The importance of underground foods

in female gelada (*Theropithecus gelada*) socioecology

by

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Abstract

Food plays a foundational role in animals' lives, particularly during periods of food scarcity. Foods consumed only during times of food scarcity, "fallback foods", exert strong selective forces in shaping behavior and life history. However, the role of fallback foods has not been examined in many species. Geladas (*Theropithecus gelada*) present a particular conundrum. While geladas primarily eat grasses blades, alternative diet items, such as underground plant storage organs, are a large part of the diet, especially in the dry season, when green grasses are scarce. In this thesis, I investigate the role that these alternative diet items have in gelada foraging and behavioral ecology in a population of wild geladas in the Simien Mountains National Park, Ethiopia, from January, 2015 - January, 2016.

I asked the following questions: (1) How much of the gelada diet (across seasons) is comprised of grass? And, (2) to what extent do geladas utilize "fallback foods"? I quantified monthly diet profiles of adult geladas from eight study units (n=37 females, 17 males) using instantaneous scan samples (n=7,533 feeding scans), and seasonal above- and underground food availability. I compiled data from published gelada feeding studies and compare the relative importance of underground foods in the gelada diet. Geladas preferred green grasses year-round (up to 93.4% of monthly foraging time), but spent a large amount of time consuming underground foods in the dry season (up to 58% of monthly foraging time). Grass consumption was positively correlated with grass availability, and underground food consumption was negatively correlated with green grass availability. In contrast with grasses, underground food availability did not vary seasonally, which supports the hypothesis that underground foods are important fallback foods for geladas.

Next, I examined the role that underground foods play in shaping gelada social relationships among females. Socioecological models predict that female competition should increase when food resources are clumped and defensible. Female geladas thus represent a puzzle for socioecology; they feed on dispersed resources that cannot be monopolized, yet they exhibit aggressive competition and a strict dominance hierarchy. I hypothesized that female geladas must routinely contest underground resources during times of scarcity. To test this hypothesis, I used behavioral data from adult females (n=32 females; 1,424 observation hours) collected in the dry and wet seasons to assess the effect of behavioral context, season, and on the probability of receiving aggression. I found that females were more likely to receive aggression from within-unit females than from females outside of their unit, that aggression was highest during the dry season when geladas were *not* feeding on a widely-dispersed resource (grass) but rather were feeding on underground foods, that aggression was higher during a feeding context than a non-feeding context, and even more so when the feeding was on underground food items, and that low-ranking females were the most likely to receive aggression in these contexts. Therefore, the results of this study support the hypothesis that female aggression (and the dominance hierarchy that ensues) functions to usurp lower-ranking females from their underground excavations that expose valuable underground foods. These excavations represent an investment of time, energy, and a level of uncertainty as to whether the effort will uncover a valuable food resource, all of which can be eliminated or reduced for a high-ranking individual that can acquire the "patch" without investing any of the effort. In sum, the results presented here support the hypothesis that fallback foods can be contestable resources, and can be influential in shaping social relationships among female geladas.

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Table of Contents

Chapter 1
Beyond graminivory: the gelada diet depends on fallback foods during the dry season

Introduction

Animals cope with food scarcity by using a variety of strategies. A common strategy is to shift to consuming alternative diet items, or "fallback foods", which are typically less nutritious, less preferred, yet nevertheless comprise a critical part of a species' diet (Brockman & van Schaik 2005). Fallback foods are defined as "foods whose use is negatively correlated with the availability of preferred foods" (Marshall & Wrangham, 2007: p.1220; Altmann 1998). While these foods are often not the most frequently consumed diet items, the increased complexity associated with processing, handling, and digesting them can exert strong selective pressures. For example, a severe drought in the Galapagos caused rapid selection of beak size in one species of finch (*Geospizia fortis;* Boag & Grant 1981). The drought caused a drastic reduction in the abundance of preferred seeds, and individuals that had larger body and beak sizes were able to harvest the large seeds of *Tribulus cistoides*, which are ignored during periods of highly-preferred food availability. As a result, birds with larger beaks had lower mortality rates, and the subsequent generations of these finches had larger beak sizes (Boag & Grant 1981). Since this pivotal study, behavioral ecologists have focused much more research effort towards understanding evolutionary adaptations during food shortages rather than during periods of food abundance.

The use of fallback foods has been invoked to explain morphological adaptations for processing foods. For example, the thick dental enamel of grey-cheeked mangabeys (*Lophocebus albigena*) has been argued to be an adaptation for puncturing and crushing bark and seeds, which are exploited during times of preferred food scarcity (Lambert et al. 2004). Variation in dental morphology of the great apes is consistent with the mechanical properties of their fallback foods (Constantino et al. 2009). In addition to shaping morphological traits, the abundance and distribution of fallback foods can also shape population density, movement, and grouping patterns of a species. For instance, fallback foods influenced both the population density and group size of Japanese macaques (*Macaca fuscata*) (Hanya et al. 2006), the movement patterns of the black-fronted titi monkey (*Callicebus nigrifrons*) (Nagy-Reis & Setz 2016), and habitat use of chimpanzees (*Pan troglodytes*) during times of preferred food scarcity (Furuichi et al.

2001). Fallback foods have also been shown to both limit the population density (e.g., gibbons (*Hylobates albibarbis*); Marshall et al. 2009) and facilitate the formation of extremely large groups during times of preferred food scarcity (e.g., snub-nosed monkeys (*Rhinopithecus bieti*); Grueter et al. 2009), Angolan colobus monkeys (*Colobus angolensis*); Fashing et al. 2007).

Sympatric species with considerable dietary overlap of preferred foods often partition fallback foods. For example, gorillas (*Gorilla beringei graueri*) in the Kahuzi-Biega National Park rely on low quality, abundant fallback foods (e.g., bark and leaves) which enable them to stay in cohesive groups across a variety of different habitats regardless of fruit abundance, while sympatric chimpanzees rely heavily on ripe fruits, and consume higher quality fallback foods that enable them to inhabit small home ranges, but restricts the range of suitable habitat types and reduces group cohesion (Yamagiwa & Basabose 2009).

The importance of fallback foods in shaping behavior, ecology, and evolution has received considerable attention in primatology and paleoanthropology (e.g., Constantino & Wright, 2009). Yet, the role of fallback foods for many species has not been investigated. Geladas (*Theropithecus gelada*) are one such species. Geladas are a graminivorous primate, restricted to an altitudinal range of 1700-4200 m in the Ethiopian highlands (Dunbar 1998). The majority of gelada foraging time is spent feeding on green graminoid (grasses and sedges, hereafter "grasses") leaves, with *some months* reaching over 90% of foraging time (Iwamoto, 1993) – but, importantly, with some months also reaching as low as 30% of foraging time (Fashing et al. 2014). Fashing and colleagues (2014) found that forb leaves are the most preferred diet item for one population of geladas, but that these leaves are not sufficiently abundant to be a primary food source throughout the year. Green grass blades are also preferred foods; in the height of the dry season, when green grass cover is severely reduced, geladas still spend a large portion of total foraging time feeding on green grass blades (Dunbar 1977, Iwamoto 1979, 1993; Hunter 2001, Fashing et al. 2014). However, geladas consume other plant genera and plant parts that make up a substantial part of foraging time (Dunbar 1977, Iwamoto 1979, 1993; Hunter 2001, Fashing et al. 2014). Of these alternative diet items, underground plant storage organs (e.g., roots, rhizomes, and corms) comprise a considerable proportion of gelada foraging time and caloric intake in the dry season (Hunter 2001).

Underground storage organs – hereafter "underground foods" – are swollen, starchy masses of tissue used to store water and carbohydrates during harsh conditions (Dominy et al. 2008), and are a common plant adaptation in habitats with extreme dry seasons (Laden & Wrangham 2005). Underground foods are important food resources during the dry season in open-plains savanna habitats (Struhsaker 1967) and have been recognized widely as important fallback foods for a variety of mammals including early hominins, baboons (e.g., *Papio* spp.), ursids, and suids (Barton 1993, Dominy et al. 2008; Hatley & Kappelman 1980; Laden & Wrangham 2005, Altmann 1998). The ability of hominins and baboons to exploit underground foods has been used to explain how they have managed to persist in savanna habitats (Laden & Wrangham 2005). Corms and tubers, in particular, are considered important fallback foods for baboons (*Papio aunbis, P. cynocephalus,* and *P. ursinus*) (Altmann 1998, Barton 1993, Hamilton et al. 1978, Byrne et al. 1993). It is then reasonable to hypothesize that geladas, a close relative of baboons that also inhabit regions with intense dry seasons, would also use underground items as fallback foods.

Previous feeding studies have reported that geladas switch to consuming underground foods in the dry season (Dunbar 1977, Iwamoto 1979, 1993; Hunter 2001, Fashing et al. 2014). Researchers have suggested that underground foods are fallback foods because consumption is higher when green grasses are scarce (Fashing et al. 2014) and because underground foods (e.g., roots and rhizomes) are extremely tough and difficult to fracture (Venkataraman et al. 2014, Dominy et al. 2008). However, we cannot confidently conclude that geladas prefer grass leaves unless we can demonstrate that underground food items remain available during times when grass is consumed. Therefore, we must test the alternative hypothesis that consumption rates of above- and underground foods are simply based on what is available seasonally.

