Western lowland gorilla (*Gorilla gorilla gorilla*) diet and activity budgets: effects of group size, age class and food availability in the Dzanga-Ndoki National Park, Central African Republic

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Abstract

Variation in food availability, body size and group size are known to influence primate diet and activity budgets. Due to greater difficulties in habituating western lowland gorillas (Gorilla gorilla gorilla) very few studies have been carried out to describe their diet and activity budgets based on direct observation. In this study I report how seasonality in terms of food availability, group size and age differences may shape the diet composition and activity patterns of two western lowland gorilla groups. First of all I compared food availability between the home ranges of the two groups by monitoring the leafing and fruiting patterns of major gorilla food trees. Next I compared the activity budgets and diet composition of the groups while outlining differences between the different age classes and seasons. I obtained data on gorilla activity by continuous recording of the activity of focal animals rotated daily. I found that western gorillas spent most of their time feeding (38.8 %), followed by resting (33.1 %), traveling (19.1 %) and only a small proportion of time for social activities (5.3 %). Also based on the amount of time spent consuming different food items I found that the diet of western lowland gorillas consisted mainly of fruits (35.7 %), followed by stems (24.0 %), leaves (21.4 %), insects (14.2 %) and bark (2.5 %). Both groups spent significantly less time feeding, traveling and socializing; and consumed significantly more fruits, less leaves and bark during the season of high frugivory in comparison to the season of low frugivory. Adults were significantly different from immatures only in social behaviour. Time spent resting and the proportion of stems and insects in diet showed no seasonality. My results show that western gorilla activity budgets and diet composition vary more in response to ripe fruit availability rather than group size or age differences.
Acknowledgements

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Mbusa, Kotto et al. Without their kind support, expert forest knowledge and exceptional tracking skills none of this would have been possible. It has been an honour for me to lead this team.

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Chapter 1-General introduction

Variation in food availability, climate and anthropogenic activities alongside body size and group size, are known to influence primate diet diversity and activity patterns (Dunbar, 1992; Hanya, 2004; Brockman and Van Schaik, 2005; Masi et al., 2009; Brockman & Van Schaik, 2011). Primates in tropical rainforest face local, seasonal and inter-annual variation in food availability (Van Schaik et al., 1993; Morellato et al., 2000; Brugiere, 2001; Hemingway & Brynum, 2005; Van Schaik & Pfannes, 2005) and as a result they frequently show more flexible behaviour and can modify their diet and activity patterns in order to survive. Therefore even within-species within the same contiguous forest, diet can vary across the population (Chapman et al., 2002), as well as between different seasons and different years (Doran & McNeilage, 2001; Chapman et al., 2002). Knowing how primates of different group sizes exposed to fluctuating food availability modify their diet and activity pattern to survive is therefore a key element to understanding their socioecology (Harcourt & Stewart, 2007). This knowledge is vital for calculating area and range requirements to conserve viable populations as well as to safeguard tree species for populations out of protected areas (such as logging concessions); therefore invaluable in planning and managing conservation projects.

Most studies on gorilla behavioural ecology have focused on the well-habituated mountain gorillas, Gorilla beringei beringei (Watts, 1996; reviewed in Doran and McNeilage, 1998, 2001). However, in recent years there have been increasingly more studies carried out on WLGs yielding further information on their behavioural ecology. Through indirect evidence from feeding trails and faecal analyses (Calvert, 1985; Rogers et al., 1990; Williamson et al., 1990; Nishihara, 1995; Kuroda et al., 1996; Remis, 1997; Goldsmith, 1999; Doran et al., 2000) and direct observation (Masi et al., 2009; Doran-sheehy et al., 2009), it has been shown that western lowland gorillas (hereafter WLGs) change their diet and activity pattern according to the seasonal availability of fruits. However no study has been able to investigate how the effect of group size might influence diet and activity patterns.
In collaboration with the Primate Habituation Programme of Dzanga-Sangha Protected Areas in Central African Republic, this study aims to understand how two WLG groups (of different size) cope in the face of local differences and seasonal changes in food availability and how this may influence their feeding behaviour and activity patterns.

1.1. Food availability, diet and activity pattern

Rainforest is characterised by alternating seasons, with climatic conditions that vary seasonally and inter-annually, thereby causing an irregular availability of vegetative and reproductive plant parts. As a result, primary consumers face periods of food peaks and scarcity (Morellato et al., 2000; Brugiere et al., 2002; Bollen & Donati, 2004). Phenological monitoring depicts spatial and temporal variation in the availability of young leaves and ripe fruits in tropical forests with climate playing a key role [see review by Van Schaik et al. (1993)]. According to Chapman et al. (1999), significant variation in fruit availability can occur even between adjacent sites in similar forests. Different primates respond to variation in food availability in diverse ways. They can either increase or decrease their daily range and/or time spent traveling during periods of food scarcity in order to optimise foraging effort or they may switch their diet by either consuming different food categories, different items within the same food categories or rely primarily on fall-back foods (see review by Hemingway & Bynum, 2005). As a result there is seasonal variation in the behavioural ecology of rainforest primates with those that prefer ripe fruits being directly affected by the phenology of fruiting trees (Brockman & Van Schaik, 2005). For example, orang-utan diet ranges from 100% fruit during fruit peaks to very low fruit and more bark intake during periods of fruit scarcity (Galdikas, 1988; Knott, 1998). As fruit distribution is patchy compared to other food resources (which can be more evenly distributed/widespread) and generally occurs in small patches, not only do primates have to walk further to find fruit but it is also a monopolisable resource so not all group members have access.
Detailed diet analyses show that western gorillas, like other great apes, are highly selective ripe fruit opportunists seeking sweet succulent fruits high in energy (Rogers et al., 1990; Doran-Sheehy et al., 2009). However when compared with sympatric chimpanzees, gorilla diet is more varied and flexible (Head et al., 2011). In seasons of high fruit availability WLGs consume more fruits and overlook some less nutritious fibrous foods, but in seasons of fruit scarcity they increase consumption of low quality and less preferred fibrous fallback foods such as leaves, pith, stems and bark (Rogers et al., 1990; Remis et al., 1997; Tutin et al., 1997; Doran & McNeilage, 2001; Oates et al, 2003). During periods of fruit availability, WLG increase their foraging effort as they actively move from one fruit tree to another searching for fruits (Rogers et al., 2004) thereby resulting in an increase in their day journey length (Tutin, 1996; Yamagiwa et al, 1996; Doran-Sheehy et al., 2002; 2004; Cipolletta, 2004).

