49

^a = Total number of patches.

^b = Patches where 40-100% of vegetation cover consists of short graminoids (MSG: graminoids with highest energy score).

^c = Patches where 40-100% of vegetation cover consisting of tall graminoids (MTG: graminoids with lowest energy score).

Both adult females and adult males had significantly longer mean residence time in rich-quality patches than in poor-quality patches (Table 5). On average adult males spent longer time duration per patch and had significantly longer patch residence time in rich-quality patches compared to adult females. Little variation in patch residence time was found in poor-quality patches between the sexes. Both adult females and adult males engaged in a higher number of shuffle events in rich-quality patches than in poor-quality patches. On average adult males engaged in a higher number of shuffle events in rich-quality patches compared to adult females, but little variation was found in poor-quality patches.

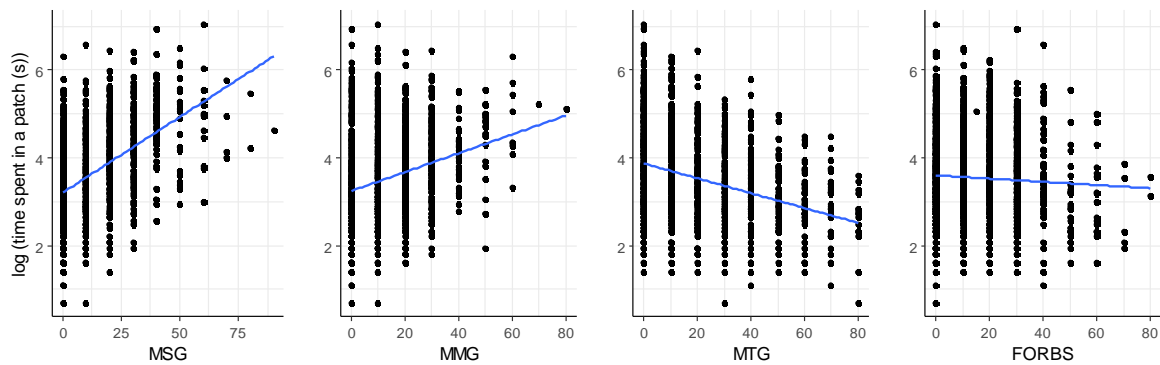


Figure 10. Linear regressions of time spent in patch with increasing percentage of vegetation ground cover composed of plant categories: MSG, MMG, MTG and forbs ($n = 1366$). Time spent in a patch is positively correlated with % MSG cover ($p < 2.2e^{-16}$) and % MMG cover ($p < 2.2e^{-16}$), and is negatively correlated with % MTG cover ($p < 2.2e^{-16}$). No correlation was found between time spent in a patch and % forbs cover ($p = 0.056$). Juveniles were not included in these analyses.

The geladas adjusted the time spent in patches according to the quality (energy yield) of vegetation in a patch by increasing time in a patch with larger percentages of high-quality graminoids (MSG: $p < 2.2e^{-16}$, and MMG: $p < 2.2e^{-16}$, $n = 1366$ feeding patches over 45 days; Figure 10), in contrast, they decreased the time spent in patches with increasing ground cover composed of low-quality graminoids (MTG: $p < 2.2e^{-16}$). Autocorrelations in the residuals were detected for these analyses, though they were found to be low. Addressing this is not within the scope of the present project. However, since the autocorrelations was low and the p-values from the tests were far below the significance level (0.05), the autocorrelations are not

expected to cause any large changes in the outcome of these tests and will not be considered further.

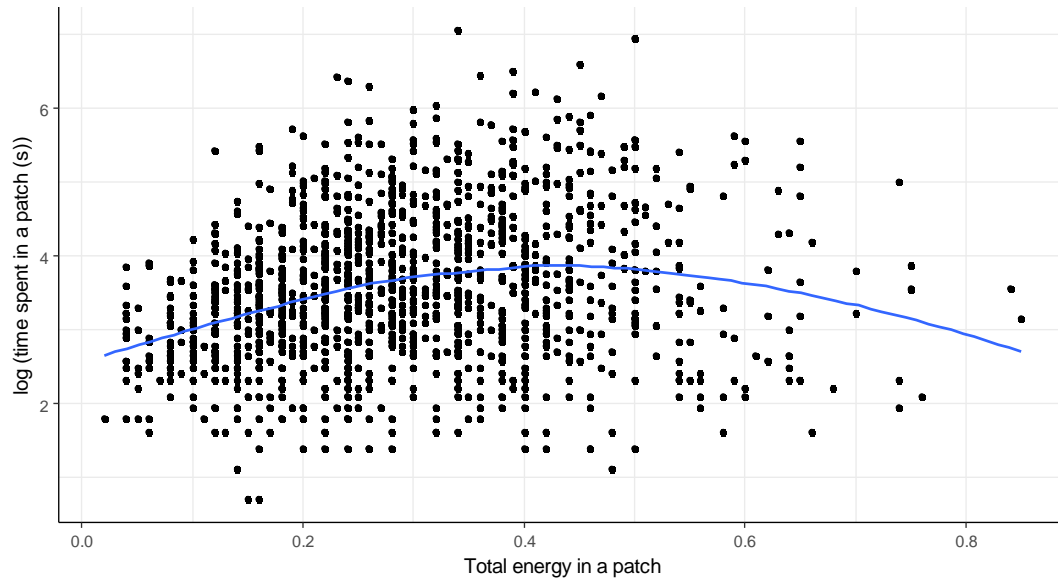


Figure 11. Correlation between time spent in a patch and total energy yield in a patch ($n = 1366$). Lowest curve. Time spent in a patch is quadratically correlated ($p < 2.2e^{-16}$) with optimum energy score at: 0.44