Here, I summarize data from published studies of gelada feeding ecology and compile results from original data to answer two questions. First, I asked how much of the gelada diet (across seasons) is comprised of grass? The idea that gelada diet consists almost entirely of grass blades has been preserved for decades, and originated from a study conducted by Dunbar and Dunbar (1974) that was neither designed nor intended to quantify the annual diet of geladas. While the study did capture some degree of both the wet and dry seasons, the study months were biased towards the wettest months, and the putative "dry season" months from the study were

months when moderate rains can occur, triggering leaf growth. This region also represents the lower altitudinal limit of the gelada range (Iwamoto & Dunbar 1983), and thus the climate and ecology are not representative of typical gelada habitat. Yet, this diet profile ("grasses account for more than 95% of the diet", Dunbar & Dunbar 1974: p. 49) has been popularized to the extent that it has become conventional wisdom (e.g., Gron 2008, Primate Info Net).

Second, I asked to what extent do geladas utilize alternative diet items, or "fallback foods", primarily underground storage organs? I investigate the relationship between underground storage organ consumption and ecological variables to test whether underground storage organs are, indeed, a fallback food for geladas. To establish that underground storage organs are fallback foods, I examine first whether there is a seasonal shift between aboveground grass consumption and underground food items. Second, I establish whether underground food items are equally available during both time periods. I quantify aboveground (e.g., grass) and underground (e.g., underground storage organs) food availability seasonally and relate this to patterns of gelada diet.

Methods

Study species and site

Geladas (*Theropithecus gelada*), a unique grazing primate, are endemic to the Ethiopian highlands and the only extant species of their genus. Geladas have a multi-level social structure (Dunbar & Dunbar 1975, Snyder-Mackler et al. 2012); the smallest unit of the social group is the one-male unit, which consists of related females and their offspring, a dominant "leader" male, and may include one or more subordinate "follower" males that are either former leader males or bachelor males that regularly associate with the group (Dunbar & Dunbar 1975). Multiple one-male units that associate with each other more than 50% of the time form "bands" of 50-200 individuals (Snyder-Mackler et al. 2012); and, multiple bands join to form "herds" of up to 1,200 individuals that forage together throughout the day (Crook 1966, Snyder-Mackler et al. 2012).

I collected behavioral data from all adult males and females across 8 one-male units (n=37 females, 17 males). All individuals were habituated to the presence of observers and individually recognizable by natural markings. Females that reached maturation during the dry season ($\leq$ 4 months into the study) were included in the dataset.

I conducted this study in the Sankaber region of the Simien Mountains National Park, Ethiopia (Figure 1.1) as part of the University of Michigan Gelada Research Project, which has been collecting behavioral and demographic data on a population of habituated wild geladas since 2006. Sankaber is located in the uplands of the Simien Mountains (~3250 m a.s.l.), and considered to be Afroalpine grasslands, characterized by undulating grassland plateaus, scrublands, and Ericaceous forests (Puff & Nemomissa 2005). More detailed site descriptions can be found in Dunbar (1977), Kawai (1979), Iwamoto (1979, 1993), and Hunter (2001).

Climate and weather data

The typical rainy season in the Simien Mountains occurs from June to October and the typical dry season runs from November to May. Months with more than 400 mm of cumulative precipitation from the previous 90 days were considered "wet season" months (after Venkataraman et al. 2014). Occasionally, there also is a short rainy period from February to March. I recorded daily minimum and maximum temperature (˚C) and twice a month recorded hourly temperature from 7 a.m. to 7 p.m. using a digital weather station. I recorded daily cumulative rainfall (mm) using a rain gauge. Across a 10-year period (2006-2015) the mean temperature was 13.66 °C (SD=0.49); maximum temperature was 17.57 °C (SD=0.59); mean minimum temperature was 8.18°C (SD=1.08). Mean annual precipitation was 1702.2 mm (SD=427.19). See Figure 1.2 for mean monthly temperatures and precipitation.

Data collection

Feeding behavior

I collected feeding records from individuals using instantaneous scan samples (Altmann 1974) at 10-minute intervals from Jan 2015 to Jan 2016 (n=7,533 feeding scans; data from Aug 2015 to Jan 2016 were collected by C. Hawley). Consistent with previous studies of gelada feeding behavior (e.g. Dunbar 1977, Iwamoto & Dunbar 1983, Fashing et al. 2014), an individual was considered feeding if observed handling food, chewing, swallowing, or digging. I recorded the diet item(s) the individual was foraging for and/or consuming and collapsed diet items into four categories ("grass", "forbs", "underground", and "other") as follows: "grass" included all *aboveground* plant parts (e.g., leaves, seeds, stems) of grass and sedge species; "forbs" included all *aboveground* plant parts of non-woody herbaceous diet items,

"underground" included all underground plant storage organ consumed by geladas (e.g., roots, rhizomes, corms, tubers); "other" included invertebrates, fruits, flowers, crops, water, and algae.

Aboveground food availability

To quantify aboveground food availability, I established 25 m vegetation transects (n=30) randomly stratified, representative of the relative area of habitat types across the home range. I then measured aboveground food availability using the point-intercept method (Jonasson 1988, *sensu* Rubenstein 2010). The point intercept method is among the most objective methods for assessing ground cover (Norbury & Sanson 1992) and ideal for vegetation communities with height < 3 feet (Caratti 2006). Measurements were collected monthly from February 2015 to January 2016. I dropped a metal pin vertically at 1 m intervals along the transects and recorded all plants and part of the plants hit by the pin as well as hits of bare ground and rock. Vegetation was classified as either grass or forb, and whether the vegetation was green (i.e., live) or brown (i.e., dead). I used percent green grass leaves (as a proportion of all grass leaf hits) as a measure of aboveground food availability. Percent green grass was calculated for each transect and averaged by month:

% green grass/transect = total # of green grass leaf hits/ total # of all grass leaf hits x 100

Underground food availability

To quantify underground food availability, I collected soil cores (6.35 cm wide, 20 cm long) along random intervals at the 30 transect locations used for aboveground food measurements (2 cores/transect). Cores were collected in April (the end of the dry season, n=54) and November (the end of the wet season, n=60). I was unable to reach 20 cm at some of the transect locations in the dry season due to the hardness of the soil. After collection, material was sorted using a sieve, and vegetation items were dried and weighed on a digital scale. All underground plant storage organs, such as roots, rhizomes, and corms, were considered as diet items. I report the sample weights as $g/6.35\ cm^2$ (or g/core; the core size approximates the size of the typical hole dug by a gelada (personal observation).

Cross-study diet comparison

I summarized feeding data results from all published studies of gelada feeding behavior and report the results expressed as percent of feeding time for the annual and seasonal diets. All studies used scan sampling to quantify diet (Altmann 1974). Seasonal importance of the diet categories was assessed using the respective percentage of foraging time.

Statistical analysis

All statistical analyses were performed using R v 3.3.0 (R Core Team 2016). I compared monthly green grass availability to the monthly percent foraging time of each diet category using Pearson's correlation coefficients to assess the relationship between preferred food availability and consumption. I tested the relationship between green grass availability and rainfall to assess the validity of using rainfall as a proxy for food availability using Pearson's correlation coefficient. I tested whether season affected underground food availability using a Mann-Whitney U test.

Results

Geladas prefer grass when available

The gelada diet shifted from being almost entirely aboveground grass parts in the wet season (ranging from a minimum of 83.1% of the diet in May to a maximum of 93.4% of the diet in November) to a much greater reliance on underground foods in the dry season months, with January and February reaching a higher reliance of underground items than grass (58.9% and 49.8%, of the diet, for January and February 2015, respectively) (Table 1.1). Grass consumption was positively correlated with green grass availability (r=0.826, p<0.01), and underground food consumption was negatively correlated with green grass availability (r=-0.823, p<0.01) (Figure 1.3). The consumption of forbs and other diet items had no relationship with green grass availability (r=-0.242, p=0.45, and, r=-0.539, p=0.071, respectively).

Rainfall is a good proxy for aboveground food

Aboveground food availability was highly correlated with rainfall. The strongest predictors of green grass availability were cumulative rainfall from (1) the previous 90 days (r =0.94, df =10, p< 0.01) and (2) the previous 60 days (r=0.92, df=10, p<0.01). Rainfall from

the previous 30 days was also correlated with percent green grass (r=0.48, df=10, p<0.01), but to a lesser degree. This relationship was also observed by Fashing et al. (2014) and Hunter (2001).

Underground food availability

Perhaps most importantly, underground food availability did not vary between the dry and wet seasons (Mann-Whitney U Test, W=1633, p=0.94). Mean dry weights for April (dry season) and November (wet season) were 0.91 g/core (SD=0.72) and 0.94 g/core (SD=0.79), respectively (Figure 1.4).

Cross-study comparisons

The proportion of grass in the annual diet varied substantially across the 6 studies on gelada feeding ecology; the lowest estimate at 50.6% (Fashing et al. 2014) and the highest estimate at 96.6% (Dunbar & Dunbar 1974), (Table 1.2). Of all studies that recorded sufficient feeding behavior across both seasons, the dataset from my study demonstrated the highest percent of grass in the annual diet (75.5%) as compared to the lowest estimate of 50.6% (Fashing et al. 2014). Underground foods made up a substantial part of geladas' dry season diet in all gelada studies, but varied in importance across study site and study year. The geladas in the Sankaber region of the Simien Mountains National Park appear to consistently consume the highest percentage of underground foods (25.2%, this study; 56.6%, Hunter 2001; 63%, Dunbar 1977). In the study sites at higher elevations and more intact ecosystems, Gich (3900 m) and Guassa (3450 m), underground foods were not as heavily consumed in the dry season (14.9% and 18.0% of diet in Gich and Guassa, respectively), and forbs were more heavily consumed during the dry season than underground foods (forbs: 23.8% and 32.3% of the diet for Gich and Guassa, respectively).