Doran-Sheehy et al (2002) made a comparison of WLG diet at 4 different sites (in Republic of Congo, Gabon, and CAR) but the study was based on indirect analyses of faecal sample and feeding trails. Results showed that fruit consumption increased with increases in its availability, but fibre remained present in the diet throughout the year. However indirect sampling of diet provides just a broad estimate; to totally understand inter-individual, inter-group and inter-site diet variation, a direct observational study of habituated animals is required. A later comparison of data from 6 different gorilla sites showed that WLGs feed on many of the same types of food between sites but at different frequencies (Rogers et al., 2004). These data showed that WLG can consume up to 230 different food types from 180 different species (Rogers et al., 2004). However most of the latter data are again from indirect evidence, and are likely an underestimate of diet. As habituated animals became available, Doran-Sheehy et al. (2009) and Masi (2008) provide a more detailed account of gorilla diet and foraging behaviour by systematic focal observation and nutritional analysis of gorilla foods at Mondika Research Centre in the Republic of Congo and Bai Hokou in Central African Republic. During the same overall study, Masi et al. (2009) provide a detailed account of WLG activity budgets by direct observation of a well-habituated group, finding that WLG can spend about
70% of their time feeding and less than 1% on social activities. During the season of high fruit availability there was an increase in the time spent traveling and a resulting decrease in time spent feeding.

**1.2. Group size/structure**

Generally most primates live in stable and cohesive social units (Van Schaik & Kappeler, 1997). There are many benefits of group-living, however as a consequence social primates are faced with increased intra-group competition for food which limits individual access depending on food patch size (Clutton-Brock and Harvey, 1977; Chapman and Chapman, 2000). Group size therefore influences primate diet and activity patterns. The larger the group the greater the competition for food resources as each group member strives to increase their foraging effort to maintain their required food intake. This competition takes two forms. Contest competition is the basis of the development of group hierarchies and usually results in certain individuals switching to less expensive resources (potentially increasing diet breadth) which may be associated with a reduction in group cohesiveness. However, when a large group of animals forages on a food patch that cannot be monopolised, each individual ‘scrambles’ for the reduced food available and hence longer distances need to be travelled to find sufficient food for all (scramble competition/ ecological constraints model, Chapman & Chapman, 2000; Harcourt & Stewart, 2007). For gorillas, this hypothesis has been proven to be true in mountain gorillas in Bwindi and Karisoke (McNeilage, 1995; Ganas & Robbins 2005) as well indirectly for western gorillas which travel longer distances in fruit seasons when preferred food is in smaller patches (Remis, 1994, 1999; Goldsmith, 1999; Cipolletta, 2004; Doran-Sheehy et al., 2004; Ganas & Robbins, 2005).

Stable WLG groups always consist of one silverback, with an average of 3 to 5 adult females, and their offspring (Breuer et al., 2009). Age boundaries of life-history classes for western lowland gorillas were reassessed as follows by Breuer et al. (2009): silverback (over 18 years), young silverback (14-18 years), blackback (11-14 years), adult females (over 10 years), subadult male (7.5-
11 years), subadult female (7.5-10 years), Juvenile (4-7.5 years) and infants (0-4 years). Average group size is approximately 8 to 10 individuals (Tutin, 1996; Yamagiwa et al., 2003; Robbins et al., 2004) although higher group sizes are observed (Bermejo, 2004; Doran &and McNeilage, 2001; Ando et al 2008; this study).

1.3. Project details

1.3.1. Aims and objectives

The aims of this study are (1) to understand how two western gorilla groups of differing size cope in the face of changing food availability and (2) to provide information that will contribute to the conservation management of gorilla habitats.

Objectives:

- Compare the variation in food availability within the home ranges of two WLG groups living about 10 km apart by examining local phenological differences in young leaves and fruit production.
- Determine the activity budget of the two groups of differing size (Group Makumba, N=9 and Group Mayele N=15) by Continuous Focal Sampling and investigate how it might be influenced by food availability, group size and age class differences.
- Compare the diet composition of the two groups with emphasis on the amount of time dedicated to the consumption of different food types.

1.3.2. Research questions and hypothesis

Three major research questions will be answered;

1) Is there a variation in the phenology of fruits and young leaves of major gorilla food trees between two WLG habituation sites, Bai Hokou and Mongambe within the Dzanga-Ndoki National Park?
2) How does group size, age class and food availability (phenology of fruits and young leaves) influence the activity pattern of these two groups?

3) What is the role of group size, age class and food availability on the diet of these two groups?

From the above review I predict that (1) there are detectable differences in the leafing and fruiting patterns of major gorilla food trees between the two sites. (2) As a result of its larger group size, I predict that the Mayele group will spend more time feeding than the smaller group since it might have to incorporate more non-fruit dietary items which take longer to process, are lower in energy content and need to be ingested in greater quantity, thus requiring more feeding time. However, since non-fruit items (leaves, stems, bark, and insects) are more evenly distributed and home range size might be limited by density-dependent factors, the larger group might not to travel farther to meet its energy requirements. Thus I predict that (3) there will be no differences between the proportions of time both groups spend traveling. Since social time is the parameter that bonds primate groups and the amount of social time is positively correlated with group size (Dunbar, 1992), I predict that (4) the larger group will spend proportionally more time for social activities than the smaller group. As a result of high sexual dimorphism in gorillas (Breuer et al., 2007) adult males have high daily energetic costs to maintain body size and adult females need extra energy to meet the cost of reproduction (Bean, 2004). I therefore expect considerable differences in the diet and activity budgets of adults and immatures. I predict that (5) adults will spend more time feeding and traveling in search of food than immatures in order to meet these extra energy requirements. As a consequence of the higher feeding and traveling time, (6) I expect adults to dedicate less time to social activities.

1.3.3. Thesis structure

- Chapter 1. General introduction and project aims
• Chapter 2. General methods

• Chapter 3: Research Article: ‘The role of food availability and group size on activity budgets of western lowland gorillas (Gorilla gorilla gorilla) in the Dzanga-Ndoki National Park, Central African Republic’. This chapter is written in the form of a journal article to be submitted to the International Journal of Primatology (IJP). This multidisciplinary journal publishes current research in fundamental primatology and diverse disciplines. This article provides information on western lowland gorilla behaviour in the face of varying food availability by comparing two groups of varying sizes living within the same forest. The paper adheres to author guidelines as laid out by the journal.

• Chapter 4: Research Article: ‘The role of food availability and group size on diet of western lowland gorillas: case study of Bai Hokou and Mongambe in Central African Republic’. This chapter is written in the form of a journal article to be submitted to the American Journal of Primatology (AJP). This journal publishes articles from many disciplines aimed at understanding primates better. This article provides information to improve knowledge on feeding behaviour of western lowland gorillas. The paper adheres to author guidelines as laid out by AJP

