Seasonal and altitudinal effects on glucocorticoid metabolites in a wild primate (Theropithecus gelada)

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Abstract

Behavioral ecologists are increasingly adopting sophisticated non-invasive methods for measuring glucocorticoids from "excreta" because samples are easy to collect, animals are left undisturbed, and measures may be more reflective of external events than serum samples. Some of the most common predictors for hormone profiles in wild animals are seasonal changes in ecology and behavior. For example, we might expect baseline glucocorticoid levels to track changes in food availability or other seasonal stressors such as unusually high or low temperatures. Geladas (Theropithecus gelada) are one of the few non-human primates that live at extremely high altitudes where nighttime temperatures often dip below freezing. However, the physiological effects of this relatively inhospitable environment have never been examined in this species. Here we validate a "field-friendly" method of hormone extraction from gelada feces and demonstrate that this method can be used to detect seasonal and altitudinal differences in glucocorticoid metabolites for this species. We use two years of climatological and hormonal data from a wild population of geladas to test the hypothesis that geladas exhibit elevated glucocorticoids under environmentally "challenging" conditions — mainly, when temperatures and rainfall are low and altitude is high. Our results indicate that cold temperatures and high altitude predicted elevated glucocorticoids, but low rainfall did not. Therefore, we suggest a metabolic hypothesis (as opposed to a nutritional hypothesis) to explain this result. However, at the present time, we cannot rule out a behavioral stress hypothesis.

1. Introduction

In vertebrates, the concentration of glucocorticoids in plasma is widely used as one indicator of physiological stress [1–5]. However, much like Heisenberg's uncertainty principle, it can be difficult to obtain accurate glucocorticoid values from serum because the invasive process of drawing blood can itself induce a stress response — thus, changing the variable of interest. This "observer effect" is due to the transient nature of plasma glucocorticoid values, which rise with the onset of a stressor within 2–3 min. Particularly for studies of wild animals (where habituation or training to blood draws is not a feasible option), it is optimal to have non-invasive alternatives for measuring hormones. Consequently, sophisticated methods have been developed for measuring glucocorticoids from "excreta" [6] — mainly, urine [7–10] and feces [11] — but increasingly also saliva [14–16]. In many cases, such samples can be collected easily and without disturbing an animal, thereby allowing frequent sampling over long time periods. Furthermore, because collection protocols are non-invasive, animal welfare considerations are minimal and special permits and/or animal handling expertise are usually not required. Moreover, because fecal sampling has been shown to smooth short-term fluctuations and diurnal variation, fecal measures can actually improve the ability to distinguish between normal pulsatile changes and genuine physiological responses to external events [17]. It is not surprising, therefore, that behavioral ecologists are increasingly adopting such methods to incorporate hormonal measurements into their long-term studies.

Nevertheless, for such non-invasive methods to be utilized in a new species, proper validation is critical [6,18–20]. There are three steps involved in validation. First, because hormones (or, more accurately, their metabolites) extracted from excreta represent “downstream” products of normal metabolism, one must identify the metabolized hormone products present in the sample. Second, it must be established that the relative amounts of the measured metabolized product either (a) reflect levels of the circulating hormone in the blood [but see 6 for problems with this validation technique], or (b) reflect a pharmacological stimulation (e.g., an ACTH challenge) or suppression of the circulating hormone. Third, as with conventional plasma hormone assays, an appropriate antibody that demonstrates cross-reactivity with the hormone of interest (or its metabolites) must be analytically validated to demonstrate parallelism (or dilutional linearity), accuracy, and precision prior to general use.
field workers, an additional consideration, is the feasibility of a particular method for use in a field setting. For example, many methods require samples to be frozen or dried within 2 h of collection. This requirement can hamper the simultaneous collection of behavioral data. Thus, methods that allow behavioral sampling to continue relatively uninterrupted by hormone sampling might be particularly useful.