Discussion

Underground storage organs are important diet items for geladas during the dry season. Although underground foods were available year-round, geladas only spent time foraging on them when green grass availability was low. Additionally, despite the low availability of green grass during the dry season months, geladas nevertheless spent a disproportionately high amount of time trying to feed on aboveground grass parts. Therefore, geladas appear to prefer green grass to underground foods, even when it is sparse and presumably difficult to harvest (Dunbar

1977, Iwamoto 1979, 1993; Hunter 2001, Fashing et al. 2014). Supporting Hunter's study (2001), we also demonstrate no significant differences in seasonal abundance of underground food. This suggests that underground foods are indeed fallback foods (i.e., that the consumption of underground food is not influenced by availability, but rather by the lack of green grass availability; Marshall & Wrangham 2007).

Geladas may have other preferred food items. We do not dismiss the possibility that other diet items may be preferred to green grass blades. For example, fruits from *Rosa abyssinica* (Hunter 2001) and *Rubus apetalus* (Fashing et al. 2014), and invertebrates (e.g., Desert locust outbreak observed by Fashing et al. 2010) may be preferred foods, but these items so rarely are available that the selectivity and importance of these diet items is difficult to assess with our current dataset. Geladas may be subsisting primarily on fallback foods, and grasses may, in fact be a "staple" fallback food (consumed year-round and can comprise 100% of the diet), while underground foods are "filler" fallback foods (only consumed during certain periods, and are never 100% of the diet) (Marshall & Wrangham 2007). The importance of these foods in gelada diet may not be captured adequately using the traditional method of scan sampling the quantify diet because this does not account for variations of intake rates and nutritional value of each diet item (Dunbar 1977, Hunter 2001).

The gelada diet is not 90% grass. Although geladas exhibited variability in the amount of grass in their diet across studies, all studies report that at least half of the gelada diet is grass (and at least 69.6% during the wet season). However, only Dunbar and Dunbar (1974) report the oft-quoted figure that the gelada diet is comprised of >95% grass – a study conducted for only 6 months, which included primarily wet season months. We advise against use of this figure to represent the percentage of grass in the gelada diet – except as an extreme upper bound.

The reliance on underground foods is variable across studies and years. The amount of time geladas spent feeding on underground foods in the dry season was quite variable by study site, and by study year for Sankaber. This may be due to several factors. First, the length of study varied substantially between studies from 3-15 months. Fashing and colleague's (2014) study from the Guassa geladas and our study were the only studies that captured a full year of feeding data; results from the other studies were from data collected during months in the height of the dry and wet seasons. These studies necessarily miss the transitional periods from dry to wet

season where underground food consumption steadily decreases with the onset of the beginning of the wet season. Second, variation in rainfall likely contribute to the differences between studies. For example, in Hunter's study (2001), May to October accounted for 79.5% of total annual rainfall, while this period accounted for 95.4% of annual rainfall in our study. In other words, the dry season was drier during Hunter's study, and we thus expect green grass availability to be lower, forcing geladas to spend more time feeding on underground foods. Third, elevation may also play a role in the dietary differences. The studies in the Guassa Conservation Area and the Gich region of the Simien Mountains took place at higher elevations than the Sankaber region. Temperatures are lower at higher elevations, which requires more energy for thermoregulation, and may require geladas to consume a higher proportion of grass and forbs to maintain adequate protein consumption (Iwamoto & Dunbar 1983). Fourth, land use also certainly plays a role in shaping the gelada diet. When comparing the Sankaber, Guassa, and Gich study sites, Sankaber routinely experiences the most grazing pressure by domestic livestock and the geladas living in this area must rely more heavily on underground foods in the dry season due to the drastic reduction grass cover (Iwamoto & Dunbar 1983). The Gich area is also grazed by domestic livestock but to a lesser extent than at Sankaber during the time of Iwamoto's (1979) study. The Guassa Conservation Area is the only intact ecosystem of the gelada feeding studies, and has substantially more aboveground biomass than Sankaber (personal observation). These differences in grass availability are consistent with our observations of underground food consumption. If green grass availability remains higher in the dry season, underground foods should constitute less of the dry season diet. This hypothesis remains to be tested.

Fallback foods may be an important factor in gelada socioecology. Fallback foods are known to influence behavior, morphology, and physiology in other primate species. Yet despite the profound seasonal importance of underground storage organs for geladas, little attention has been given to the abundance, distribution, or foraging effort required to extract these food resources. While previous studies have acknowledged geladas' specialized behavioral and morphological adaptations to utilize all parts of the grasses (Dunbar & Dunbar 1974, Dunbar 1977, Iwamoto 1979, Iwamoto 1993), and how this ability enables them to maintain such high biomass in grassland plateaus (Crook 1966), the effects of underground food availability on gelada behavioral ecology have not been quantified. Gelada diet has been oversimplified to encompass only green grass leaf availability; this basic assumption underlies many studies which

have hypotheses about population density (Crook 1966, Dunbar 1977, Iwamoto 1993), ranging (Dunbar & Dunbar 1974), grouping patterns (Pappano et al. 2012), and female feeding competition and social relationships (Wrangham 1980). This has led to the assumption that grasses are the only food that has shaped gelada evolutionary and behavioral ecology. This is unlikely to be the case for geladas.

Unanswered questions. There remain several unanswered questions related to gelada fallback foods. First, more detailed research on specific species and plant parts of underground foods eaten will help illuminate whether geladas exhibit preferences for specific types of underground foods. There is some evidence that geladas consume underground foods from different species in the wet and dry seasons (Dunbar 1977); for example, rhizome nodules of *Meredera abyssinica* found in soil samples were only consumed by the geladas during the wet season (Hunter 2001). Whether the consumption of all underground food items is due to relative availability or preference remains a question that deserves further study.

Second, in addition to underground foods, Venkataraman and colleagues (2014) suggested another candidate as a fallback food for geladas: the blades of *Festuca macrophylla,* a common tussock grass species in the Ethiopian highlands (Puff & Nemomissa, 2005). The data from this study are not resolved to the species level to test the relationship between preferred food availability and consumption of *F. macrophylla*, but I did observe geladas feeding on blades of this species only in the dry season, which supports observations made at Sankaber (Dunbar 1977) and the Guassa Conservation Area (Venkataraman et al. 2014).

Finally, in this study cumulative precipitation for the previous 1-3 months proved a reliable proxy for green grass availability – and therefore the consumption of underground foods. In drier years, geladas will rely more heavily on underground storage organs than in wetter years, which was the case when comparing dry season diets between the current study and the study by Hunter (2001). Further, the length of the rainy season should also influence underground food consumption. Geladas should spend more time eating underground foods in more months when the rainy season is short, compared to years with more months experiencing high rainfall. The relationship between elevation and underground food consumption deserves to be further explored. Particularly since geladas are highly constrained by time they can dedicate to foraging as elevation increases (Dunbar et al. 2009). This is of concern in areas of high altitude that are

heavily grazed by livestock. Geladas may not be able to cope with the severe reduction of grasses at the upper limits of their suitable habitat.

Conclusion

I demonstrated that underground storage organs are a fallback food for geladas. Geladas depend more on underground storage organs when green grass blades are scarce. The role that underground foods play in shaping gelada socioecology has largely been ignored and should be investigated in future research. Spatial and temporal patterns of underground food abundance, distribution, and the subsequent effects on behavior should be examined closely to gain a better understanding of gelada behavioral and evolutionary ecology.
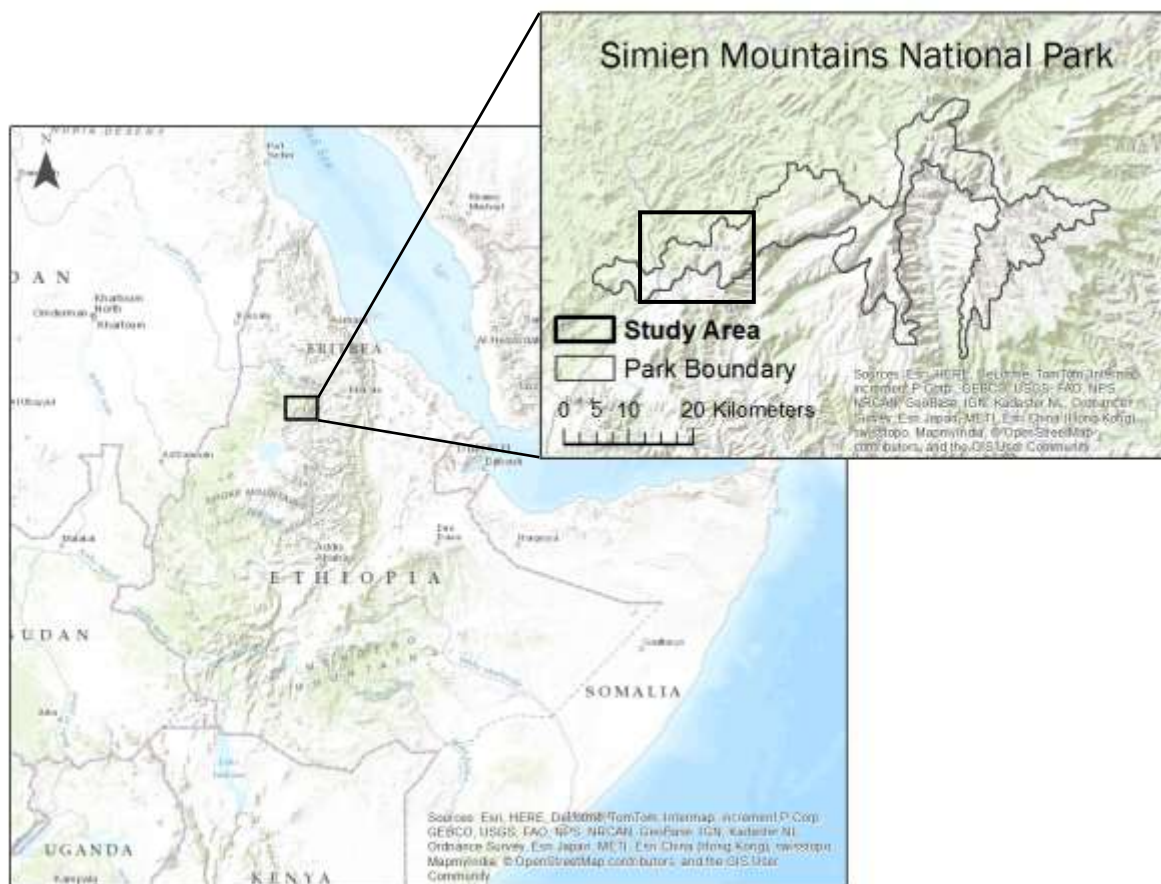
Chapter 1: Figures and tables