• Chapter 5. General conclusions
Chapter 2 - General Methods

2.1. Study area

Bai Hokou (20°50' N, 160°28' E) and Mongambe (2°55'N, 16°23'E) are situated in the Dzanga sector of the Dzanga-Ndoki National Park (DNNP) in south-western Central African Republic (Figure 1). The park is part of Dzanga-Sangha Protected Areas (DSPA) and co-managed by the CAR government and WWF (World Wildlife Fund). DSPA are a subset of a 25,000 km² complex of protected areas called the Sangha Tri-National complex (known by its French acronym TNS) additionally including Lobeke National Park in Cameroon and Nouabale-Ndoki National Park in the Republic of Congo. The TNS was named a World Heritage Site by UNESCO (United Nations Education, Scientific, and Cultural Organization) in 2012 in an effort to safeguard its high biodiversity including large populations of African forest elephants (*Loxodonta africana*), western lowland gorillas (*Gorilla gorilla gorilla*), central chimpanzees (*Pantroglodytes troglodytes*), and other threatened species that occur in this area (e.g. Carroll, 1988; Fay, 1989; Fay and Agnagna, 1992; Turkalo and Fay, 2001; Blom et al., 2001). The Regional Action Plan for the Conservation of Chimpanzees and Gorillas in Western Equatorial Africa outlines the TNS as an exceptional priority area for their conservation. The Dzanga sector of the park covers an area of 495 km² part of which was selectively logged between 1972 and the 1980s mainly for two species of hardwood (one to two stems per hectare): *Entandrophragma cylindricum* (Sapele) and *Entandrophragma utile* (Sipo) (Baum et al., 1998). The topography is relatively flat with a few streams flowing from east to west through the park, towards the main Sangha River. The forest is made up of a patchwork of primary forest habitats and secondary forest with much herbaceous undergrowth. Light gaps created by natural tree falls and/or elephant activity account for almost 9.5% of the forest habitat of the sector (see Carroll, 1988). In sections, there are also networks of old abandoned logging roads now colonised by herbaceous plants resulting from previous logging activities. The climate is characterized by a three-month dry season (December-February) and a long rainy season, usually interrupted by a drier
period June-July (Bai Hokou, long term data). In 2011, mean annual rainfall at Bai Hokou was 1200 mm with temperatures varying little over the year, averaging 26.3 °C (mean monthly minimum temperature 19.8 °C and mean monthly maximum temperature 28.7 °C, Bai Hokou long term data).

Figure 1: Detailed map of study site showing the position of Bai Hokou and Mongambe in the Dzanga-Sangha protected Areas.
2.2. Study species

Following recent taxonomic classification by Groves (2001) there are two species (Eastern and Western) and four subspecies of gorillas. The two subspecies of western gorillas (Groves, 2001) are: the western lowland gorillas \((\text{Gorilla gorilla gorilla})\) inhabiting Equatorial Guinea, Cameroon, Gabon, Central African Republic, Republic of Congo and Angola, and, the Cross River gorillas \((\text{Gorilla gorilla diehli})\) found in Nigeria and Cameroon. Both subspecies of western gorillas are Critically Endangered (IUCN, 2012) based on threats and population decline caused by poaching, habitat destruction and disease outbreak (Walsh et al., 2003).

Figure 2: Adult female western lowland gorilla at Bai Hokou CAR
2.3. Study groups

This study was carried out from July 2011 to January 2012 on two groups of western lowland gorillas (WLGs), group Makumba (Figure 3) and group Mayele (Figure 4) both ranging in the Dzanga sector of the park, but not neighbouring groups. Both groups are well habituated to human presence. Habituation of group Makumba started in 2000 and tourists started to visit the group by the end of 2004.

Figure 3: The Makumba group family tree showing the silverback at the top, adult females in the middle and offspring at the bottom. *** represents adult females that left the group before the study period

Figure 4: The Mayele group family tree showing the silverback at the top, adult females in the middle and offspring at the bottom.
At the time of the study, the group had nine individuals consisting of one silverback, two adult females, one black back, four juveniles and one infant (age/sex classification from Breuer et al., 2009). Habituation of group Mayele commenced in 2005 and the group started to receive tourists in 2010. During the whole study period this group had 15 individuals consisting of one silverback, four adult females, three sub-adults, four juveniles and three infants (Breuer et al., 2009).

Figure 5: Individuals of the Makumba group in Bai Hokou, CAR

2.4. Data collection

Data were collected over a six months period from July to August 2011 and October 2011 to January 2012. Phenology data were collected by trained research assistants and trackers while all western gorilla behaviour and diet data were collected by Terence Fuh.
2.4.1. Tree phenology

The phenology of new leaves, flower and fruit production of important gorilla food trees (occurring for more than 1% of gorilla feeding time, Masi, 2008 and Bai Hokou long term data) were monitored during the six months of study as an indicator of food availability in the gorilla habitat (Chapman et al., 1994). A total of 365 individual trees for 32 species of gorilla food were monitored along permanent transects in Bai Hokou and 314 trees of 34 species in Mongambe within the home range of each group. Only trees with a diameter at breast height (DBH) of more than 10 cm within 5 m from trails were selected. The target was to mark at least 10 trees of each species but some species were scarce in Mongambe and were replaced by different important gorilla fruit trees, hence resulting in more species. In both sites each tree was marked with tags and revisited once per month. Observations were made by a long-term field assistant and a Ba’Aka tracker with binoculars in each study site. To assess the availability of young leaves, flower, and fruits we used scores 0 – 4 (0 = no young leaves, 1 = rare, 2 = few, 3 = common and 4 = abundant). Both fruits on the ground and on the tree were considered and ripe fruits scored separately from unripe fruits.

2.4.1 Behavioural data

I collected behavioural data during half-day observation periods either during the morning (between 6:30 to 11:30) or afternoon (between 11:30 to 17:00) for both study groups (Makumba N = 54 days; for Mayele N = 42 days). Data collection started once contact was made with the group, usually after 6:30 am for morning periods and after 11:00 am for afternoon sessions. Every target animal was observed for an average of 3.5 hours per day. When the group was further away from camp it took longer to make contact resulting in lower observation time on those days; when tourists visited the group, data collection was halted until they left. Continuous Focal Sampling (Altmann, 1974) data were collected for seven days per month on group Mayele and 8-9 days per month on group Makumba, for both choosing a different focal animal on daily rotation. For group Makumba, all group members were sampled ensuring comparable sampling between morning and afternoon periods for each individual. For group Mayele, for logistic reasons only seven of the 15
group members were chosen as focal animals during this study as representative sample of the study group: the silverback, two adult females, one sub-adult male, two juveniles and one infant. Therefore, each individual of both groups was sampled at least once per month ensuring comparable sampling between morning and afternoon periods for each individual. Data were collected on activity, position (ground or tree) and the food consumed (species and type of food such as fruit, leaves, stem, bark, flower or insect) by the gorillas. Identification of gorilla foods was made by experienced Ba’Aka trackers and the local names noted. Activities were classified into five main categories (modified from Masi et al., 2009 and Watts 1988): feeding (including foraging and food processing), travelling (walking, running, climbing up or down trees), resting (stationary, sitting or lying down with eyes open or closed, autogrooming), social (playing, vocalisations, displays towards other individuals) and other (vigilance, nest construction, drinking and any other activity).