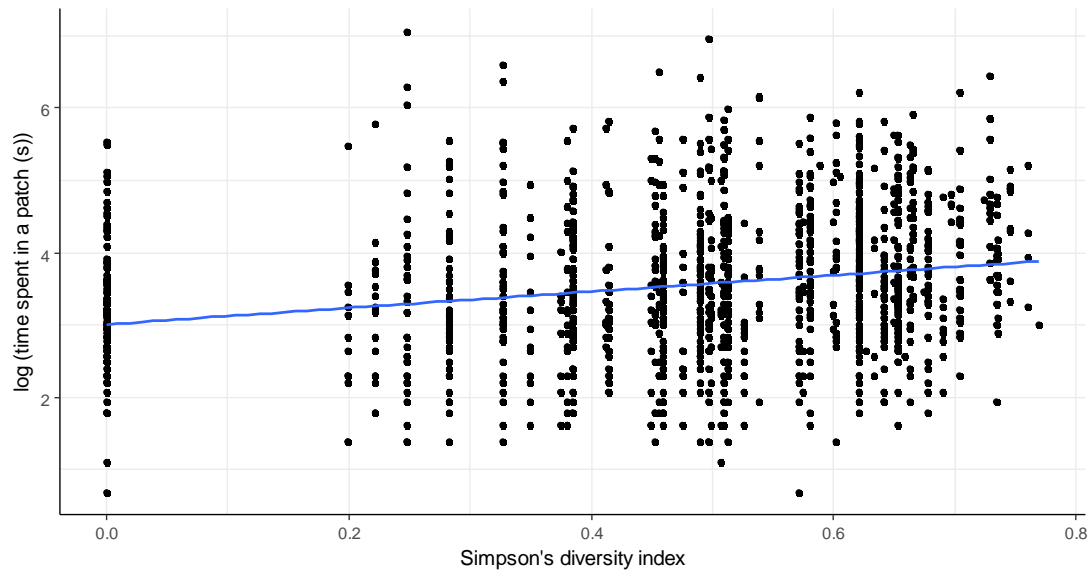


Figure 12. Linear regression of time spent in a patch against Simpson's Diversity Index ($n = 1366$). Time spent in a patch is positively correlated with species richness and diversity (p -value: $2.74e^{-15}$) in the patch.

The longest time spent in a patch was found to be in patches of intermediate energy yield (0.44; Figure 11). Time spent in a patch was positively correlated with the Simpson's diversity index for a patch (Figure 12). These results show that the geladas increased time spent in a patch with increasing plant category richness and plant category diversity.

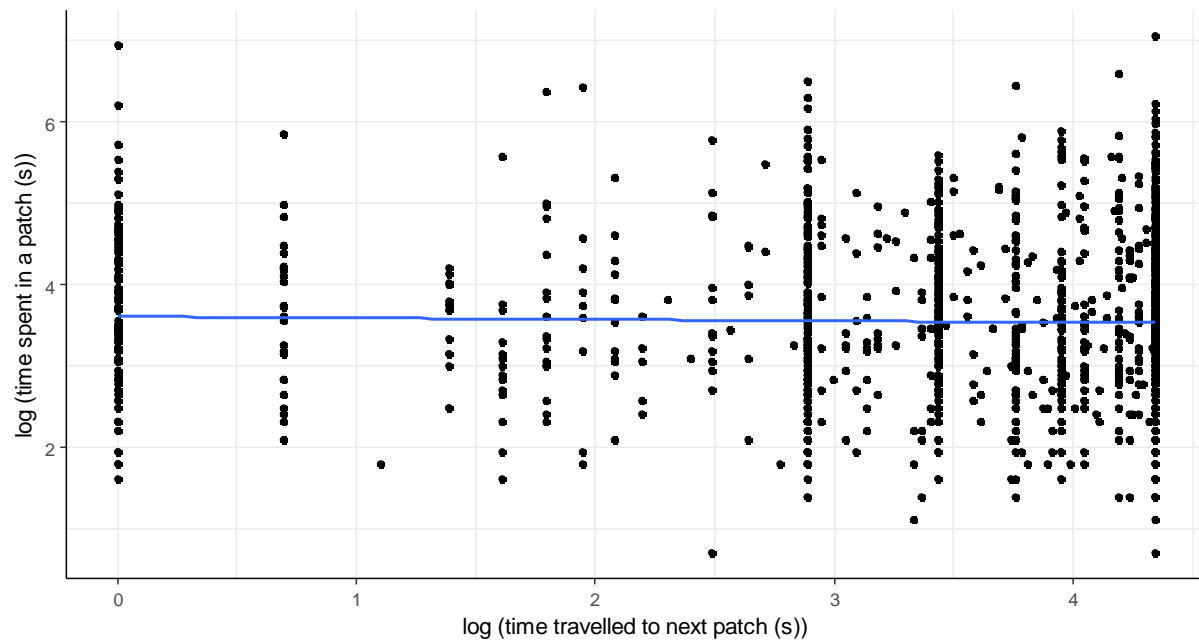


Figure 13. Linear regression of time spent travelling to the next feeding patch against time spent in the previous patch ($n = 1366$). No correlation was found ($p = 0.393$).

No correlation was found between time spent in a patch and times spent travelling to the next patch ($p = 0.3927$; Figure 13).