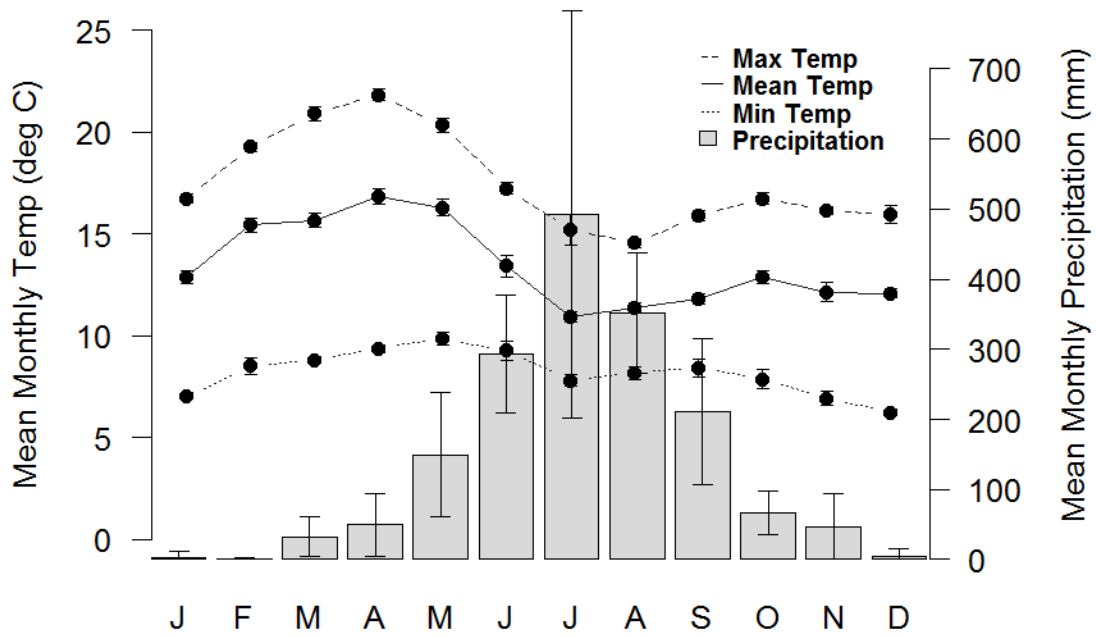**Figure 1.1.** I conducted the study in the Sankaber region in the Simien Mountains National Park, Ethiopia.

Figure 1.2. Mean monthly temperatures (± SEM), and mean cumulative monthly precipitation in Sankaber (± SD), from January 2006-January 2016). The rainy season typically occurs from June to October, and the dry season typically occurs from November to May.
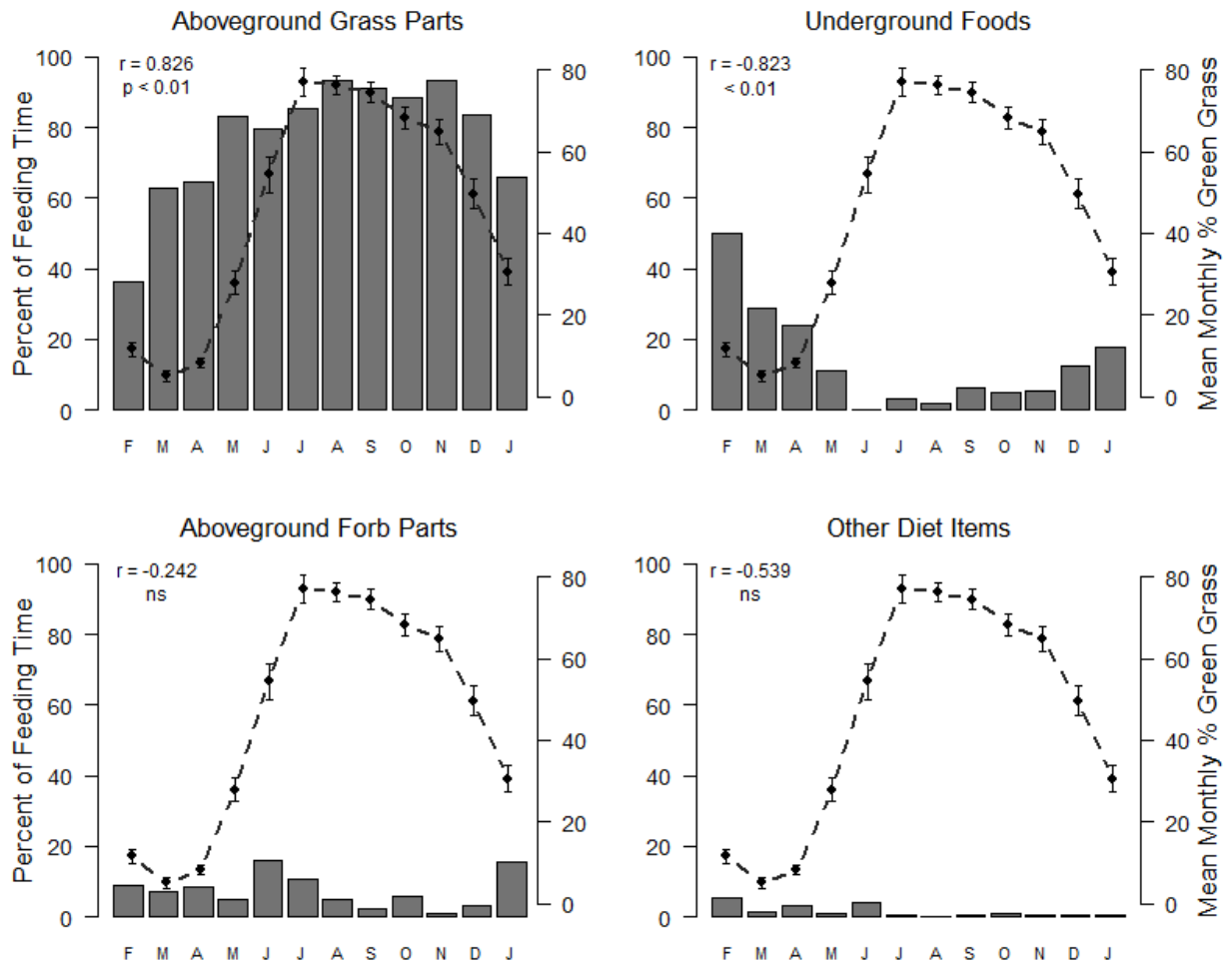
Figure 1.3. Monthly feeding records for aboveground graminoid parts (grasses and sedges), underground foods, aboveground forbs parts, and other diet items in relation to mean monthly green grass availability. Bars depict percent of feeding time; dots depict the mean monthly percent green grass (±SEM). Geladas foraged mainly on grasses throughout the year, but shifted to spending more foraging time on underground foods from December to May.
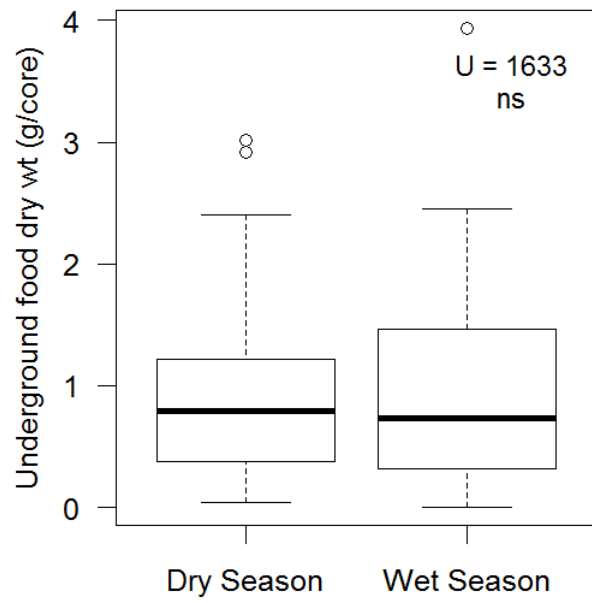
Figure 1.4. Dry weights (g/6.35 cm^2, or g/core) of underground food from soil cores collected in the dry and wet seasons.

Table 1.1. Percent monthly feeding time of diet categories by geladas in Sankaber from January, 2015 – January, 2016.