Table I: Total hours of focal per member of group Makumba and Mayele

<table>
<thead>
<tr>
<th>Individual</th>
<th>Age</th>
<th>Group</th>
<th>Total hours of focal</th>
</tr>
</thead>
<tbody>
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<td>Makumba</td>
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<td>Makumba</td>
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<td>Makumba</td>
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<tr>
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<td>Makumba</td>
<td>19.7</td>
</tr>
<tr>
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<td>Makumba</td>
<td>21.3</td>
</tr>
<tr>
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<td>Makumba</td>
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<td>Mayele</td>
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<td>Mayele</td>
<td>18.8</td>
</tr>
<tr>
<td>Ellli</td>
<td>adult female</td>
<td>Mayele</td>
<td>18.9</td>
</tr>
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</tr>
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<td>juvenile</td>
<td>Mayele</td>
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<td>Moangale</td>
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<td>Mayele</td>
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</tr>
</tbody>
</table>
2.5 Statistical analysis

Following Remis (1997) and Remis et al. (2001) and Masi et al. (2009), who showed seasonality in gorilla behaviour at Bai Hokou, I divided the study period into two seasons: High Fruogivory (HF) season (July and August 2011) and the Low Frugivory (LF) season (October 2011 to January 2012). Due to the small sample size, I merged the age/sex categories into two age classes, “adults” (silverback and adult females) and “immature” (sub adults and juveniles). Infants were not included in the analysis. I used SPSS for statistical analyses.

For Phenological data, I calculated the percentage of trees fruiting, flowering and leafing per month per site. Trees with at least one fruit were considered to be fruiting, trees with at least one leaf as leafing and same for flower. I used nonparametric test for related samples to test for normality of the phenology data (SPSS: Friedman’s Two-Way Analysis of Variance by Ranks). Since the data were not normally distributed, I used Wilcoxon Signed Rank Test to compare phenological profiles for the two sites.

For focal follows, for each individual gorilla I calculated the daily, average monthly and average seasonal percentages of time spent in each activity. The daily proportion of feeding time spent on each food category (fruits, leaves, stems, bark, insects and other food types or unidentified food items) was also calculated. The proportion of time spent feeding on each food category was taken as an estimate of consumption (Wrangham et al., 1998). Daily, average monthly, and average seasonal food diversity was calculated as the average number of different food species consumed by each individual gorilla per focal sample.

To analyse differences between the two groups in seasonal activity budgets I used Mixed Model Repeated Measures ANOVA with activity (feeding, resting, traveling, social, and other) as the dependent variable and group and season as independent predictors. One dependent variable was tested per model. I used the same analysis to test for: age-differences in seasonal activity budgets (dependent variable, activity; independent indicators, age and season); group differences in seasonal
diet (dependent variable, proportion of time spent feeding on each food type; independent indicators, season and group); age class differences in seasonal diet composition (dependent variable, food type; independent indicators, season and age class). Finally, to test for sphericity of the data (an assumption of the repeated measures ANOVA) I used Mauchly’s test. In case of violation of the assumption of sphericity I checked significance of the Greenhouse-Geisser correction (Greenhouse & Geisser, 1959).
Chapter 3-Research Article

For submission to: International Journal of Primatology

The role of food availability and group size on activity budget of western lowland gorillas (*Gorilla gorilla gorilla*) in the Dzanga-Ndoki National Park, Central African Republic

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ABSTRACT

Variation in food availability, body size and group size are known to influence primate diet and activity budgets. Due to greater difficulties in habituating western lowland gorillas (*Gorilla gorilla gorilla*) very few studies have been carried out to describe their activity budgets based on direct observation. In this study we report how seasonality in terms of food availability, group size and age differences may shape western lowland gorilla activity patterns. We compare the activity budgets of two groups while outlining differences between the different age classes and seasons. Data on gorilla behavior was obtained by continuous focal sampling of target animals rotated daily. We found that western lowland gorillas spent most of their time feeding (38.8 %), followed by resting (33.1 %), traveling (19.1 %) and only a small proportion of time for social activities (5.3 %). Additionally, both groups’ activity budgets appeared to vary more in response to differences in food availability rather than those attributed to group size and age. Both groups responded to changes in fruit availability in the same way. Individuals spent significantly less time feeding and more time traveling and socializing during the high frugivory season than the low frugivory season. The proportion of time spent resting did not vary with season. Adults were significantly different from immatures only in social behavior. Similar seasonal variations have been observed in other great apes with the exception of bonobos.

**Key words:** western lowland gorillas, activity budgets, seasonality, group size, age differences

INTRODUCTION

Understanding evolution of primate sociality and life history patterns can be only achieved by acquiring information relating on activity budgets of the different age/sex classes of the different taxa. Variation in food availability, group size, body size, climate and anthropogenic activities in the habitat can influence both primate diet and activity patterns (Dunbar, 1992; Hanya, 2004; Brockman
and Van Schaik, 2005; Masi et al., 2009; Brockman & Van Schaik, 2011). Thus, a better understanding of the adaptive mechanisms in different habitats may therefore be achieved by investigating primate behavioral responses to these varying environments.

Great apes have seen substantial reductions in population size due to habitat loss and degradation (see review by Hardus et al. 2012), thereby emphasizing the importance of understanding how they react and potentially adapt to different habitats. For example different orangutan subspecies show different flexibility/tolerance towards logging (Hardus et al., 2012). Chimpanzees are more sensitive to selective logging than gorillas (Arnhem et al., 2008; Matthews and Matthews, 2004; Morgan and Sanz, 2007) due to their high dependence on fruit resources and the territorial nature of their home ranges.

Like most primates, gorillas respond to seasonal variation in resource availability by modifying their diet and activity pattern (gorillas: Masi et al., 2009; Doran-Sheehy et al., 2009; chimpanzees: Overdorff, 1996; Doran, 1997; orangutans: Knott, 2005). Western gorillas are the least studied of the two gorilla species due to greater difficulties in their habituation (Tutin and Fernandez, 1991; Blom et al., 2004; Doran-Sheehy et al., 2007). Yet a number of studies have been carried out to understand their behavioral ecology of based on indirect evidence from trail signs and fecal samples (reviewed by Rogers et al., 2004). These studies have shown seasonal variation in both diet and activity budgets of this species in contrast to the mountain gorillas (Watts, 1998), subspecies of the Eastern species (Rogers et al., 1990; Williamson et al., 1990; Remis, 1994; Tutin, 1996; Yamagiwa et al., 1996; Remis, 1997; Tutin et al., 1997; Doran and McNeilage, 1998; Goldsmith 1999; Doran et al., 2002; Oates et al. 2003, Rogers et al., 2004; Masi et al., 2009). However, only the recent study by Masi et al. (2009) show the first detailed account of activity budgets by direct observation of a well habituated group of western gorillas at Bai Hokou site in Central African Republic (CAR). Their results show that western lowland gorillas (WLG) can spend about 67 % of their time feeding, 21 % resting, 12 % traveling and very little time (0.5 %) for social activities. However this study is based on a single
group and thus does not account for group size influence or possible variation of food between different home-ranges. A study on a different group and field site, by Doran-Sheehy et al. (2009), shows that western gorillas dedicate 43-44% of the time feeding, but this study is based on just one silverback and several adult females and does not provide information on other activities different from feeding. Moreover, the tropical forest where western gorillas live is characterized by large fluctuation in raining patterns and consequently in fruit availability (Van Schaik et al., 1993; Morellato et al., 2000, Brugiere, 2001). Consequently, western gorillas are greatly affected by this seasonality in terms of ranging, activity patterns, diet and even health (Remis, 1994; Remis, 1997; Goldsmith, 1999; Cipolletta, 2004; Masi, 2008; Masi et al., 2009). Like most of great ape species, they increase their travelling time, daily travel distance and/or home-range as fruit consumption increases (Wrangham, 1977; Doran, 1997; Remis, 1997; Goldsmith, 1999; Yamagiwa et al., 2003; Cipolletta, 2004; Doran-Sheehy et al., 2004; Ganas & Robbins, 2005; Masi, 2008; Masi et al., 2009). Western gorillas spend less time feeding when integrating more energy rich fruit in the diet as a consequence of higher availability of fruit in the habitat (Masi, 2008; Masi et al., 2009).