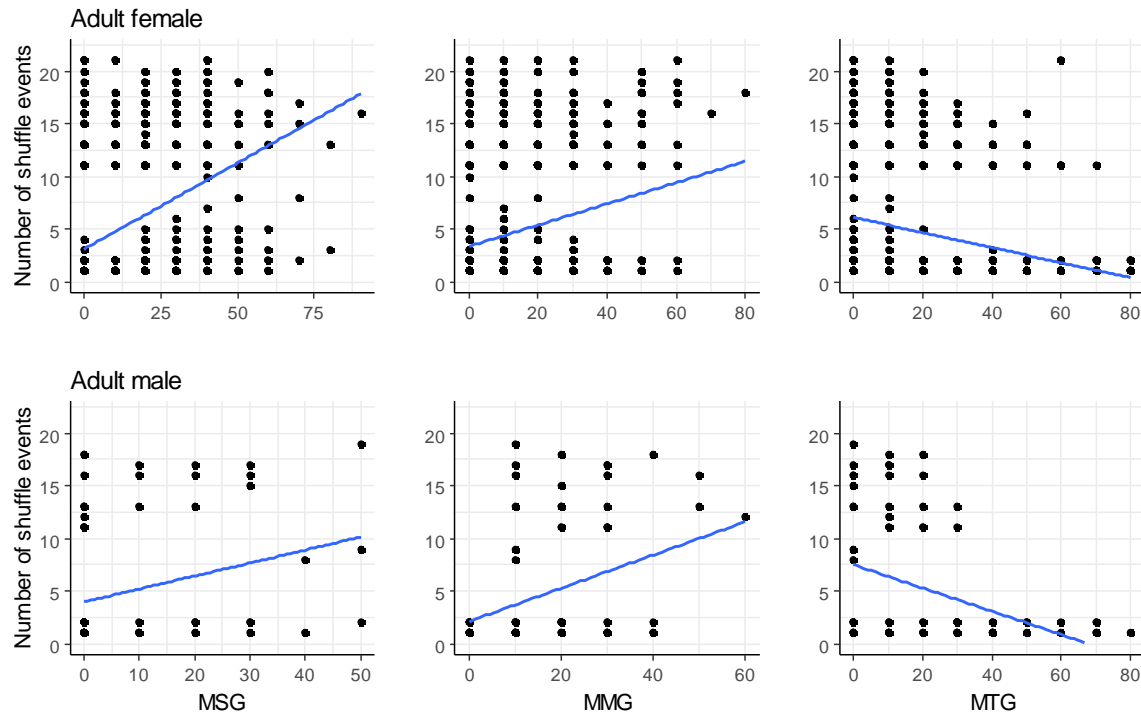


Figure 14. Linear regressions of number of shuffle events with increasing percentage of vegetation ground cover composed of plant categories: MSG, MMG and MTG in a patch (adult female: $n = 1280$, adult male: $n = 86$). Number of shuffle events positively correlated with % MSG cover (adult female: $p < 2.2e^{-16}$; adult male: $p = 0.009$) and % MMG cover (adult female: $p = 5.667e^{-16}$, adult male: $p = 5.4e^{-04}$). Number of shuffle events negatively correlated with % MTG cover (adult female: $p < 2.2e^{-16}$; adult male: $p = 1.8e^{-04}$).

A positive correlation was found between shuffle events and ground cover composed of increasing percentage of MSG (adult female: $p < 2.2e^{-16}$, adult male: $p = 0.0089$; Figure 14) and MMG (adult female: $p = 5.667e^{-16}$, adult male: $p = 5.4e^{-04}$), in contrast to a negative correlation with shuffle events and increasing percentage of MTG (adult female: $p < 2.2e^{-16}$, adult male: $p = 1.8e^{-04}$). Similarly to the previous analyses, autocorrelations in the residuals were detected also for these analyses, though they were also found to be low. Since the autocorrelations was low and the p-values from the tests were far below the significance level (0.05), the autocorrelations are not expected to cause any large changes in the outcome of these tests and will not be considered further.

Taking into consideration that the increased number of shuffle events in MSG and MMG patches could simply be a result of the individuals remaining in those patches longer, shuffle events were tested using a Poisson regression: $\text{shuffle} \sim \text{plant category value} + \text{offset}(\log(\text{time}))$. The offset means that the number of shuffle events per time unit were modeled as a function of plant category value. Of the three plant categories MSG scored the lowest p-value ($p = 2.18e^{-11}$). By using manual step-wise-up model building by first incorporating MMG ($p = 4.13e^{-05}$), MSG was still found to have the highest effect on shuffling (MSG: $p < 0.2e^{-16}$ versus MMG: $p = 2.27e^{-12}$). Adding MTG showed that the effect of MSG ($p = 4.71e^{-13}$) and MMG ($p = 1.26e^{-10}$) explains the apparent correlation between number of shuffle events and MTG ($p = 0.72$), showing that MTG is not a significant factor in regard to number of shuffle events. When testing for linearity versus quadratic trend, MSG shows a quadratic correlation while MMG showed no correlation. Therefore, it can be concluded that the best model is: $\text{Shuffle} \sim \text{MSG}^2 + \text{MMG} + \text{offset}(\log(\text{time}))$. Which means that there is an amount of MSG that leads to a maximum amount number of shuffle events, however, since the correlation is quadratic the maximum number of shuffle events do not occur at the maximum amount of MSG but instead in patches of mixed vegetation.