Some of the most common predictors for hormone profiles in wild animals are seasonal changes in ecology and behavior. In seasonal breeders, we expect to find an increase in gonadal activity prior to the onset of breeding. However, in both seasonal and non-seasonal breeders, we might also expect baseline glucocorticoid levels to track changes in food availability or other seasonal stressors such as unusually high or low temperatures. Indeed, nutritional stress, heat stress, and cold stress have been associated with elevated glucocorticoids in a variety of species [21–32]. For many behavioral ecologists, the link between climatological variables and physiological stress is critical for understanding the adaptive nature of behavioral variables such as migration patterns, mating behavior, and foraging behavior. For example, geladas (close relatives to the well-studied Papio baboons) are one of the few non-human primates that live at extremely high altitudes where nighttime temperatures often fall below freezing [33]. The pressure that these low temperatures impose on thermoregulation in geladas is compounded when coupled with the wind-chill factor and the high levels of humidity, especially during the rainy season [33]. Previous research on wild geladas found that groups spend more time feeding to fulfill their nutritional needs as altitude increases and temperature decreases, presumably due to the metabolic costs of thermoregulation [34]. However, the physiological effects of this relatively inhospitable environment have never been examined in geladas.

Here, we validate a modification of a “field-friendly” method of hormone extraction from fecal samples for a new species—the gelada (Theropithecus gelada). The method is particularly useful for field researchers because it does not require immediate access to a freezer, lyophylizer, or an oven for processing and storing samples. Furthermore, this method has been used to successfully measure glucocorticoid metabolites (GCMs) in close relatives of geladas, the baboons (Papio spp.) [35–37]. Following the validation, we demonstrate that this method can be used to detect seasonal and altitudinal differences in GCMs. Therefore, we will primarily be focused on one form of excreta (feces) and one class of hormones (glucocorticoids). We use two years of climatological and hormonal data from a wild population of geladas that lives at very high altitudes in the mountainous regions of Ethiopia. Geladas are non-seasonal in their breeding, and groups are organized into a multi-leveled society [57]. The smallest levels are (1) the reproductive unit, or harem, comprising a leader male, several adult females and their offspring (and possibly 1–2 follower males) and (2) the bachelor group, comprising only young adult males. Harems and bachelor groups that share a home range are called a band, and bands join together to form herds that can number over 1000 individuals. Geladas are unique among primates in having a highly specialized diet, with over 90% of their diet comprising high-protein fescue grasses [38,39,33]. The geladas modify their diet across the year by utilizing parts below ground (roots and storage organs) during the wet season (May–Oct) and parts below ground (roots and storage organs) during the dry season (Nov–Apr) [33]. With such a restrictive diet, it seems probable that gelada nutrition is affected by rainfall. Additionally, as temperatures drop below freezing during some months of the year, we expect that thermoregulation might be an important problem in this species. Finally, as altitude increases, both ambient temperature and forage quality declines. Therefore, we expect that gelada populations living at higher altitudes will have higher metabolic costs. In the present study, we test the hypothesis that geladas will exhibit elevated GCMs under environmentally “challenging” conditions—mainly, when rainfall and temperatures are low and altitude is high.

2. Methods — validation on captive geladas

2.1. Physiological validation

To validate this method for use on wild geladas, an ACTH challenge was conducted on four captive geladas (2 adult males, 2 adult females), housed at the Wildlife Conservation Society’s Bronx Zoo, Bronx, NY. All captive research was approved by the Wildlife Conservation Society’s Institutional Animal Care and Use Committee (IACUC).

An ACTH challenge involves the administration of ACTH to naturally stimulate the adrenal gland to produce corticosteroids [e.g., 13,40]. To measure baseline GCMs, we collected one fecal sample/morning/subject during the three days prior to ACTH injection. On the day of injection, subjects were shifted individually into a transfer chute with a restraint device where males received 27.6 IU and females received 18.4 IU (administered i.m.) of ACTH suspended in 16% gelatin to provide a prolonged adrenal corticoid release (H.P. ACTHAR gel; Questcor Pharmaceuticals, Inc., Union City, CA). Subjects were not anesthetized prior to injection and routinely entered the transfer chute as part of normal husbandry practices. Due to zoo operating hours, we were unable to collect samples on night and therefore timed the injection to maximize our chances of detecting peak GCM excretion (which, based on their high fiber diet, we anticipated to be earlier than that of baboons at 26 h post-injection). Therefore, between 16–25 h post-injection, we collected all fecal samples excreted by subjects (range: 3–8 samples/subject). For the next three days, we resampled collecting one fecal sample/morning/subject.