In this study we make the first comparison between activity budgets of two habituated WLG groups of different size (Group Makumba, N = 9 and Group Mayele, N = 15) living in home ranges less than 10 km apart. We aim at investigating how seasonality in terms of food availability, group size and age differences may shape their activity patterns. Comparison of food availability between the two sites during the study period by monitoring of the phenology of young leaves and fruits are reported elsewhere (Chapter 4). Our main objective is to compare the group activity budgets while outlining differences between the different age classes and seasons. We expect both groups to spend less time feeding during the high frugivory (HF) than the low frugivory (LF) season (Masi, 2008; Doran-Sheehy et al., 2009; Masi et al., 2009). However we predict that (1) as a result of its larger group size, the Mayele group will spend more time feeding than the smaller group since it might have to incorporate more non-fruit items to its diet which are lower in energy and need to be ingested in greater quantity, thus requiring more feeding time. As a consequence of the above hypothesis we
expect a lower resting time in the larger group. We also expect both groups to travel more during the HF than the LF season as they search for fruits which are patchily distributed within their home ranges (Masi et al, 2009) however we predict that (2) there will be no significant difference in time spend traveling by the two groups since individual groups can move faster if they have a longer distance to cover (Williamson & Dunbar, 2001). As reported by earlier studies (Masi et al., 2009) we expect both groups to spend more time for social activities during the High frugivory season. However since social time is what bond primate groups and the amount of social time required is positively correlated with group size (Dunbar, 1992), we predict that (3) the larger group will spend more time for social activities than the smaller group. As a result of high sexual dimorphism in gorillas (Breuer et al., 2007) adult males have high daily energetic cost to maintain boy size and females need extra energy to meet the cost of reproduction (Bean, 2001). We therefore predict that (4) adults will spend more time feeding and traveling to search for food than immatures in order to meet up these extra energy requirements. As a consequence of the higher feeding and traveling time, (5) we expect adults to dedicate less time to social activities.

**METHODS**

**Study site**

[See section 2.1]

**Study species**

[See section 2.2]

**Study groups**

[See section 2.3]
Data collection
[See section 2.4]

Statistical analysis
[See section 2.5]

The research complied with protocols approved by the American Society of Primatologists with ethical guidelines for the treatment of non-human primates, was approved by the appropriate animal care and use committees (i.e. Oxford Brookes University, UK) and followed Central African Republic’s protocol for foreign researchers.

RESULTS

Food availability
We found no significant difference in food availability between the two sites. Detailed results of the comparison of leafing and fruiting of major gorilla food trees between the two sites are reported elsewhere (Chapter 4).

Seasonal and group effect on activity budgets
Both groups spent most of their time feeding (mean = 38.8 ± SE 2.0 %), followed by resting (mean = 33.1 ± SE 3.1 %), traveling (mean = 19.1 ± SE 1.3 %), social activities (mean = 5.3 ± SE 1.5 %) and other activities (mean = 3.7 ± SE 0.4 %).

Feeding time was significantly affected by season (Table II). Both groups spent more time feeding during the LF (Makumba = 52.1 ± SE 4.7 % and Mayele = 42.1 ± SE 5.4%, Figure 6b) than the HF season (Makumba = 27.6 ± SE 4.5 % and Mayele = 34.2 ± SE 5.2 %, Figure 6a). However, we found no significant difference in the proportion of time each group dedicated to feeding within the same season (Table II, Figure 6). Even though the overall mean proportion of time that the Makumba
group spent feeding (43.3 ± SD 12.5 %) tended to be higher than that of the Mayele group (38.3 ± SD 10.8 %), overall, group effect had no significance on feeding time (Table II).

Figure 6: Activity budgets of the Makumba and Mayele groups of western lowland gorillas during the high frugivory (a) and low frugivory (b) seasons.
Table II) Effects of season and group on western gorilla time-budget according to mixed model repeated measures analyses of variance (ANOVA)

<table>
<thead>
<tr>
<th>Activity budget</th>
<th>season</th>
<th>group</th>
<th>Season*group</th>
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<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>Feeding</td>
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<td>0.018</td>
<td>2.300</td>
</tr>
<tr>
<td>Resting</td>
<td>0.069</td>
<td>0.771</td>
<td>0.379</td>
</tr>
<tr>
<td>Travelling</td>
<td>7.777*</td>
<td>0.016</td>
<td>0.161</td>
</tr>
<tr>
<td>Social</td>
<td>4.810*</td>
<td>0.049</td>
<td>1.018</td>
</tr>
<tr>
<td>Other</td>
<td>3.678</td>
<td>0.079</td>
<td>0.071</td>
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</tbody>
</table>

Results of separate Mixed model repeated measures ANOVA with time spent feeding, resting, traveling, social activities and other activities as dependent variables and season as group as independent predictors. Values are F-values and significance values at P<0.05 is represented by *

Season had no significant effect on the time gorillas spent resting (table II). Also we found no significant difference in the time both Makumba and Mayele spent resting within the same season (Table II). During the HF season Makumba spent 33.9 ± SE 6.4 % of the time resting, while Mayele spent 34.1 ± SE 7.4 %, while during the LF season, time spent resting by Makumba was 28.5 ± SE 4.7 % and for Mayele 36.0 ±SE 5.5 % (Figure 6). Overall group effect had no significance on resting time (table II).

Season significantly affected the time gorillas spent traveling (table II). Both groups spent significantly more time traveling during the HF (Makumba = 22.7± SE 2.8 % and Mayele = 22.3 ± SE 3.2 %, Figure 6a) than the LF season (Makumba = 14.4 ± SE 1.6 % and Mayele = 16.8 ± SE 2.0 %, Figure 6b, Table II). However we found no significant difference between the proportions of time each group spent traveling within the same season (Table II). Overall, the effect of group on the time gorillas spent traveling was not significant (table II).

Seasonal differences also significantly affected the time gorillas spent for social behaviors (table II). Both Makumba and Mayele groups spent significantly more time for social activities during the HF season (Makumba = 11.0 ± SE 3.4 % and Mayele = 5.4 ± SE 4.0 %) than the LF season (Makumba = 2.7 ± SE 1.2 % and Mayele = 2.2 ± SE 1.4 %). We found no significant difference between the
proportions of time each group spent for social activities within same seasons (Table II, Figure 6). The effect of group on time spent for social activities was non-significant (table II).