4 Discussion

4.1 Activity budget

The geladas in the present study spent the majority of their time feeding (46.1%) and walking (26.5%). Other studies also found geladas to spend a large proportion of their time feeding (Fashing et al. 2014: 56.8%, Wrangham 1976: 48.1%, Dunbar 1977: 45.2%). Because of their unusual diet, geladas spend more time feeding than other primate species (Passamani 1988, Prates & Bicca-Marques 2008, Matsuda et al. 2009). Compared to other graminivorous mammals, geladas feed less than the grazing ungulate plains zebra (*Equus quagga*: 60%), but a similar amount of time to grazing ungulates such as African buffalo (*Syncerus caffer*: 48%) and sable antelopes (*Hippotragus niger*: 45%: Owen-Smith & Goodall 2014). The geladas in the present study spent more time walking than buffalo (12%) and zebras (15%) and about the same amount of time walking as sable antelopes (0.8%: Owen-Smith & Goodall 2014).

Activity budget was found to be correlated with sex and age. Adult females and juveniles spent significantly more time feeding than adult males. Adult males spent significantly more time resting compared to adult females and juveniles. The activity budget hypothesis predicts that larger individuals will spend more time resting to digest food due to their larger digestive tracts (Ruckstuhl & Neuhaus 2002), which will consequently lead to variations in activity budgets in dimorphic species (Gaulin 1979, Rothman et al. 2011). Indeed, this pattern of activity budget variation has been reported for several dimorphic species: squirrel monkeys (*Saimiri oerstedii*: Boinski 1988), long tailed macaques (*Macaca fascicularis*: van Noordwijk & van Shaik 1986), black howler monkeys (Bicca-Marques & Calegro-Marques 1994), merino sheep (*Delaine merino*: Michelena et al. 2006) and Soay sheep (*Ovis aries*: Perez-Barberia et al. 2007). The trend is that larger bodied adult males spend more time resting while smaller sized adult females and juveniles spend more time feeding.

4.2 Diet: Plant category consumption

4.2.1 Age-sex classes

Nutritional analysis of plant species known to be eaten by the geladas at Guassa (Fashing, Nguyen, Venkataraman & Rothman unpub. data) was used to establish energy scores for each plant category. From the nutrition data, it was confirmed that representative species of MSG (mixed short graminoids) had the highest level of energy per 100g and scored 0.5 on energy yield. Energy contents declined with increasing graminoid length, with MMG (medium height graminoids) and MTG (mixed tall graminoids) scoring 0.4 and 0.2 respectively. Forbs scored higher in energy (1.0) than any of the graminoid categories. These scores fit with the expectation that tall species have a lower nutrition value (Westoby 1974, Owen-Smith & Novellie 1982, Rothman et al. 2012). Thus, even though taller graminoids offer higher biomass, they have a lower energy yield (carbohydrates and protein) per 100g. Short and medium height graminoids were also found to have a higher level of fat (Fashing et al. unpub. data). In addition, taller species contain higher levels of fiber that make them mechanically tough and more challenging to ingest and digest. Due to these reasons, tall graminoids are the plant category of lowest nutritional quality.

In general, all age-sex classes of geladas in the present study were found to consume a relatively large percentage of mixed short graminoids (MSG, highest energy graminoid, see below) in their diet compared to nearly all other plant categories. This was expected since the present study was conducted in the rainy season and short graminoid consumption is known to correlate with rainfall from the previous months (Figure 4; Fashing et al. 2014). Accordingly, the geladas show preference for short graminoids (Leighton 1993, Fashing et al. 2014, the present). Preference for high-quality food items has also been shown in other primate species (Oates 1994, Oates et al. 1980, McKey et al. 1981, Estrada 1984, Milton 1984, Barton & Whitten 1994, Fashing 2001, Mekonnen et al. 2010) and in large non-primate herbivores (Albon & Langvatn 1992, Parsons et al. 1994).

Plant category consumption was strongly correlated with sex and age. Adult females and juveniles showed greater selectivity of high energy plant categories (MSG, MMG and forbs) than adult males. In addition, juveniles fed significantly more on MSG and forbs than adult females. Adult males and adult females did not vary significantly in MSG and MMG consumption, but adult females fed a little more on MSG and more on forbs compared to adult males. Adult females fed significantly more on the three highest energy and quality plant categories together (MSG, MMG and forbs) than adult males, who fed significantly more on MTG. Juveniles were rarely found to ingest MTG. Larger animals are able to utilize lower-energy and potentially fiber-rich food items because of their larger digestive tracts (Ruckstuhl & Neuhaus 2002). In addition, as body size increases, energy requirements per body unit decrease, resulting in larger individuals having lower energy requirements per unit of body mass, which according to the Jarman-Bell principle means that larger individuals can afford to feed on lower quality foods (Bell 1971, Jarman 1974). The opposite may explain why smaller sized juveniles select for energy-rich, but less abundant forbs at Guassa (Fashing et al. 2014).

In dimorphic primates, adult females and juveniles have been found to feed more on higher quality food items than adult males (Gaulin 1979). Juvenile long tailed macaques were reported to feed significantly more on small, high-protein fruits, and avoid fruits with tough skins or rinds (van Noordwijk & van Schaik 1986). In Soay sheep, adult females have also been found to feed more on higher quality graminoids than adult males (Perez-Barberia 2007). Similarly, in many African ungulates, the relationship between body size and diet quality follows expectations that smaller species and smaller individuals within a species require higher energy yields from their food in order to maintain greater metabolic rates (Codron et al. 2017).