2.2. Hormone extraction and storage

Hormones were extracted from feces using a modified version of a method described previously [41,42]. Specifically, within minutes following deposition, the entire fecal sample was mixed thoroughly with a wooden spatula, and an aliquot of the mixed sample (~0.1 g wet feces) was placed in 3 ml of a methanol/acetone solution (4:1). To keep collection relatively consistent from sample to sample, we added fecal matter until the solution was displaced to the 3.4 ml mark on a graduated 15 ml polypropylene tube. The solution was immediately homogenized for 1 min using a battery-powered vortexer (BioVortexer, BioSpec Products, Inc., Bartlesville, OK). Because fecal hormone values are expressed as ng of hormone per g of dry feces, the exact weight of the dry fecal matter was later determined using a battery-powered, portable scale to ±0.001 g (Ohaus Scout Pro, Pine Brook, NJ). Approximately 6–8 h after sample collection, 2.5 ml of the fecal homogenate was filtered through a 0.2 μm polytetrafluoroethylene (PTFE) syringeless filter (Whatman, Florham Park, NJ), and the filter was subsequently washed with an additional 1 ml of methanol/acetone (4:1). We then added 7 ml of distilled water to the filtered homogenate, capped and mixed the solution, and loaded it onto a reverse-phase C18 solid-phase extraction cartridge (Sep-Pak Plus, Waters Corporation, Milford, MA) with a luer-lock syringe (needle removed). Prior to loading, Sep-Pak cartridges were prepped according the manufacturer’s instructions (with 2 ml methanol followed by 5 ml filtered water). After the sample was loaded, the cartridge was washed with 1 ml of a sodium azide solution (0.1%). All samples were stored on cartridges in separate sealed bags containing ~2 g of silica beads. Cartridges were stored at ambient temperatures for either 2 h (in the captive setting) or up to 10 days (in the field setting — see below), after which all samples were stored at subzero temperatures (~10 °C) until transported to the University of Michigan for analysis. Steroid hormones stored on cartridges were shown to be stable for up to four weeks at ambient temperature [10]. In the laboratory, steroids were eluted from cartridges with 2.5 ml 100% methanol and subsequently stored at ~20 °C until the time of RIA.
2.3. Radioimmunoassay

To measure glucocorticoids, we used a double-antibody, corticosterone 125I RIA kit (MP Biomedicals, Orangeburg, NY). The primary antibody in this kit cross-reacts 100% with corticosterone, 0.34% with deoxycorticosterone, 0.1% with testosterone, 0.05% with cortisol, 0.03% with aldosterone, and 0.02% with progesterone. Although cortisol is the primary GC in primates, we selected the MP Biomedicals corticosterone antibody for our study for several reasons: (1) After testing several antibodies (including at least one with a high affinity for cortisol), Wasser et al. [13] demonstrated that the primary antibody in the MP Biomedicals kit had relatively high affinity for the major cortisol metabolites present in feces during peak excretion following both radiolabel-infusion and adrenal activation. The authors concluded that the MP Biomedicals corticosterone antibody may be a group-specific antibody, with cross-reactivities to multiple GC metabolites excreted in feces. (2) Wasser et al. [13] reported that the MP Biomedicals antibody was superior to other antibodies for measuring GC metabolites in feces of a wide range of mammalian species, including baboons. (3) The primary antibody in this kit has been successfully validated for use in baboons [Papio spp., 13,42–44].

Prior to RIA, all samples were incubated at room temperature for 1 h, and an aliquot of each sample was reconstituted in working buffer. Internal controls were run in every assay and consisted of three pooled fecal samples and two immunoassay controls provided with the RIA kit. All standards were run in triplicate, all controls and samples were run in duplicate, and mean concentrations are expressed as ng/g. For the assay protocol, see the University of Michigan’s Endocrine laboratory website (www2.lsa.umich.edu/psych/research/caf/).