Season had no significant effect on the time the gorillas spent for other activities (table II). Within the same seasons there was no significant difference between groups for the proportions of time they spent for other activities. While during the LF season both groups dedicated almost the same time for other activities (Makumba = 2.7 ± SE 1.2 %; Mayele = 2.2 ± SE 1.4 %, Figure 6b), during the HF season, this time was double for the smaller group (Makumba: 11.0 ± SE 3.4 %) in comparison to the larger group (Mayele: 5.4 ± SE 4.0 %, Figure 6a). However, the effect of group on the time spent for other activities was non-significant (table II). The main activity in “other” category in both groups was vigilance (95-100 % of time spent for other activities).

**Age class differences on activity budgets**

Adults (HF = 31.3 ± SE 5.4 %, LF = 45.6 ± SE 5.9 %) and immatures (HF = 29.8 ± SE 4.7 %, LF = 48.8 ± SE 5.1 %) did not differ significantly in the percentage of time they spent feeding within the different seasons (table III, Figure 7). Also the effect of age class differences did not significantly affect the overall time the gorillas spent feeding (table III). We found no significant difference between the percentages of time that each age class spent resting within the same season (Table III, Figure 7). Even though the percentage of time that adults spent resting (HF = 41.6 ± SE 6.8 %, LF = 34.7 ± SE 5.6 %) tended to be higher than that of the immature (HF = 28.3 ± SE 5.9 %, LF = 29.4 ± SE 4.8 %) in both seasons, the effect of age class had no significance on resting time (table III).

Within the same season time spent traveling by adults was not significantly different from that spent by the immature (HF season: adults = 20.6 ± SE 3.1 %, immature = 24.0 ± SE 2.7 %; LF season: adults = 15.4 ± SE 2.0 %, immature = 15.5 ± SE 1.8; Table III). In overall the effect of age class had no significance on the time that the gorillas spent traveling (table III).
Figure 7: Activity budgets of adult and immature western gorillas during the high frugivory (a) and low frugivory (b) seasons.
Table III: Effects of season and age class on western gorilla time-budget according to mixed model repeated measures analyses of variance (ANOVA)

<table>
<thead>
<tr>
<th>Activity budget</th>
<th>season F</th>
<th>season P</th>
<th>Age class F</th>
<th>Age class P</th>
<th>Age*season F</th>
<th>Age*season P</th>
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<td>Resting</td>
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<td>2.604</td>
<td>0.133</td>
<td>0.467</td>
<td>0.507</td>
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<tr>
<td>Travelling</td>
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<td>0.526</td>
<td>0.482</td>
<td>0.465</td>
<td>0.508</td>
</tr>
<tr>
<td>Social</td>
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<td>0.049</td>
<td>12.652**</td>
<td>0.004</td>
<td>4.071</td>
<td>0.067</td>
</tr>
<tr>
<td>Other</td>
<td>3.678</td>
<td>0.079</td>
<td>1.688</td>
<td>0.218</td>
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</table>

Results of separate mixed model repeated measures ANOVA with time spent feeding, resting, traveling, social activities and other activities as dependent variables and season and age class as independent predictors. Values are F-values and significance values at P<0.05 and P<0.01 are represented by * and ** respectively.

Time dedicated to social activities varied significantly between adults and immature (table III). The immature dedicated a significantly higher percentage of time for social activities than the adults (Figure 7, Table III). However, within the same seasons a trend was found between the percentages of time that each age class dedicated to social activities, with larger differences during the HF season; HF: immature = 14.0 ± SE 2.8 %, adults = 1.5 ± SE 3.1 %); LF: immature = 3.8 ± SE 1.1 %, adults : 0.8 ± SE 1.3 %). Playing was the main social activity among the immatures (98-100% of time spent for social activities); meanwhile vocalization was the main social activity of the adults (98-100 %). Age class differences had no effect on other activities (table III).

In summary, as expected gorillas fed less, travelled more and socialized more during the HF compared to the LF season. However contrary to our predictions we found no differences between two groups. Adults were significantly different from immatures only in social behavior.
DISCUSSIONS

Seasonality and group differences in activity budgets

While seasonality clearly affects some activity patterns of WLG (travelling, feeding and social behavior) we did not find any significant effect of group size on gorilla activity budget. Like previous study (Masi et al., 2009) the major activity in both sites was feeding (38.8 %). However the mean percentage of feeding time was lower in comparison to other studies for example 54.5 % (Remis, 1994) and 67.1 % (Masi et al., 2009). These differences in activity budgets could be due to the difference in the methodology used since their results were based on 5-minute instantaneous scan sampling of the group. Also Remis (1994) reported activities of a non-habituated group. In this study, the increased habituation and visibility of the study groups allowed us to carry out continuous sampling on focal animals. We believe these reasons and the more precise observations are responsible of the observed differences with previous studies. Our results on the percentage of time that gorillas spent feeding are closer to those reported by Doran-Sheehy et al. (2009) obtained in Mondika research site in the Republic of Congo (43-44% feeding time) who used the Focal Sampling Method as well. However their study was focused on just adult males and females. Pygmy chimpanzees (or bonobos, 40 %) and Japanese macaques (38 %) have been reported to spend a similar amount of time feeding (Bonobos: White, 1992, Japanese macaques: Hanya, 2004).

As expected from previous findings (Masi et al., 2009) both groups spent more time feeding during the LF than the HF season. Reduced feeding time in the HF season could be explained by increased consumption of ripe fruits which are higher in sugar and energy (Doran-Sheehy et al., 2009; Remis et al., 2001; Masi 2008, Masi et al., 2009) and require less time to process, thereby requiring less time to meet the energy requirement of the groups (Altmann, 1998). Both indirect evidence from trail signs and fecal samples (Calvert, 1985; Rogers et al., 1990; Williamson et al., 1990; Nishihara, 1995; Kuroda et al., 1996; Remis, 1997; Goldsmith, 1999; Doran et al., 2000) and
direct observation (Masi et al., 2009; Doran-sheehy et al., 2009) have shown that fruit consumption increase in western gorillas with increased availability. Reduced feeding time when consuming high quality food has also been shown in Japanese macaques (Hanya, 2004). Western black and white colobus monkeys on the other hand have been reported to show seasonality in their annual diet and activity budgets in response to unripe tree seed availability (Dasilva, 1992) but their response is different from that which western gorillas show to fruit availability. They spend more time feeding during the peak of unripe fruits and rest more when their diet is composed of mainly leaves (Dasilva, 1992). Contrary to our predictions the groups did not significantly differ in time spent feeding. This means that group size does not affect the time western gorillas spend feeding. However more studies with much larger groups are required before a concrete conclusion can be made on this topic. Also contrary to our predictions on resting time, we found no significant difference. Resting time in western gorillas therefore is not affected by group size. In Sulawesi crested black macaques, larger groups spend more time resting than smaller groups (O’Brien & Kinnaird, 1997). It has been shown that resting time in all primates is positively correlated with the amount of leaf in the diet, since more time is required for fermentation (Dunbar, 1998).