4.2.2 State dependent foraging decisions

Geladas at Guassa were found to exhibit state-dependent foraging strategies. The state-dependent theory predicts that in a state of hunger animals show lower selectivity of food

items (McNamara & Houston 1986). This is proposed for diurnal animals, which spend the night sleeping and resting with little to no feeding activity and are therefore assumed to experience an increased level of hunger in the early hours of the day (McNamara & Houston 1986). Plant category consumption in the geladas was found to be strongly correlated with time of day. Highest consumption of MTG (the lowest energy and quality graminoids) was recorded in the early morning (08:00-09:30). It is important to note, however, that after the geladas ascent from the sleeping cliffs, they sit on the top of the cliff basking in the sun, resting and grooming for up to about an hour (Appendix X, Wrangham 1976). These cliffs are dominated by *Festuca*, a MTG, and thus do not offer the same level of variety of plant categories as the plateau (Figure 5). Plant category consumption was also correlated with time period from the late morning (10:00-11.30), after the geladas usually reached the plateau. The geladas were found to feed more on MTG in the late morning compared to the early afternoon (12:00-13:30), late afternoon (14:00-15.30) and the evening hours before sunset (1600:17:30). In addition, in the evening hours before sunset the geladas had the highest consumption of MSG compared to any other time period of the day, showing that in this time period the geladas exhibited the highest level of selectivity. The geladas do not venture far from the sleeping cliffs on a day out foraging and have an average daily travel distance of 3.5 ± 1 km (Moua 2015). Plant category consumption was found to be significantly different between the time periods of early morning and the evening hours before sunset.

4.3 Patch utilization, travelling and locomotion

Studies on patch utilization originally focused on birds and insect prey (Krebs et al. 1974, Charnov 1976, Cowie 1977). Birds have been found to follow predictions of the OFT and MVT by adjusting time spent in a patch according to patch quality and spending longer times in higher quality patches (Krebs et al. 1974, Cowie 1977, Smith & Dawkins 1971, Gill & Wolf 1977, Krebs et al. 1978, Watanabe et al. 2014). Patch use has also been studied in several wild primates. Preference for foraging in higher quality patches has been shown for vervet monkeys

(*Cercopithecus aethiops*: Whitten 1988, Teichroeb & Aguado 2016) and Japanese macaques (*Macaca fuscata*: Agetsuma 1998). Possible evidence of energy as the currency driving patch use decisions has been found in white-handed gibbons (*Hylobates lar*), siamangs (*Hylobates syndactylus*: Grether et al. 1992) and langurs (*Semnopithecus entellus*: Sayers et al. 2010).

In the present study, an indirect version of the MVT was assessed according to the following assumptions: 1) patches with higher return rates will receive greater allocation of foraging time, 2) patches are characterized by smooth deceleration curves, and 3) deceleration curves of alternative patches do not cross but run roughly parallel. According to the results, the geladas made patch decisions according to predictions of the MVT and the “one-best-patch” rule. They spent longer time in rich-quality patches with more high-energy food items (MSG) compared to poor-quality patches with more low-energy food items (MTG). Time spent in a patch was also positively correlated with percentages of MSG (energy score 0.5) and MMG (energy score 0.4) and inversely correlated with percentage of MTG (energy score 0.2) in the patch. The geladas exhibited a high level of selectivity since the correlation between time spent in a patch and percentage of MSG is greater than that of MMG, even though the two graminoid categories only differed by 0.1 in energy score. This provides additional support for the hypothesis that geladas select for high-quality food items. Graminoid abundance in a patch seems to be the main factor driving gelada patch decisions since the percentage of forbs in a patch did not correlate with time spent in a patch. This is surprising since forbs have the highest energy score of any of the plant categories (energy score 1). This could be due to the low abundance of forbs eaten by geladas at Guassa (Fashing et al. 2014). In addition, as mentioned above (Methods), MSG and MTG were never found in the same patch, while forbs could be found in small amounts in all patches. This indicates that graminoids at Guassa show gradients of food quality within the habitat, and these gradients of graminoid quality are likely to drive the foraging decisions of the geladas. Data on juvenile patch time allocation were not collected in the present study, but it would be worth to investigate if forbs drive patch decisions for this age class, since they show a higher selectivity for forbs than adults (Table 3).

Both adult males and adult females showed the same correlation curves between patch residence time and plant category in patches with positive correlation with MSG and MMG cover and inverse correlation with MTG cover. On average, adult males spent longer time per patch visit than females (Table 5). Adult males spent significantly longer time than adult females in rich-quality patches. This could be an effect of the adult male larger body size allowing them to be less selective of food items. They could keep feeding in the patch even after all the high-quality food items were depleted and continue to feed on lower-quality food items that remained in the patch. Their larger body size could also result in higher cost of relocation, which means it will be more beneficial to stay in one patch for longer and feed on low-quality food to minimize travelling costs. However, the distinct age-sex classes showed no significant differences in time allocated to walking and the different OMU's (one-male units) in the herd could remain in close proximity while foraging. It is therefore suggested that the males feed longer time per patch and then travel further between patches to keep up with the rest of their OMU. This also allows males more time to rest, while the adult females and juveniles must keep feeding.

Although the results showed that the prediction of the "one-best-patch" rule holds for geladas, the geladas allocated the longest time in patches of an intermediate total energy score (0.44). By incorporating Simpson's diversity index, a positive correlation was found between time spent in a patch and plant category richness and diversity in the patch. This result suggests that, in addition to energy, preference for a mixed diet may be an important factor driving the geladas patch decisions. Studies of black and white colobus (*Colobus guereza*), baboons (*Papio sp.*) and mountain gorillas have also shown that other primates balance multiple nutrients while foraging (Johnson et al. 2017, Rothman et al. 2011). Partial preference and selectivity for a mixed diet is a foraging strategy commonly found in non-primate herbivores (Seagel & McNaughton 1992).