Month	# feeding scans	Grass	Forb	Underground	Other
Jan-15	270	35.9%	3.7%	58.9%	1.5%
Feb	518	36.1%	8.7%	49.8%	5.4%
Mar	941	62.8%	7.1%	28.7%	1.4%
Apr	788	64.7%	8.2%	24.0%	3.0%
May	590	83.1%	4.9%	11.0%	1.0%
Jun	676	79.7%	16.1%	0.0%	4.1%
Jul	753	85.5%	10.8%	3.1%	0.7%
Aug	59	93.2%	5.1%	1.7%	0.0%
Sep	659	91.2%	2.3%	6.2%	0.3%
Oct	673	88.3%	5.9%	4.8%	1.0%
Nov	557	93.4%	0.7%	5.4%	0.5%
Dec	579	83.8%	3.1%	12.6%	0.5%
Jan-16	470	66.0%	15.5%	17.9%	0.6%

Table 1.2. Summary of annual and seasonal gelada diets from published gelada feeding ecology studies modeled after Fashing et al. 2014. Diet items were collapsed into four feeding categories. All studies used instantaneous scan samples (Altmann 1974) to represent percent of feeding time.

Study Site	Elevation	# study months	Annual Diet				Wet Season				Dry Season			
			Grass	Forb	Under-ground	Other	Grass	Forb	Under-ground	Other	Grass	Forb	Under-ground	Other
1. Bole	2300	6	96.6	0.5	0.5	2.4	-	-	-	-	-	-	-	-
2. Gich, SMNP	3900	3	68.8	15.7	10.5	5.1	81.3	8.7	10.0	0.0	61.1	23.8	14.9	0.2
3. Guassa Conserv. Area	3450	15	50.6	28.7	11.5	9.2	69.6	21.0	5.5	3.9	46.8	32.3	18.0	2.8
4. Sankaber, SMNP	3250	5	58.6	4.4	35.3	1.7	93.0	0.5	3.3	3.2	28.8	2.8	63.0	5.4
5. Sankaber, SMNP	3250	6	55.2	5.6	32.4	6.9	85.6	2.1	8.2	4.1	28.3	9.0	56.6	6.0
6. Sankaber, SMNP	3250	13	75.5	7.8	15.2	1.5	85.5	8.3	4.8	1.4	65.6	7.6	25.2	1.6

1. Dunbar & Dunbar 1974

2. Iwamoto 1979, 1993

3. Fashing et al. 2014

4. Dunbar 1977

5. Hunter 2001

6. this study, 2015 data

Chapter 2
How underground foods, seasonality, and dominance rank influence female aggression

Introduction

  Understanding the selective forces that cause primates to live in groups and shape social relationships has been a fundamental topic in primate behavioral ecology for decades. Primatologists have developed and refined socioecological models with the goal of understanding how ecological pressures shape primate social systems (e.g., Crook & Gartlan 1966, Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck et al. 1997). Much research has focused on the relationships between ecological pressures and female social structure because female reproductive success is limited by access to food resources and environmental risk, in contrast to male reproductive success, which is limited by access to receptive females (Wrangham 1980, Koenig 2002).

  The spatial and temporal abundance and distribution of food resources are primary factors that shape the social relationships among females within and between groups (Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck et al. 1997). When limiting foods are high-quality, clumped, and defensible, females are predicted to live in philopatric groups to defend food resources collectively from other groups (Wrangham 1980). Competition over clumped foods is expected to be directly via "contest competition" (i.e., monopolization and overt aggression over food resources, and rank-related differences in food acquisition and energy intake; Isbell 1991, Saito 1996, Vogel 2005). If clumped resources are distributed in patches that are not large enough to accommodate the entire group, or there is variation in food abundance or quality within patches, females are expected to compete over food within their own group and develop a despotic, linear dominance hierarchy to aid in these contests (Isbell 1991, Sterck et al. 1997). In contrast, females in species that consume food resources that are evenly-distributed, non-defensible, or extremely rare, are expected to compete indirectly via "scramble competition" (i.e., individuals have equal access to food, but energy intake rates decrease with increasing group size; van Schaik & van Noordwijk 1988). These females, in turn, are expected to develop a more egalitarian social structure, with low levels of aggression and a weak or non-existent dominance hierarchy, possibly characterized by female dispersal (van Schaik 1989).

Socioecological models have been moderately successful in explaining female social relationships in many species. For example, vervets (*Chlorocebus aethiopis*) had higher rates of food-related aggression and stricter dominance hierarchies when feeding in habitats where resources were relatively limited and clumped (Pruetz & Isbell 2000). Feeding competition among olive baboon females (*Papio anubis*) increased in the dry season, when food patches become scarce, and are spatially clumped (Barton & Whiten 1993, Johnson 1989). Contest competition increased among female chimpanzee (*Pan troglodytes*) when food resources became defensible and group size increased (Wittig & Boesch 2003).

Although this theoretical framework has provided sufficient explanations for the social structure and competitive regimes of a number of primate species, there remain many perplexing examples of species where female social relationships do not fit the predictions of socioecological models. Geladas (*Theropithecus gelada*) have been one of the most frustrating examples.

Based on the gelada's primary food source – grass blades (a low quality, evenly distributed resource) – any socioecological model would predict that the female gelada social structure should be egalitarian, with no female philopatry and weak dominance relationships (e.g., Isbell 1991, Sterck et al. 1997). Yet, in stark contrast with this prediction, female geladas exhibit overt aggression and form matrilineal societies with strict, linear, nepotistic dominance hierarchies (le Roux et al. 2011; Tinsley Johnson et al. 2014). This apparent mismatch between social structure and ecology has offered a challenge to socioecological models. Competition and aggression in geladas are costly behaviors, so, if grasses are not "worth" fighting over, then why do female geladas exhibit high rates of aggression? And, why do females have a strong, linear dominance hierarchy?

I propose that this conundrum can be solved with a closer examination of the gelada diet. As discussed in chapter 1, geladas consume primarily green grass blades, but also consume other plant species and plant parts; they also show considerable seasonal variation in the relative proportions of time spent consuming diet items (Dunbar 1977, Iwamoto 1979, Hunter 2001, Fashing et al. 2014). Most notably, during the dry season, geladas shift their dietary focus and rely heavily on underground foods. This occurs both in our population but also across a number of other gelada feeding studies (see chapter 1). Therefore, underground foods are an important

fallback food for geladas. However, underground foods have heretofore not been included in models of gelada socioecology, and predictions were formed under the assumption that geladas eat only grasses, and thus this widely dispersed resource would be the only food item that influenced gelada female competitive regimes and social relationships (Wrangham 1980).

The modular structure of gelada social organization further complicates gelada socioecology, because there are multiple levels at which to assess social relationships. Unlike most primates, geladas have a fluid, multi-tiered social system (see chapter 1), and are constantly surrounded by others within the same unit, as well as individuals from other units (Snyder-Mackler et al. 2012). Geladas are extremely tolerant of and show a considerable degree of spatial overlap with extra-group individuals (Snyder-Mackler et al. 2012, Tinsley Johnson et al. 2014). While the abundance and distribution of grasses enable geladas to associate in such large groups (Crook 1966, Gaulin 1979), it does not explain why females are philopatric or form linear dominance hierarchies.

Here, I investigate the nature of female competition in a population of wild geladas. My main objective is to solve the gelada paradox with respect to socioecology – why might female geladas have a dominance hierarchy? Is there a more contestable resource than grass that they are fighting over? I focus on female aggression with respect to season, behavioral context, and whether the aggression takes place within or between units. I test the effects of dominance rank, season, and behavioral state on the likelihood of receiving aggression using 13 months of behavioral data from adult females.

Underground foods are fallback foods, but they are absolutely necessary to get geladas through the dry season. These foods require a high degree of processing: because they must be dug up, and digging takes time (Hunter 2001). Therefore, although these underground foods are available year-round (refer to chapter 1), they are not worth digging up until green grass is unavailable.

Importantly, once a hole has been dug, the exposed underground storage organ becomes a clumped, defensible resource – only made available by the act of digging. Although this idea is not new (e.g., Johnson 1989) this is the first time this idea has been applied to gelada socioecology and the exposure of underground foods through digging. Therefore, I propose to examine whether female aggression is used primarily in the context of fighting over underground

foods. Specifically, I predict that females will receive more aggression (1) within units, (2) during the dry season, (3) in a feeding context, while feeding on underground food items, and (4) when low-ranking.

Methods

Study species and site

I conducted this study in the Sankaber region of the Simien Mountains National Park, Ethiopia as part of the University of Michigan Gelada Research Project, which has been collecting behavioral and demographic data on a population of habituated wild geladas since 2006. All geladas are habituated to human observers and individually recognized by natural markings. The site is described more completely in Chapter 1. The Simien Mountains have a wet and dry season. Months with less than 400 mm of cumulative rainfall from the previous 90 days were considered "dry season" months (January-April, 2015 and October-January, 2016) and the rest were considered "wet season" months (June-November, 2015).

Behavioral data

I collected behavioral data using instantaneous scan samples (Altmann 1974) at 10-minute intervals during focal unit follows from adult females across 7 one-male units (n=32 females) from January 2015 to January 2016 (n=8545 scans; dry season, n=4895 scans; wet season, n=3650 scans); (C. Hawley collected all data from Aug 2015 – Jan 2016). Females that reached maturation during the dry season (≤ 4 months into the study) were included in the analyses. During each scan, I categorized each female that was visible as in one of three behavioral contexts: (1) aboveground feeding, (2) underground feeding, and (3) not feeding. An individual was considered feeding if she was searching for, handling, chewing, or swallowing food items.

I collected all occurrences of dyadic within- and between-unit aggression (i.e., visual threats, vocal threats, physical attacks, and supplants) between all adult females during focal sampling (within-unit events, n=323; between-unit events, n=123). Distance between the actor and recipient of the aggression was estimated in meters. Because aggression is instantaneous and unlikely to be captured in a group scan, I collected continuous data on aggression between scan samples. If a female was the recipient of aggression during this period, I then matched this

event to the closest previous scan sample recorded (if it occurred within the last 10 minutes) and that scan was scored as having either within- or between- unit aggression occur. I considered the behavioral context of that scan as the context of the event.