2.4. Extraction recovery

To confirm that the described extraction method was effective, we examined recovery of 200 μl of MP Biomedicals 125I corticosterone added to 10 aliquots of homogenized gelada feces (0.5 g). After incubating aliquots for 1 h at room temperature, we extracted each as described above. The recovery of 125I corticosterone following extraction was 62.6±1.0% (N=10). Because for fecal samples we are measuring immunoreactive GC metabolites (and not corticosterone itself), we also tested the recovery for 500 μl cortisol (125I cortisol, Diagnostic Products Corporation, Los Angeles, CA). The recovery of 125I cortisol was 73.9±1.0% (N=10).

2.5. Antibody validation

The MP Biomedicals corticosterone antibody was validated for use on extracts from gelada fecal samples by characterizing the antibody with respect to parallelism, accuracy, and precision. First, to determine parallelism between the RIA standard curve and a serial dilution of a gelada fecal extract pool (males only), we tested equality of slopes using an analysis of covariance (ANCOVA). A lack of significant interaction between the standard curve and serial dilution indicated that the slopes of these lines are equal (ANCOVA: R² = 0.99, F(1,11) = 0.03, p = 0.87). Second, assay accuracy (observed/expected) was determined by spiking each of the standards with a high (50 μl) and a low (25 μl) aliquot from a fecal pool and running these spiked standards as samples. Mean assay accuracy was 93 ± 3.0% for the high pool (N=6) and 94 ± 6.0% for the low pool (N=6). Finally, the precision of the antibody was determined by calculating intra- and interassay coefficients of variation (CVs). The intraassay CV for a high fecal pool was 6.3% (N=10), a low fecal pool was 8.7% (N=10), a high kit control was 6.3% (N=12), and a low kit control was 4.1% (N=12). The interassay CV for a high, mid, and low fecal pool was 15.8% (N=12), 11.8% (N=12), and 7.6% (N=12), respectively.

3. Methods — seasonal/altitudinal analysis in wild geladas

3.1. Study site and subjects

All data for the field portion of this study come from a population of wild-feeding geladas inhabiting the Simien Mountains National Park located in northern Ethiopia (13°13.5' N latitude). Two sets of data were examined in this study — one (longitudinal) to examine the seasonal effects of temperature and rainfall on glucocorticoid metabolites (GCMs), the other (cross-sectional) to examine altitudinal effects on GCMs. The longitudinal subjects for this study include 16 adult leader males from 13 different harems spread out across two bands (Michiby and Chilquanit bands) of a single herd. These target males are part of a long-term monitoring project that began in Jan 2006, therefore we have repeated fecal samples from these males across the entire study period. Although there was some variability in male ages, they were all “prime adults” (i.e., ranging between 8–13 years of age [45]) and were reproducively active across all periods of data collection. The cross-sectional subjects include additional leader males from three additional bands (Sankaber, Gich, and Chennek bands) spread out across the Simien Mountains National Park. Each of these five bands is located at different altitudes (Table 1). All field research was approved by the University Committee on Use and Care of Animals (UCUCA) at the University of Michigan and adhered to the laws and guidelines of Ethiopia and the Ethiopian Wildlife and Conservation Department.

3.2. Hormone sample collection

As described above, hormone samples were collected non-invasively by extracting hormones from fecal samples of known subjects. Although fecal collection in the field is ongoing, we restricted analyses to the first two years of sampling (Jan 2006–Jan 2008).

For the longitudinal analysis, we employed a targeted collection schedule such that we usually obtained a fecal sample from each leader male before any male was sampled twice. However, the total number of samples from each male varied as a function of male tenure as leader of a harem. For males that remained leader males through-out the study (N=6), this variation was minimal (range: 31–37 samples/meal). For males that gained or lost a harem during the study period (N=8), or were added as study subjects later (N=2), the number of samples varied in proportion to their residency as leader/subject males (range: 17–33 samples/meal). In all cases, male subjects were evenly sampled per unit time, and no male is missing samples from more than one month. In sum, we have 439 samples from 16 target males across 24 months.