According to the predictions of the MVT, herbivores should spend more time in feeding stations (patches) as biomass increases (Novellie 1978, Åstrom et al. 1990, Jiang & Hudson 1993, Langvatn & Harley 1993). However, herbivores display foraging strategies to optimize nutritional balance through the selection of a mixed diet (Seigel & McNaughton 1992). This foraging strategy was found in sheep (Parson et al. 1994). Sheep show selectivity of food items by actively choosing higher quality clover (a forb), however, mean diet is obtained from a mixture of food items (grass and clover) even when a monospecific diet of clover is available (Parson et al. 1994). Similar findings have been reported for elk (Frair et al. 2005) and red deer (Jiang & Hudson 1993, Langvatn & Harley 1993). The issue that ungulates select a more varied diet than predicted by optimal foraging theory and optimal diet was originally addressed by Westoby (1974). He suggested that since generalist herbivores have adapted to using food that is abundantly available but of low nutritional value, they must be sure to obtain a large amount of different nutrients from a relative fixed bulk of food. Since evidence for this partial preference and mixed diet was found in the present study, it is likely that geladas increase their time in intermediate energy patches because these contain a wider variety of plant categories and nutritional qualities.

The biological patch definition presented in the present study is based on the distinct foraging behavior of a grazing animal, which alternate between feeding and walking. As a gelada sits and feeds it can move through a patch by shuffling. Although it seemed clear then when shuffling occurred the gelada was relocating to a previously unharvested area, there was an obvious distinction between shuffling and walking regarding the distance of relocation as well as the energy it requires. With each shuffle event the gelada extended the patch in a radius of about 30 cm (Appendix; Table C). In comparison, one step relocates an individual about 80 cm (Appendix; Table C), but it means the individual has to stop plucking food items, stand up and use all four extremities for relocation. Since shuffling involves bipedal movement, which means the gelada does not need to stand up for locomotion, it can be assumed to be of lower energetic cost. Shuffling by bipedal movement is thought to have evolved in geladas to avoid the cost of “gear-change” or raising the hind-quarters to stand up (Wrangham 1980). It is

therefore reasonable to suppose that the geladas themselves perceive patches in a manner reflected by their two different forms of locomotion (quadrupedally walking and bipedal shuffling). Shuffling allows them to expand the size of high-quality patches, thereby lowering the cost of relocation while foraging. Since it is not possible to make this distinction for non-primate herbivores, geladas provide a unique opportunity to explore perception of patch size and quality in a grazing animal.

The MVT predicts that travelling time between patches will increase with increasing time spent feeding in patches (Charnov 1976, Winterhalder 1981). Other studies investigating patch residence time and inter-patch travelling time in primates have found that both spider monkeys (*Ateles geoffroyi*) and mantled howler monkeys (*Alouatta palliata*) increase the time spent in a patch with increasing travel time (Chapman 1988). The present study did not find a correlation between time spent feeding in patches and time spent travelling (cost), as predicted by the MVT (Charnov 1976, Winterhalder 1981). This could simply be the result of a graminivorous diet. Graminivorous animals feed on food items that are high in abundance but generally low in nutritional quality (Westoby 1974, Searle & Shipley 2008). It is therefore necessary to spend a large amount of the daily time feeding, and since feeding occupies the major proportion of foraging time, variations in walking time have only a minor influence on overall energy cost (Owen-Smith & Novellie 1982). Consequently, travel time has relatively less impact in optimal residence time in patches of homogenous habitats and is mostly affected by the overall quality of the habitat (Winterhalder 1981).

On average, both adult female and adult male geladas engaged in a higher number of shuffle events in rich-quality patches (40-100% MSG cover) than in poor-quality patches (40-100% MTG cover). Number of shuffle events were positively correlated with percentage of MSG and MMG cover and inversely correlated with percentage of MTG cover. After running the Poisson regression and the manual step-wise-up model to take into account that the correlations could simply be an effect of the differences in time spent in patches, it was detected that the effect of

decreasing number of shuffle events and MTG cover could be explained by increasing amounts of MSG and MMG. Results of the Poisson regression showed that MSG cover in a patch was the factor driving the number of shuffle events. However, the correlation was not linear. Instead, the quadratic correlation of shuffle events and MSG suggests that there is an optimum amount (intermediate amount) of MSG where the number of shuffle events are the highest. This quadratic correlation could suggest that the geladas engage in the highest number of shuffles in patches with a reasonable amount of MSG cover, but that also contain other plant categories. This once again indicates that geladas do not allocate the longest time and foraging energy in patches of the very highest energy yield, but instead, chose to allocate the longest time in patches offering a mixture of plants and therefore perhaps a mixture of nutrients.