Dominance rank

Because the effects of within-group contest competition are highly dependent on dominance rank (van Schaik 1989, Janson & van Schaik 1988, Koenig 2002), I calculated each female's rank using the Elo-rating system (Elo 1978), in the EloRating package v 0.43 (Neumann & Kulik 2014) in R v 3.3.1 (R Core Team 2016). Elo-ratings depend on how many interactions were observed and require some start up time before calculating reliable hierarchies (Neumann et al. 2011). To account for this, I used all dyadic within-unit aggressive events between adult females observed from the long-term project (data from 2009-2014) to establish a baseline rating for all individuals, and used these ratings at the starting points to calculate Elo-rating for each female during the study period. Date of maturation was used as the start time for Elo-rating calculation of all females that matured during the study. I calculated the average Elo-rating of each female using the Elo-ratings during the study period. For the models, I used the z-score of the average Elo-rating for each female (standardized around the ratings of all females in the focal female's unit, since rank relationships are established among females within a group).

Statistical models

I used generalized linear mixed models (GLMMs) to examine the effects of three covariates – dominance rank (Elo-rating), behavioral context (aboveground feeding, underground feeding, not feeding), and season (wet / dry) on a female's probability of receiving aggression (outcome variable: aggression received or not). I fit models for within-unit aggression and between-unit aggression separately. Unit and individual were included as random effects in all models to account for variation among units and individuals. All models were fit using the 'glmer' function in the lme4 package v 1.1-12 (Bates et al. 2015), using the binomial distribution and the logit link function. I compared univariate and multivariate models to assess whether one, a combination, or all covariates resulted in the best-fit model for the probability of female aggression. I then compared these models to a random-effects only model, to test whether these variables improved the model fit compared to the inherent variation among individuals and units. I used Akaike's Information Criterion (AIC) and Akaike model weights to select the best-fit

model with the 'AICtab' function in the bbmle package, version 1.0.18 (Bolker & R Development Core Team 2016).

Results

Within-unit and between-unit aggression

Females were more likely to receive aggression from females within their unit compared to aggression from females in other units (Figure 2.1). When comparing probabilities predicted from the models, high-ranking females were about equally likely to receive aggression from within- and between-unit females, however, low-ranking females were much more likely to receive within-unit aggression than between-unit aggression (Figure 2.1). Within-unit aggression occurred at closer distances than between-unit aggression (Mann-Whitney U test, W=106900, p<0.001). The median distance between individuals during within-unit aggressive interactions was 0.5 m (mean=0.87 m); the median distance between females during between-unit aggressive interactions was 1.5 m (mean=2.52 m) (Figure 2.2).

Within-unit aggression

The best-fit model for predicting within-unit aggression included behavioral context, season, and rank (Table 2.1): AIC=2487.5, ΔAIC=0.0, AIC weight=1 (Table 2.2). Females were more likely to receive within-unit aggression in the dry season (β=0.58±0.14), when feeding on underground foods (β=1.35±0.16), and when low-ranking (β=-0.93±0.15), (Table 2.1, Figure 2.3.a, 2.4.a).

Between-unit aggression

The best-fit model for predicting between-unit aggression also included behavioral context, season, and rank (Table 2.1), AIC=1253.0, ΔAIC=0.0, AIC weight=0.748 (Table 2.3). The second-ranked model for between-unit aggression included context and season, but not rank, as a predictor: AIC=1255.3, ΔAIC=2.3, AIC weight=0.236 (Table 2.3). Females were more likely to receive between-unit aggression in the dry season (β=0.95±0.22), when feeding on both aboveground foods (β=0.69±0.22) and underground foods (β=0.80±0.29), and when low-ranking, but the effect size of rank was small, and the confidence interval contains zero (β=-0.22±0.11) (Table 2.1, 2.3.b, 2.4.b).

Discussion

The results of this study supported all of the predictions. First, females were more likely to receive aggression from the females within their own unit than from females outside their unit, but only for low-ranking females. Second, aggression was highest during the dry season when geladas were *not* feeding on their preferred and widely-dispersed resource (grass) but rather were feeding on the fallback foods found underground. Furthermore, in support of the idea that females were fighting over these resources, aggression was higher during a feeding context and even more so when the feeding was on underground food items. Finally, low-ranking females were the most likely to receive aggression in these contexts. Therefore, the results of this study support the hypothesis that female aggression (and the dominance hierarchy that ensues) functions to secure access to underground foods.

Within-unit aggression

Among female geladas, I observed more within-unit aggression than between-unit aggression. Unsurprisingly, low-ranking females received the most aggression. Seasonality and behavioral context had strong effects on within-unit aggression. Females were substantially more likely to receive aggression from within their unit when foraging for underground foods, compared to feeding on aboveground foods and not feeding. This supports the hypothesis that geladas do exhibit contest competition, but that this competition is *not* over preferred foods (e.g., grass blades and forb leaves). Instead, females are competing over underground foods, an important "fallback" food in the dry season (chapter 1). Similar results have been found in female baboons: supplants occurred significantly more than expected among female baboons when feeding on corms, but less or equally as often as expected when feeding on grass or not feeding (Johnson 1989). Mountain gorillas (*Gorilla beringei beringei*) have also been reported to exhibit contest competition over nonreproductive plant parts, which are fallback foods (Wright et al. 2014). These results support the increasing evidence that fallback foods can be contestable and influence feeding competition and social relationships.

As discussed in chapter 1, underground foods represent a major part of the geladas' dry season diet. However, the models accounted for the seasonal variation in aggression. Beyond that

variation, foraging for underground foods still increased the odds of receiving aggression, regardless of season. This suggests that underground foods are a contestable food at *all* times of the year, even when green grass blades are widely abundant. In other words, the nutritional rewards of underground food items are valuable year-round, which may be explained by the differences in distribution and nutritional qualities of gelada diet items.

Foraging efforts for aboveground and underground foods vary both in what is required to obtain those foods, and the nutritional rewards gained from them. Foraging for grasses yields roughly half the caloric intake rate in the dry season compared to the wet season (Hunter 2001). On the other hand, foraging for belowground foods yields, on average, twice the caloric intake rate as foraging for grass in the dry season, and the same caloric intake rate as foraging on grass in the wet season (Hunter 2001).

However, geladas can only increase foraging efficiency of grasses by foraging faster, or finding patches with longer or a higher proportion of green grasses. There is little or nothing to gain by defending a specific patch of grass since this is a dispersed, and relatively abundant food resource. On the other hand, foraging efficiency of underground foods can be increased by digging faster, or supplanting another individual that has already excavated a hole, and thus cutting out foraging time and energy while still gaining food resources. In other words, females increase foraging efficiency of grasses through scramble competition, but increase foraging efficiency of underground foods through contest competition. Females may benefit from usurping underground resources year-round. Thus, underground foods may actually be preferred foods. There is some evidence that the availability of certain types of underground foods fluctuates seasonally. Rhizome nodules of *Meredera abyssinica* were only found in soil samples and consumed by geladas during the wet season (Hunter 2001). Future research should investigate the nutritional quality and seasonal availability of different types of underground plant storage organs.

Between-unit aggression

Between-unit aggression was low overall among female geladas, and had little to do with dominance rank. This is not surprising, because dominance relationships are established only among females within a unit. Due to the stable linear dominance hierarchies, the "winner" of within-unit interactions is relatively predictable, and females can target other individuals that

rank below them. By contrast, as yet, we have no evidence that females recognize the dominance ranks of females in other units. Further, we have no evidence that the units themselves are "ranked" in any order. However, both these findings remain untested and are therefore possible. Even if females do not recognize the relative ranks of other females outside of their unit, attempting to supplant or threaten a between-unit female has the potential to be more disruptive than a within-unit conflict because all of the females in the unit often intervene on behalf of the subjects. Because I only investigated dyadic interactions, and many between-unit interactions involved coalitionary support from group members, these results may have underestimated between-unit aggression overall. A detailed investigation of these events may provide additional insight to the factors that influence between-unit aggression. High-ranking females may have been slightly less likely to receive between-aggression because they were more centrally located within their unit and had less overlap with between-unit individual, or because there is some degree of rank, or individual recognition by between-unit females. These ideas remain to be tested.

Between-unit aggression increased in the dry season, but this is unlikely to be food-related, because geladas consume only 1-3% of plant biomass (Crook 1966). Geladas are probably not limited by food, but rather by the time needed to forage (Iwamoto & Dunbar 1983, Dunbar et al. 2009). Alternatively, the seasonal increase in between-unit aggression may be influenced by social factors that cause geladas to forage at closer distances than tolerable. For example, spacing among geladas within a unit and between units decreases when bachelor males are present (Pappano et al. 2012), which may force geladas to forage closer to each other, and at higher densities, than tolerable. Because bachelors challenge leader males more frequently in the dry season, causing increased social turmoil (Pappano & Beehner 2014), females may pass some of this aggression along to one another.

Thus, geladas may face a tradeoff in the dry season between reducing scramble competition and reducing the risk of a challenge or takeover. Additionally, this study population spends a large amount of time foraging in agricultural fields, and among domestic livestock, and come into frequent conflict with humans, particularly in the dry season, during planting and harvesting (personal observation). These conflicts with humans may also force geladas to forage at closer distances, and cause increased aggression.