For the cross-sectional fecal collection, we located one of three additional bands and collected fecal samples from as many leader males as possible on that day (on any given day, no male was sampled twice). To control for seasonal variation, all samples for cross-sectional analyses were collected during the month of March in 2006 and 2007. Gich and Chennek were each sampled twice (2006, 2007) and Sankaber was only sampled once (2006 only). To facilitate comparisons with the longitudinal data from the Michiby and Chilquanit bands, the

<table>
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<tr>
<th>Band</th>
<th>Altitude (m)</th>
<th>Total number of males sampled</th>
<th>Sampled in Mar 2006</th>
<th>Sampled in Mar 2007</th>
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<td>✓✓</td>
</tr>
<tr>
<td>Chennek</td>
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<td>12</td>
<td>✓✓</td>
<td>✓✓</td>
</tr>
</tbody>
</table>

Table 1

Samples for the altitudinal analysis for five different bands
cross-sectional data was used in conjunction with longitudinal data collected only during March of both years. In sum we have 72 samples from 16 target males and 49 samples from 25 additional males for Mar 2006 and Mar 2007.

### 3.3. Climatological data

Climate data was collected at a central location in the geladas’ home range. Precipitation (mm) was measured using a rain gauge and temperature data (daily maximum and minimum, °C) was measured using a digital max–min thermometer placed in a permanently shaded area. Climate data were recorded on a near-daily basis, with a mean for each month calculated for temperatures (Max Temp, Min Temp) and a cumulative total for each month calculated for rainfall (Rain). All months had at least 22 days of temperature data recorded, and for 15 of the 18 months of this study, we had fewer than two days without temperature data. Because evaporation was minimal due to the narrow opening of the gauge, even when researchers were absent from the camp, rainfall was able to be recorded upon their return. Therefore, our temperature and precipitation data are thought to be accurate representatives for each month.

### 3.4. Data analysis

For the ACTH challenge, hormone data were evaluated with one-way ANOVA followed by a Tukey’s post-hoc test to determine pairwise differences.

For the seasonal analysis, we used a general linear mixed model (GLMM) to assess the effect of three continuous independent variables (Max Temp, Min Temp, and Rain) on one continuous dependent variable (GCMs) for all leader males. A GLMM (in contrast with the general linear model) is able to account for multiple measures from the same subjects by including each subject (i.e., each leader male) as a random factor in the model (each with their own random intercept and slope). Due to the high correlation between variables (Max Temp and Min Temp were...
positively correlated (Pearson’s correlation: \( r = 0.61, p < 0.001 \)) and Max Temp and Rain were negatively correlated (Pearson’s correlation: \( r = -0.66, p < 0.001 \)).

For the altitudinal analysis, we analyzed March hormone samples from all five bands. Because individual males from the Sankaber, Gich, and Chennek bands were only sampled once per year, each sample represents one male. For the Michiby and Chilquanit bands (with multiple samples/male for the months of March), we used one mean/male/year in the analysis. Thus, we ensured that no one male from the Michiby and Chilquanit bands accounted for a disproportionate amount of each monthly mean value. Differences in hormones across bands were analyzed using one-way ANOVA.

Because our hormone variable was not normally distributed, we log-transformed hormone values prior to statistical analysis. GCMs were normally distributed following transformation (Kolmogorov-Smirnov test: \( p > 0.05 \)), thus facilitating the use of parametric statistics. All statistical analyses were performed using SPSS (16.0), and the statistical threshold for all analyses was set at \( p < 0.05 \).

4. Results

4.1. ACTH challenge

During the 24 h period after the ACTH injection, GCMs were significantly higher than the baseline and the 72 h post-injection period (ANOVA: \( F(4,56) = 9.30, p < 0.001 \)), and marginally higher than the 48 h post-injection period (Fig. 1a). Even after removing one particularly high post-injection sample for one female (see Fig. 1b), the results remain the same (ANOVA: \( F(4,55) = 9.31, p < 0.001 \)), with 24 h post injection values significantly higher than baseline (Tukey’s post-hoc test: \( p < 0.001 \)) and 72 h post-injection values (\( p < 0.01 \)), and marginally higher than 48 h post-injection (\( p = 0.054 \)).