4.4 Future studies

The present study was conducted in the rainy season when food for the geladas is known to be abundant (Fashing et al 2014). The “active” foraging strategy predicts that as food availability declines animals will devote more time to foraging in order to obtain enough energy to survive (Norberg 1977), which could lead to variation in optimal activity budgets. In general, seasonal variation seems to be a common feature of primate diets (Hill 1996). Variations in diet in response to seasonal changes have been reported for many primates (e.g., Hu et al. 1980, Shi et al. 1982, Agetsuma and Nakagawa 1998, Zhang & Watanabe 2006)). The gelada foraging decisions at Guassa have also been found to be affected by season, with the geladas consuming lower quality graminoids (MTG) and underground storage organs as fallback foods in the dry season (Fashing et al. 2014). Future studies should compare activity budgets between seasons and assess how season influences diet across age-sex classes. Furthermore, studies should also assess if patch utilization and residence time are affected by seasonality, by testing the prediction that an individual should stay longer in a patch regardless of quality and if individuals decrease travelling time between patches as general quality of the habitat decreases.

Social behavior and hierarchy can also affect foraging strategies and decisions in primates (Nakagawa 1990, Kazahari & Agetsuma 2008) and an individual's behavioral decisions and activities can be affected by his/her position in the social hierarchy. For example, aggression and rank differences have been shown to affect energy intake in patches for capuchin monkeys (Vogel 2005). It would be interesting to see if rank influences patch quality choices in geladas by incorporating rank values of adult females into data analyses. For example, do higher ranking adult females feed in higher quality patches than lower ranking adult females? Does rank affect the time individuals stay in a specific patch? Patch residence time of lower ranking individuals could be affected by dominant individuals pushing them away. The present study did not incorporate the effects of social behavior on movement decisions.

Geladas are social primates that live in unusually large groups (Bergman & Beehner 2013). Number of co-feeders has been shown to positively affect patch use in Japanese macaques (Kazahari & Agetsuma 2008). Thus, it is critical to incorporate social factors, on a group level, to further investigate gelada foraging strategies. An interesting aspect would be to look at all of the different factors affecting foraging decisions (e.g. plant nutrients and energy or patch qualities, time of day, sex and age, reproductive status, hierarchy rank, number of co-feeders, rainfall) and run an ordination test to get a clearer picture on the relative impacts of the factors driving gelada foraging decisions.

4.5 Implications for conservation

Geladas are categorized as "Least Concern" by the IUCN (Gippoliti & Hunter, 2008), even though gelada habitat is still under threat due to an increase of grassland conversion to settlements, farms livestock grazing areas as well as from climate change (Fashing & Nguyen, 2015). The gelada is the last remaining member of a genus that during the Pleistocene was one of the most widespread terrestrial primates (Dunbar 1998, Jablonski 1993). Today most of the

remaining populations of geladas are found above 3,000 m.a.s.l., due to a dramatic increase in the Ethiopian human population (from 8 million in 1910 to 100 million today) and the resulting conversion of gelada habitat to farmland in recent decades.

The geladas in the present study showed a preference for a mixed diet, though it is also clear that they actively select for high-quality food items (MSG, MMG and forbs). Thus, decreases in the abundance of these plants could lead to energetic stress among the geladas at Guassa and result in population decline. The *Festuca* graminoids (MTG) at Guassa are already being conserved through the 400-year old local indigenous management program known as the *Qero* system (Ashenafi & Leader-Williams 2005), so further efforts to conserve gelada habitat at Guassa should focus on areas of high-quality food. It has been shown, from other study sites, that geladas can sustain their metabolic requirements on high-quality, short graminoids (Dunbar & Dunbar 1974, Wrangham 1976), but little is known about the geladas ability to survive on a diet composed mainly of lower quality, tall graminoids. Gelada habitat converted to cultivated land at Guassa takes place in the mountain plateau where the diversity of plant species is greater. The continuous increase in cultivated land could ultimately restrict the geladas to the cliff edges where tall graminoids (low-quality food items) are dominant. It will therefore be important that high-quality food areas for geladas at Guassa are effectively conserved.

Climate change is a major long-term threat to the cool and wet climate of Afroalpine ecosystems (Dunbar 1998). Productivity of vegetation is affected by temperature, with high temperatures leading to desiccation of graminoids in the dry season (Dunbar 1988). Geladas prefer to consume green graminoids which are more nutritious and when graminoid productivity is low geladas must compensate by increasing daily travel length (Iwamoto 1993, Erskine 2016). Climate change could result in geladas being restricted to small mountain peaks, leading to significant reductions in existing populations (Dunbar 1998).

5 Conclusion

The present study provided novel evidence that geladas feed according to predictions of the MVT and the “one-best-patch” rule, by allocating longer time in patches with increased percentage of high-energy plant cover and shorter time in patches with high percentage of low-energy plant cover. However, the results showed that geladas allocated the longest time per path in those patches with the highest diversity of plant categories, even though these were of intermediate total energy yield. This provides evidence that geladas select for a mixed diet, similarly to non-primate herbivores which obtain a mixture of nutrients from a relatively fixed bulk of food. The results also showed that geladas selected for high-quality food items, that their foraging strategies reflected the abundance and distribution of food items in their habitat, and that the individual’s state of hunger affected foraging decisions. In addition, differences in activity budget, feeding behavior and diet composition reflected the differing demands of optimal activity and energy allocation between different sex-age classes.

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Appendix

Table A. Percentages of (a) the ground cover accounted for by the different plant species surveyed and (b) the plots (0.7m x 0.7m; n=300) in which each species appeared.