Also as expected from previous study (Masi et al., 2009), both WLG groups travelled significantly more during the HF than the LF season. Previous research reported longer daily path lengths when gorillas increased fruit consumption (e.g. Cipolletta, 2004; Doran-Sheehy et al., 2004; Ganas& Robbins, 2005; Goldsmith, 1999; Remis, 1994,1997) and increased travel time (Masi et al., 2009). Fruit trees are patchily distributed in the home range of the gorillas and since western gorillas are selective ripe fruit opportunists (Doran-Sheehy et al., 2009) they need to travel long distances to access these fruits. The opposite situation was found in Sulawesi crested black macaques in which distance moved reduced as fruit consumption time increased (O’Brien & Kinnaird, 1997). In support of our predictions, we found no significant difference between the percentages of time each group spent traveling. Despite Mayele’s larger group size they spent the same time traveling as the Makumba group. Moreover, the daily path lengths of another smaller group of Bai Hokou did not
decrease when the group was reduced to less than half its original size (Cipolletta, 2004). Therefore, the time spent traveling by western gorillas does not seem to be affected by the group size. It could be argued that individuals in larger groups experience more within-group competition, and need to increase travel cost in order to meet the nutritional requirements of all group members (Dunbar, 1988; Janson, 1992; Wrangham et al., 1993; Chapman & Chapman, 2000; Clutton-Brock and Harvey, 1977; Harcourt & Stewart, 2007). This has been shown in Sulawesi crested black macaques where larger groups spent more time travelling than smaller groups (O’Brien & Kinnaird, 1997). However individual primate groups can move faster if they have a longer distance to cover as seen in baboons (Williamson & Dunbar, 2001). Individuals of the Mayele group were always spread out when feeding such that the adult females and their offspring could go as far as 400 m from each other and the silverback while the Makumba group was always cohesive (Personal observation). Therefore, we could hypothesized that western gorillas may respond to increased within-group competition (due to larger group size) to the cost of group cohesion, thus, increasing group spread (Harcourt and Stewart, 2007) rather than travelling longer distances. However, we studied just two groups and there may be inter individual differences of silverback behavior: for example Mayele, the silverback of the larger group is more relaxed about group cohesion than Makumba, the silverback of the smaller group (Personal observation).

In support to our expectation from the previous study (Masi et al., 2009) both WLG groups dedicated significantly more time for social activities during the HF season. The extra energy gained from fruit consumption and possibly the extra time gained from reduced feeding time during this season may explain this pattern (Dunbar 1992; Bronikowski & Altmann 1996; Masi et al. 2009). The mean percentage of time spent for social activities (5.3 %) was similar to that of bonobos (6.3 %, White, 1992) but the types of social behaviors were different. The main social behaviors in both western gorilla groups were play (immature) and vocalization (adults) while the major social behavior for bonobos was grooming (White, 1992). Japanese macaques (16 %) and Sulawesi macaques on the other hand dedicated more time to social activities (O’Brien & Kinnaird, 1997; Hanya, 2004).
Contrary to our predictions we found no significant difference in the time each group dedicated for social activities. Therefore we could hypothesize that in western gorillas the amount of time dedicated to social activities varies with food available rather than by group size. However since immature western gorillas dedicate more time to social activities than adults (Masi et al., 2009) we could argue that the larger group was under represented (three immature individuals out of ten). Therefore more detailed studies need to be carried out to arrive at a concrete conclusion.

We found no significant difference in the percentage of time each group spent for other activities. The main activity in the “other” category was vigilance.

**Age differences**

The effect of age class was significant only for the time dedicated to social activities. We found no significant difference between the percentages of time that both adults and immature spent feeding. A previous study on western gorillas reported lower feeding time in adult males than females and immature (Masi et al., 2009) while another study found no difference in overall time that males and females spent feeding (Doran-Sheehy et al., 2009). Adult male spider monkeys have been shown to feed less than females (Symington, 1988). This is similar to orangutans where adult females and sub adult males feed more than adult males (Mitani, 2005). As a result if high sexual dimorphism in western gorillas adult males need extra energy to maintain large body size as well as group cohesion, compete with other males and guard mates and offspring (Alberts et al., 1996). Adult females on their part need extra energy to cover the increased cost of reproduction since fertilization, pregnancy, lactation and infant dependency are energy consuming; meanwhile the immature need energy to meet the cost of growth (Altmann, 1980). Our study however grouped adult males and females into one category (adults) and sub adults and juveniles into another (immature) due to low sample size, pooling individuals may have had confounded effects on our results. However adult great apes have energy constrains as a result of the high sexual dimorphism and cost of reproduction (Bean, 2001) but the large body size of males my restrict them from
accessing some areas of food patches (such as outer tree branches) while the young might not be strong enough to exploit some resources (such as stripping of bark and breaking of termite mounts). Also smaller animals (females and immature) can be displaced from food sources (Bean, 2001). These factors might also influence the proportion of time that gorillas spend feeding. However more detailed studies are required to give a concrete comparison of adult and immature western gorilla diet.

The percentage of time that adults spent resting was slightly higher (but not significantly) than the time spent by immatures. Most of the time when the adults were resting, the immatures continued playing among themselves (personal observation). This increase in social time is likely the reason for reduced resting time. Age class difference had no effect on the time spent traveling. A previous study reported higher travel time in adult males than females and juveniles (Masi et al., 2009). Adult female and sub adult orangutans spend more time traveling than adult males (Mitani, 2005). Also male sider monkeys have been shown to travel more than females (Symington, 1988). The more cohesive nature of western gorilla groups may imply that individuals spend similar amounts of time traveling.

The immature gorillas dedicated a significantly higher percentage of time for social activities than the adults. A previous study on western gorillas has also yielded the same results (Masi et al., 2009). Immature western gorillas like other young primates need play for proper social development. Through play the basis for adult dominance hierarchy can be set, individuals can be socially integrated into the group structure and could learn how to communicate with/and understand each other (Poirier & Smith, 1974). Theoretically, adult males spend more time and energy guarding the females and immature and maintaining group cohesion while the females spend more energy for reproduction and maternal care.

In conclusion we found that western gorilla activity budgets varied more in response to ripe fruit availability rather than group size and age differences. Both groups responded to these changes
in fruit availability in the same way. Individuals spent significantly more time feeding, traveling and socializing during the high frugivory season than the low frugivory season. The proportion of time spent resting did not vary with season. Adults were significantly different from immatures only in social behavior. Seasonal behavior has also been shown in chimpanzees (Doran, 1997), orangutans (Galdikas, 1988; Knott, 1998; Mitani, 2005), other gorillas species (Watts, 1998), Japanese macaques (Hanya, 2004) and many other primate species (Dunbar, 1992; Hanya, 2004; Brockman and Van Schaik, 2005; Brockman & Van Schaik, 2011). On the contrary very little or no seasonal patterns have been observed in bonobos (White, 1992; 1998). Also a study on Sulawesi crested black macaques reported that group differences were more pronounced than seasonal differences (O’Brien & Kinnaird, 1997). More studies involving larger western gorilla groups and both age and sex categories are required to better understand seasonality in activity budgets.

ACKNOWLEDGMENTS

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CHAPTER 4- Research Article

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The role of food availability and group size in the diet of western lowland gorillas: case study of Bai Hokou and Mongambe in Central African Republic.