For one female, we were able to detect a peak in GCM excretion (61.1 ng/g) at 18 h post-injection (Fig. 1b), with elevated GCMs extending from 16–25 h post-injection. For the other three animals, we were able to detect elevated GCMs (also from 16–25 h post-injection) but not a peak during this period. Because we were unable to resume sample collection until 16 h post-injection (see Methods), we probably missed peak excretion for these other three animals. Therefore, the range for peak fecal GCM excretion is sometime before 16 h but up to 18 h post-injection, followed by continued GCM elevation until at least 25 h post-injection.

4.2. Diurnal variation

To determine if fecal GCMs reflect the diurnal hormone secretion patterns observed in serum samples, we collected morning and afternoon fecal samples from the same individuals on the same day (\( N = 8 \) adult males, 16 samples). We extracted and processed all samples as described above. We found no difference in GCMs between morning and afternoon samples from the same individuals (Wilcoxon signed ranks test: \( Z = -1.4, p = 0.161 \)).

4.3. Seasonal effects

For the longitudinal dataset, the two models with the lowest AIC (i.e., the best fit) included only Max T or Min T as the independent variable. As mean monthly maximum or minimum temperature increased, individual male GCMs significantly decreased (GLMM Max Temp: \( F(1,16) = 6.07, p < 0.05 \); Min Temp: \( F(1,16) = 6.82, p < 0.05 \); Fig. 2a–b). When included in the model with Min Temp, rainfall had no effect on male GCMs (GLMM Rain: \( F(1,15) = 0.03, p = 0.87 \); Fig. 2c).

4.4. Altitudinal effects

Using the cross-sectional dataset, an ANOVA followed by a Tukey’s multiple comparison’s test indicated that fecal GCMs were significantly different across bands (\( F(4,56) = 9.76, p < 0.001 \)) with bands at the highest altitudes (Gich and Chennek) exhibiting the highest GCMs (Fig. 3). The bands at lower altitudes (Chilquanit, Michiby, and Sankaber) were not significantly different from each other, but all three exhibited significantly lower GCMs than Chennek, and all but Chilquanit were significantly lower than Gich.

5. Discussion

5.1. Method validation

The method described for extracting GCMs from fecal samples was successfully validated for use in geladas. First, an ACTH challenge demonstrated that biologically meaningful elevations in GCMs were detected in gelada fecal samples, with a lagtime between GCM secretion (into the bloodstream) and peak excretion (into the feces) of approximately 18 h. This lagtime is slightly shorter than that proposed for the closely-related baboons [26 h, 13], and is probably due to the high fiber diet of geladas [over 90% grass, 38, 39, 33] as compared with the omnivorous diet of baboons [46–49]. Second, the MP Biomedicals corticosterone primary antibody, used successfully across a wide variety of species [13], was also shown to be linear, accurate, and precise for geladas, and hormone recovery following the described extraction method was high (60–75%) for both corticosterone and cortisol. Finally, diurnal changes in hormone levels, a factor that must be considered when using hormones in serum or excreta such as urine or saliva, do not appear to be a factor for gelada GCM fecal measures. This result was also found for baboons [10], and is consistent with the general finding across many mammalian species that fecal GCMs represent a cumulative “average” of adrenal activity over a period of time [50,6,19].