Species	Family	Category ^a	% Coverage ^b	% Plots
<i>Festuca macrophylla</i>	Poaceae	graminoid, tall	15.30	72.67
<i>Thymus schimperi</i>	Lamiaceae	forb (not eaten)	14.35	73.33
<i>Alchemilla abyssinica</i>	Rosaceae	forb (not eaten)	12.72	82.67
Bare ground (soil)	---	soil	9.36	73.67
Other tall graminoids	Poaceae/Cyperaceae	graminoid, tall	6.20	73.33
Mixed short graminoids	Poaceae/Cyperaceae	graminoid, short	5.46	57.67
<i>Euryops pinifolius</i>	Asteraceae	shrub	5.46	43.33
<i>Helichrysum splendidum</i>	Asteraceae	shrub	4.59	49.00
Rock	---	rock	3.63	25.67
<i>Carex monostachya</i>	Cyperaceae	graminoid, tall	2.88	10.00
<i>Trifolium</i> spp.	Fabaceae	forb	2.02	66.33
<i>Agrocharis melanatha</i>	Apiaceae	forb	1.85	66.66
<i>Erica arborea</i>	Ericaceae	shrub	1.51	10.67
<i>Commelina africana</i>	Commelinaceae	forb	0.83	58.67
<i>Agrolobium ramosissimum</i>	Fabaceae	forb	0.78	44.33
<i>Kniphofia foliosa</i>	Asphodelaceae	forb	0.48	1.33
Unidentified lichen	Unidentified	lichen	0.43	7.67
<i>Ranunculus</i> sp.	Ranunculaceae	forb	0.35	18.00
<i>Haplosciadium abyssinicum</i>	Apiaceae	forb	0.30	14.33
<i>Kniphofia insignis</i>	Asphodelaceae	forb	0.30	14.00
<i>Hypericum revolutum</i>	Hypericaceae	shrub	0.21	3.00
<i>Aeonium leucoblepharum</i>	Crassulaceae	forb	0.17	0.67
<i>Rubus apetalus</i>	Rosaceae	shrub	0.10	1.33
<i>Lobelia rhynchoptalum</i>	Lobeliaceae	forb	0.10	1.00
Unidentified fern	Unidentified	fern (not eaten)	0.10	1.00
<i>Anthriscus sylvestris</i>	Apiaceae	forb	0.07	2.33
<i>Galium simense</i>	Rubiaceae	forb	0.05	1.67
<i>Carex simensis</i>	Cyperaceae	graminoid, short	0.05	1.67
<i>Carduus nyassanus</i>	Asteraceae	forb	0.05	1.33
Mixed herbs	Unidentified	forb	0.04	1.67

Species	Family	Category ^a	% Coverage ^b	% Plots
<i>Hebenstretia angolensis</i>	Scrophulariaceae	forb (not eaten)	0.03	0.67
<i>Salvia merjamie</i>	Lamiaceae	forb (not eaten)	0.03	2.33
<i>Helichrysum formosissimum</i>	Asteraceae	shrub	0.02	0.67
<i>Silene burchellii</i>	Caryophyllaceae	forb	0.02	3.00
<i>Anthemis tigreensis</i>	Asteraceae	forb	0.01	2.33
<i>Delosperma schimperi</i>	Aizoaceae	forb	0.01	1.33

- ^a Entries categorized as '(not eaten)' were taxa that geladas were never observed consuming.
- ^b Approximately 10% of the ground cover within the plots consisted of plant species we were unable to identify. (Taken from Fashing et al. 2014).

Table B. Activity time budget (frequency %) of geladas at Guassa August-October 2016 organized by time periods.

Activity	N ^a	Early morning	Late morning	Early afternoon	Late afternoon	Evening hours before sunset
Feeding	510	18.0	50.6	46.1	70.6	44.6
Walking	620	11.8	23.0	43.6	21.2	33.6
Grooming	590	32.2	15.3	5.4	1.7	15.3
Resting	525	33.5	8.0	3.4	3.8	3.8
Other	400	4.5	3.1	1.5	2.7	2.7

^a = Total number of records.

Table C. Measurements obtained from female and male geladas on shuffle length, step length and foraging width.

Measurements (cm)										
Age-Sex	N ^a	Shuffle length			Step length			Foraging width		
		Mean	Median	Mode	Mean	Median	Mode	Mean	Median	Mode
Adult female	85	30.0± 4.3	30.5	35.0	79.3± 7.5	80.5	84.0	51.0± 4.8	51.0	50.0
Adult male	25	31.6± 6.0	32.0	35.0	80.0± 7.8	81.0	82.0	51.6± 7.0	52.0	50.0

^a = Sample size.

Table D. Comparative data of gelada feeding activity and diet across study sites in Ethiopia.

Field site	Season	Months	Proportion of time feeding	Plant consumption as proportion of diet							Source
				Graminoids			Graminoid seeds	USOs	Forbs	Other	
				Short	Medium	Tall					
Guassa	Rainy season	3	46.1	33.1	28.0	9.7	3.0	9.2	16.8	0.2	Present study
Guassa	Rainy and dry season	15	56.8	8.7		41.9 (tall and medium)	2.2	4.0	37.8	5.4	Fashing et al. (2014)
Simien Mountains	Rainy season	2	48.1	91.6		1.4	1.7	1.1	3.0	1.2	Wrangham (1976)
Simien Mountains	Rainy and dry seasons	3	70.9 (males) 73.0 (females)		(68.8)		5.1	8.0	18.1		Iwamoto (1979, 1993)
Simien Mountains		5	45.2		(45.0)		23.2	24.5	2.8	4.5	Dunbar (1977)
Bole		6			(91.4)		5.0	0.5	0.3	2.8	Dunbar and Dunbar (1974)
Simien Mountains	Rainy and dry seasons	6		55.2		0.0	1.8	11.9	26.1	5.0	Hunter (2001)

Blank cells = no data available.