Females were only slightly more likely to receive aggression from females outside of their unit when they were feeding, compared to not feeding. This result supports socioecological model predictions, and previous observations that between-unit competition is low among female geladas (Mori 1979, Wrangham 1980). Further investigation on spatial position and proximity relative to between-unit individuals may provide additional insight into understanding the factors that influence between-unit aggression.

The gelada paradox. This study highlights the proximate benefits of dominance in female geladas – access to calorically-rich food resources while saving foraging effort and time. Rank has been linked to ultimate benefits such as increased energy intake and expenditure (Janson 1985, Vogel 2005, Wright et al. 2014), increased reproductive success (Whitten 1983, Harcourt 1989, Holekamp et al. 1996, Pusey et al. 1997, van Noordwijk & van Schaik 1999), and lower rate of parasite infections (Foerster et al. 2015).

Contest competition is traditionally argued to be over food resources that are distributed in discrete, well-defined patches (e.g., fruiting tree) that can be monopolized or usurped (Wrangham 1980, van Schaik 1989). Food patches, however, may not need to be *spatially* or *temporally* clumped to be monopolized. Underground food resources, consumed by geladas, are a prime example. Underground foods are not distributed in spatially discrete, defensible patches; furthermore, they are available year-round. Yet, the foraging effort that must be invested to expose and then extract these underground resources can be defended or usurped (i.e. the hole an individual has excavated). This hole represents an investment of time, energy, and a level of uncertainty as to whether the effort will uncover a valuable food resource, all of which can be eliminated or reduced for a high-ranking individual that can acquire the "patch" without investing any of the effort. Therefore, the excavation itself is the contested resource.

Conclusion

This study provides evidence that female gelada social structure does fit within the predictions of socioecological models, when we have more detailed analyses of foraging. Females exhibit contest competition over fallback foods, rather than preferred foods. For female geladas, there may be a benefit to dominance – saving valuable time and energetic costs on foraging, while still having access to those food resources, particularly in a time of resource

scarcity and potential nutritional stress. This study highlights the importance of considering the effect fallback foods in shaping female social relationships.

Limitations & Future Directions

Phylogenetic inertia. These results do not entirely dismiss the possibility that female gelada social structure has been preserved through phylogenetic inertia (Di Fiore & Rendall 1994). To address the role of phylogeny in gelada social structure, future research should investigate the intensity and context of female aggression among an interbreeding population of geladas under different ecological conditions (as proposed by Chapman & Rothman 2009) to assess the role that ecology plays in shaping social structure. Comparing aggression rates across populations merits future research, since the dependence on underground foods is quite variable across elevation and ecological conditions (as discussed in chapter 1).

Spatial variation in food quality and availability. I did not consider the potential variation within diet categories (e.g., the relative nutritional quality among grass species and leaf stages; Koenig et al. 1998) or the spatial variability in food resource abundance and distribution within habitats and patches (Phillips 1995). Both nutritional and spatial variation could influence aggression among female geladas, and should be quantified from the perspective of individuals (Vogel & Janson 2011).

Considering multiple levels of association. A limitation to this study was that I did not consider differences in aggression at all levels of the gelada social system. While social relationships are confined to within-unit individuals, unit association patterns are not random. Units form multiple levels of association: teams (recently fissioned units), and bands are groups of units that regularly associate with each other (Snyder-Mackler et al. 2012). Units may be more tolerant of units that they regularly associate with, and be more at risk of receiving aggression from units that do not regularly associate with them. That is, the likelihood of receiving aggression from between-unit females may be conditional on the identity of the unit. I was not able to account for this potential variation, since 6 of the 7 study units were members of the same band, and 2 units were daughter units that had previously fissioned from the same unit. Future research should investigate the effects that team and band identity may have on female aggression.

Chapter 2: Figures and tables

Table 2.1. Results of the within-unit and between-unit received aggression models. Feeding behavior, season, and dominance rank (Elo-rating) were all significant predictors of within- and between-unit aggression.

Predictors	*Within-Unit Aggression Model* β ± SE	p-value	*Between-Unit Aggression Model* β ± SE	p-value
Intercept	-4.60 (0.30)	<0.001	-5.34 (0.29)	<0.001
Aboveground Feeding	0.15 (0.14)	0.279[a]	0.69 (0.22)	0.002[a]
Underground Feeding	1.35 (0.16)	<0.001[a]	0.80 (0.29)	0.006[a]
Dry Season	0.58 (0.14)	<0.001[b]	0.95 (0.22)	<0.001[b]
Elo-rating	-0.93 (0.15)	<0.001	-0.22 (0.11)	0.040

[a] Above and underground feeding scans were compared to non-feeding

[b] Dry season scans were compared to wet season scans.

Table 2.2. Results of model comparison of all models fit for within-unit aggression. Models are ordered by ΔAIC.

Model	Model Description	Syntax (aggression received ~)	df	AIC	ΔAIC	AIC weight
m1	context + season + Elo-rating + Unit/ID (random effects)	context + season + Elo-rating + (1|Unit/ID)	7	2487.5	0.0	1
m4	context + Elo-rating + Unit/ID (random effects)	context + Elo-rating + (1|Unit/ID)	6	2503.7	16.2	<0.001
m7	context + season + Unit/ID (random effects)	context + season + (1|Unit/ID)	6	2514.7	27.2	<0.001
m6	context + Unit/ID (random effects)	context + (1|Unit/ID)	5	2531.2	43.7	<0.001
m3	season + Elo-rating + Unit/ID (random effects)	season + Elo-rating + (1|Unit/ID)	5	2559.2	71.7	<0.001
m5	season + Unit/ID (random effects)	season + (1|Unit/ID)	4	2585.8	98.3	<0.001
m2	Elo-rating + Unit/ID (random effects)	Elo-rating + (1|Unit/ID)	4	2600.3	112.8	<0.001
m0	Intercept + Unit/ID (random effects)	(1|Unit/ID)	3	2627.2	139.7	<0.001

Table 2.3. Results of model comparison of all models fit for between-unit aggression. Models are ordered by ΔAIC.

Model	Model Description	Syntax (aggression received ~)	df	AIC	ΔAIC	AIC weight
m1	context + season + Elo-rating + Unit/ID (random effects)	context + season + Elo-rating + (1|Unit/ID)	7	1253.0	0.0	0.7477
m7	context + season + Unit/ID (random effects)	context + season + (1|Unit/ID)	6	1255.3	2.3	0.2364
m3	season + Elo-rating + Unit/ID (random effects)	season + Elo-rating + (1|Unit/ID)	5	1261.2	8.2	0.0123
m5	season + Unit/ID (random effects)	season + (1|Unit/ID)	4	1263.7	10.7	0.0035
m4	context + Elo-rating + Unit/ID (random effects)	context + Elo-rating + (1|Unit/ID)	6	1271.3	18.3	<0.001
m6	context + Unit/ID (random effects)	context + (1|Unit/ID)	5	1273.5	20.5	<0.001
m2	Elo-rating + Unit/ID (random effects)	Elo-rating + (1|Unit/ID)	4	1282.1	29.1	<0.001
m0	Intercept + Unit/ID (random effects)	(1|Unit/ID)	3	1284.5	31.5	<0.001

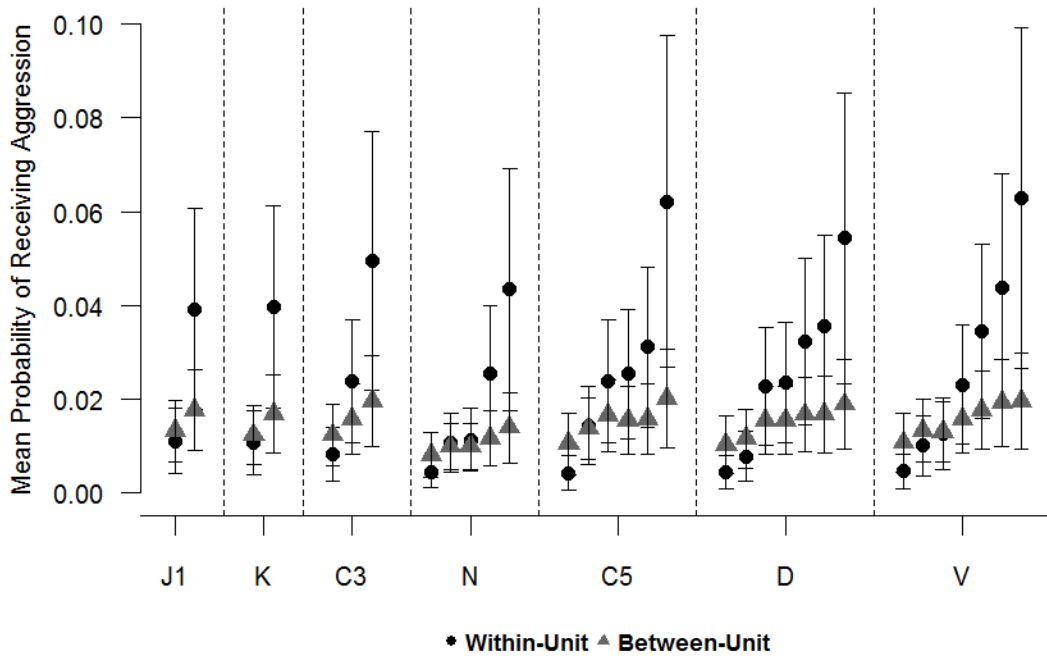**Figure 2.1.** Predicted probabilities (±2*SE) of all females of receiving within-unit (circles) and between-unit (triangles) aggression. Each bar within a group represents an individual female. Females are ordered by unit and Elo-rating (highest-ranked female in each unit is on the far left). Low-ranking females are considerably more likely to receive aggression than high-ranking females.
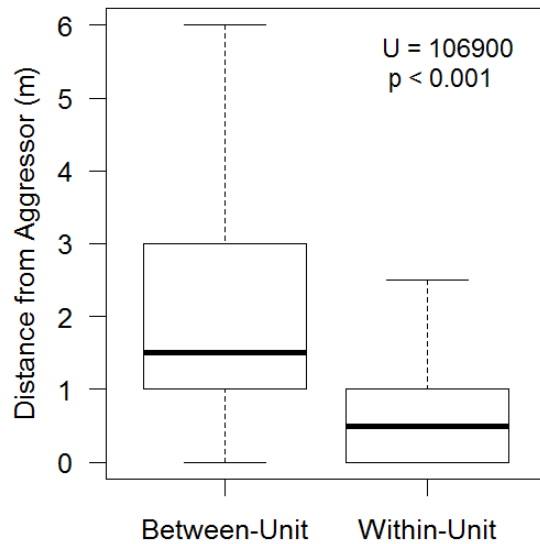