5.2. Seasonal and altitudinal analysis

Geladas, once found throughout sub-Saharan Africa [51], are now restricted to the mountainous regions of Ethiopia where high winds
and freezing nighttime temperatures present a climatological challenge to this species. Comparing physiological profiles across the year, we found that gelada males exhibited significantly higher GCMS during colder times of the year (typical July-Jan), suggesting that a decrease in both daytime (Max Temp) and nighttime (Min Temp) temperatures may be related to signs of cold-stress in this population. Cold-stress has been demonstrated to have a detrimental impact upon health and physiology across several vertebrate species [32,33], including humans [34]. Generally, animals that face cold ambient temperatures have adaptive responses that include morphological features (such as increased fat deposits or fur), physiological adaptations (such as a lower metabolic rate), or more immediate behavioral responses (such as shivering or increased food intake). Previous research has indicated that geladas have at least two adaptations to the cold weather, mainly an increase in hair density and an increase in feeding time for groups living in colder climates [34]. However, our results are the first to find a physiological response to cold-stress in this species. A similar study conducted on chacma baboons living in a highly seasonal environment in South Africa also found that the strongest correlate with GCMS was cold temperatures [29].

Several possible explanations may account for the relationship between GCMS and monthly temperatures. First, elevations in GCMS during colder periods may reflect the geladas' inability to keep up with temperature-dependent metabolic requirements. When ambient temperatures fall below a critical threshold, warm-blooded animals must either reduce their activity or increase their food consumption to maintain their body temperature [55]. This imposes a major constraint on geladas' behavioral ecology, since a diet based on grass already requires a bulk feeding strategy to extract the nutrients needed [38,39]. Compared with similar-sized primates, geladas must dedicate a larger percentage of their activity budget to feeding over other activities [34,33]. Although geladas were found to spend more time feeding when it is cold [34], perhaps they are still not able to meet their thermoregulatory needs with a granivorous diet — particularly if they have to increase their activity level to expand their foraging. However, in a detailed study on how far gelada groups traveled in a day, Hunter [33] found that geladas significantly reduced (rather than increased) their daily journey length during cold months. In sum, when faced with cold temperatures, geladas manage to (a) increase their dietary intake, (b) decrease their activity, yet still (c) exhibit elevated GCMS concentrations.

Contrary to expectations, geladas did not show elevated GCMS during the dry season. Despite increases in primary productivity during the rainy season [33] and the geladas' preference for above ground resources, we found no evidence that geladas suffer from decreased nutrition during dry months. One probable explanation is that geladas are extremely good at utilizing subterranean storage roots during dry periods [33]. This switch to underground resources may provide adequate nutrition for geladas across the year. In a study on the same population, Hunter [33] reports that geladas not only spent more time foraging but actually ingested a greater number of calories during the dry season as compared to the rainy season. Thus, it appears that a foraging strategy to extract the nutrients needed [38,39] Conversely, we do see a dramatic drop in GCMS during cold months before we can rule out a behavioral stress hypothesis (i.e., that elevated GCMS are due to behavioral factors). For example, if rates of aggression or grooming are more prevalent during some months than others, then perhaps this might better explain the seasonal differences in GCMS than temperature variables. Currently, we are in our first continuous year of behavioral collection with which we will address this possible effect.

Acknowledgements

We would like to thank the Wildlife Conservation Society/Bronx Zoo for their support and collaboration in this study. We are additionally grateful to the Ethiopian Wildlife Conservation Department, the Amhara National Regional State Parks Development and Protection Authority, and the wardens and staff of the Simien Mountains National Park for granting us the permission to conduct this research. At the Bronx Zoo, we would like to thank Florence Klecha for her help with data collection and Dr. Bonnie Raphael and Claudia Wilson for their assistance and supervision of the ACTH challenge. In Ethiopia, we would like to thank Haile Gelaye for over two years of assistance with climatological and hormonal data collection. Finally, we thank Thore Bergman, Laurence Gesquiere and two anonymous reviewers for helpful comments on an earlier draft of this manuscript. Funding was provided by the Wildlife Conservation Society (SSF Gr#: 67250), the National Geographic Society (NGS Gr#: 8100-06), the L.S.B. Leakey Foundation, the National Science Foundation (BCS-0715179), and the University of Michigan. This research was approved by the Wildlife Conservation Society's Institutional Animal Care and Use Committee at the Bronx Zoo (IUCUC protocol #05-06), the University Committee on Use and Care of Animals at the University of Michigan (IUCUA protocol #09554), and adhered to all the laws and guidelines of Ethiopia.

References