Figure 2.2. Boxplot comparing the distances the actor and recipient of dyadic within-unit and between-unit aggression events.
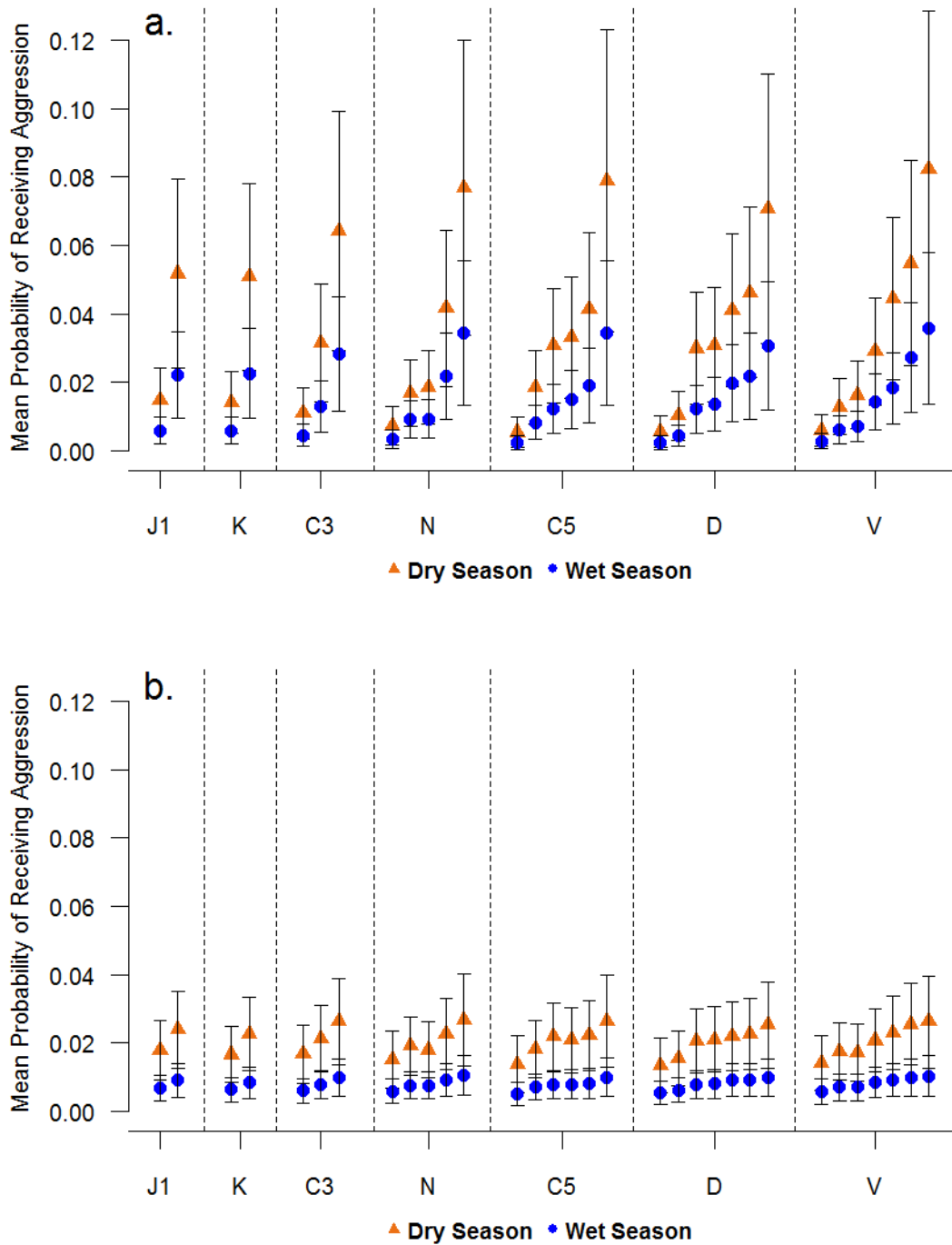
Figure 2.3. a. Predicted probabilities (±2*SE) of all females of receiving within-unit aggression by season. Each bar within a group represents an individual female. Females are ordered by unit and Elo-rating (highest-ranked female in each unit is on the far left), **b.** Predicted probabilities (±2*SE) of all females of receiving between-unit aggression by season. Each bar within a group represents an individual female. Females are ordered by unit and Elo-rating (highest-ranked female in each unit is on the far left).
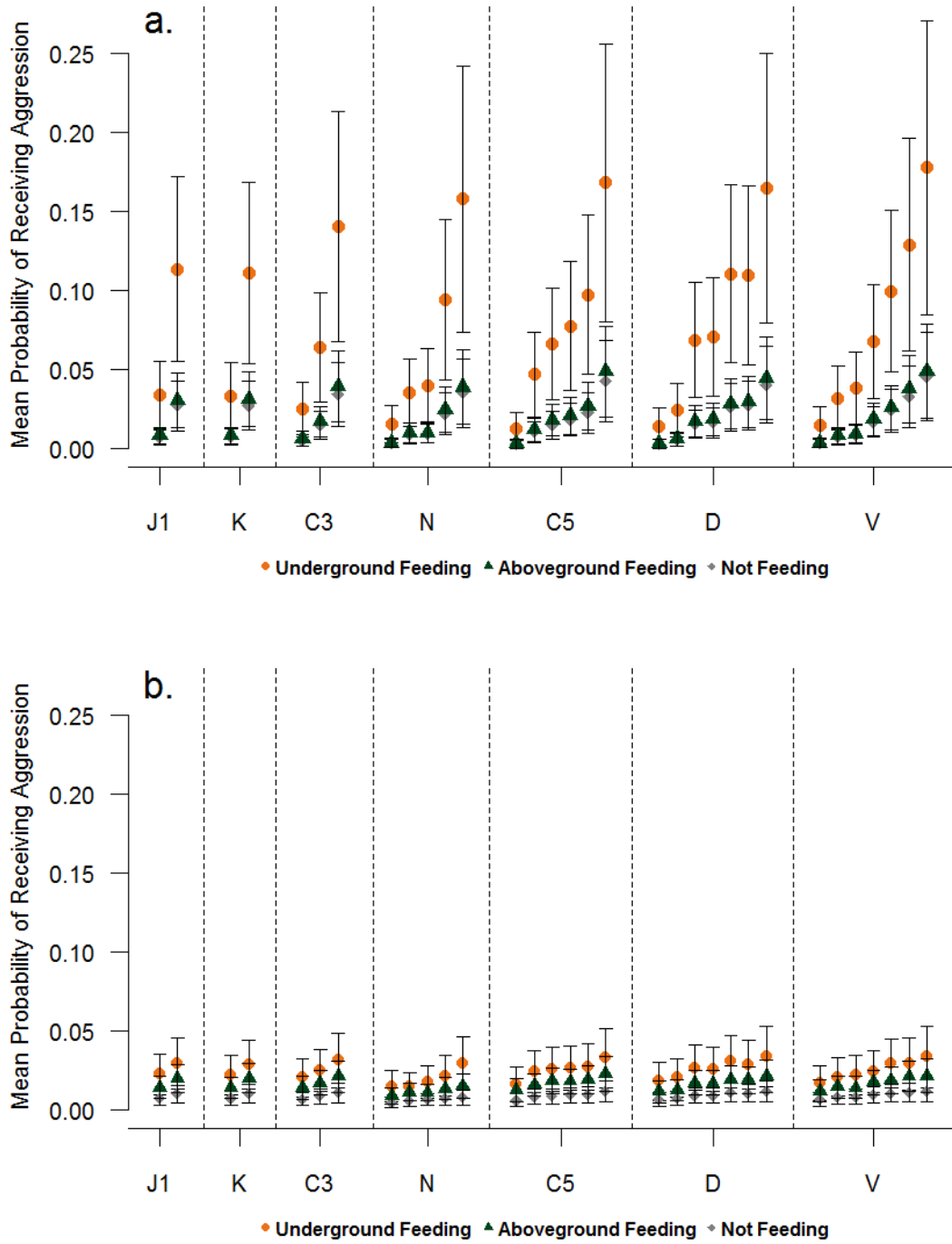
Figure 2.4. a. Predicted probabilities (±2*SE) of all females of receiving within unit-aggression by behavioral context. Each bar within a group represents an individual female. Females are ordered by unit and Elo-rating (highest-ranked female in each unit is on the far left). **b.** Predicted probabilities (±2*SE) of all females of receiving between-unit aggression by behavioral context. Each bar within a group represents an individual female. Females are ordered by unit and Elo-rating (highest-ranked female in each unit is on the far left).

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