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ABSTRACT

Variation in food availability, body size and group size are known to influence primate diet. Very few studies have been carried to describe the diet composition of western gorillas (Gorilla gorilla) based on direct observation. Also no studies so far have compared the feeding behavior of adult and immature western gorillas. In this study we report the effect of season, group size and age class on western gorilla feeding behavior. First of all we compared food availability between the two sites by monitoring the leafing and fruiting patterns of major gorilla food trees. Next, we compared data on the proportion of feeding time dedicated to the consumption of different food types and the diet diversity between the two seasons, two groups and between adults and immatures obtained by Continuous Focal Sampling method. We found that the diet of western gorillas consisted mainly of fruits (35.7 %), followed by stems (24.0 %), leaves (21.4 %), insects (14.2 %) and bark (2.5 %). Time spent consuming fruits, leaves and bark varied with season. We found no difference between the diet composition of the two groups and the two age classes. We then conclude that seasonal variation in fruit availability is more significant in the feeding behavior of western gorillas than the effect of group size. Western gorillas remain selective ripe fruit opportunist and will track fruits when available irrespective of group size or age class. Insects and stems of terrestrial herbal vegetation are staple western gorilla food and their consumption is not affected by seasons, group size or age class. Leaves and bark act as major western gorilla fallback resources during periods of fruit scarcity and are ingested in greater quantities than fruits; as a result western gorillas spend more time feeding during periods of fruit scarcity.

Key words: western gorillas, feeding behavior, age differences, group size, seasonality

INTRODUCTION

Information on the foraging strategy of primates and their response to changes in resource availability is crucial to understand the evolutionary history of the different primate taxa (Schoener,
1971; Dunbar, 2002). Unlike folivorous primates, frugivorous primates face the challenge of varying food availability due to fluctuating spatial and temporal distribution of fruiting trees (Van Schaik et al., 1993; Morellato et al., 2000; Brugiere, 2001; Hemingway & Bynum, 2005; Van Schaik & Pfannes, 2005). According to Hemingway and Bynum (2005) primates are flexible with their diet but might optimize their energy budget by either minimizing the time spent on food intake or maximizing the energy intake at the expense of time requirements in line with evolutionary life history analyses (Schoener, 1971; Brockman & Van Schaik, 2005). Therefore by investigating the foraging strategies of primates albeit seasonal changes in food availability, we seek to understand the mechanisms leading to their diverse adaptations to different environments.

Comparisons between feeding strategies of apes and old world monkeys revealed that, ape diet varies with availability of fruits while diet of old world monkeys remains diverse and stable all year round (see review by Doran-Sheehy, 2009). Different ape species, however, show different levels of flexibility to fluctuating food availability. For example orangutan diet may vary from 100% fruit during fruit peaks to very low fruit and more bark intake (up to 50%) during periods of fruit scarcity (Galdikas, 1988; Knott, 1998). Chimpanzees are highly selective ripe-fruit specialists depending on availability but can switch to lower energy foods during periods of scarcity (Wrangham et al., 1998). Bonobos on the other hand show no seasonal variation in their fruit-rich diet composition (White, 1998). In contrast, mountain gorillas at Karisoke consume relatively large amount of foliage (up to more than 90% of their diet) throughout the year (Watts, 1984, 1998). Western gorillas live sympatric to chimpanzees in many habitats and they are ripe fruit opportunists showing a diverse diet and large flexibility to fluctuating food availability (Head et al., 2011). However, till recently most of the information on western gorilla diet was based on indirect studies using faecal samples and trail signs rather than direct observation due to the difficulty of habituating western gorillas to human presence in the tropical rain forest (Tutin and Fernandez, 1991; Blom et al., 2004; Doran-Sheehy et al., 2007). Earlier studies on indirect evidence (reviewed by Rogers et al., 2004) showed seasonal changes in diet and activity of western gorillas such as increasing the intake of high-energy
succulent ripe-fruit during periods of high fruit availability accompanied by increase in distance travelled and home range. Conversely, during the periods of fruit scarcity the diet of the western gorillas rely on low energy foliage such as fibrous fruits, leaves, stems and bark (Rogers et al., 1990; Williamson et al., 1990; Remis et al., 1994; Tutin, 1996; Yamagiwa et al, 1996; Remis, 1997; Tutin et al., 1997; Doran and McNeilage, 1998; Goldsmith 1999; Doran et al., 2002; Oates et al 2003,). These studies provided a broad overall understanding of the diet diversity and pattern of fruit consumption but more recent systematic studies done on habituated groups made available more detailed assessment of the quantity and quality of western gorilla food (Doran-Sheehy et al., 2006; Cipolletta et al., 2007; Doran-Sheehy et al., 2009; Masi et al., 2009). These studies indicate large variations in the percentage of time spent feeding by western gorillas. Doran-sheehy et al. (2009) reported that western gorillas in Mondika, Republic of Congo spent 43-44 % of their time feeding while Masi et al. (2009) reported that gorillas in Bai Hokou, CAR spent 67 % of the time feeding. Similarly the proportion of fruit consumption time in overall feeding scans reported also vary, ranging from 14% to 36% (Cipolletta et al., 2007; Doran-Sheehy et al., 2006, 2009; Masi et al., 2009). However, most of these studies have been based on data from a single male (Cipolletta et al., 2007; Doran-Sheehy et al., 2006), a single group (Masi et al., 2009) and a comparison between just the silverback and adult females of a group (Doran-Sheehy et al., 2009). There is therefore the need to further investigate and compare between group variations in order to have a better understanding of western gorilla diet.

In this study we report western gorilla diet based on systematic direct observation of two western lowland gorilla groups living in areas about 10 km apart, Bai Hokou and Mongambe, in the Dzanga-Sangha National Park of Central African Republic. We therefore aim to provide the first concise comparison of the diet of two western gorilla groups of different size and composition living in similar forests, thus likely to be exposed to similar conditions of food availability during the same period. Given however that significant variation in food availability could occur even between adjacent sites sharing similar plant and animal species and experiencing similar climatic systems
(Chapman et al., 1999), our first objective is therefore to compare the availability of food in both sites by comparing the phenology of young leaves, flower and fruits of major gorilla food trees during the period of study. Following this objective, our first prediction therefore is that (1) there exist some difference between the leafing and fruiting patterns of major gorilla fruiting trees in Bai Hokou and Mongambe. Our second objective is to evaluate the proportion of feeding time dedicated to the consumption of different food types and the diversity of species consumed (dietary breadth) by providing a concise comparison between the groups, the different age classes and seasons. We predict that (2) the diet of the smaller group (Makumba, N = 9) will contain a greater proportion of fruits than the larger group (Mayele, N = 15) since the larger group size of Mayele might not be sustained by the fruit trees present in its home range. The Mayele group should be able to switch to a less fruity diet to meet is energy requirements (Brockman & Van Schaik, 2005; Hemingway & Brynum, 2005). Also we predict that (3) the larger group will have a greater diet diversity and breadth and spend more time feeding than the smaller group. We expect a strong correlation between fruit consumption and ripe fruit availability in both sites (as observed by Masi et al., 2009; Doran-Sheehy et al., 2009) however we predict that (4) the larger group will have a stronger correlation to fruit availability since this is a more limiting resource for them and when fruit is available they will track it more tightly. We would expect to (5) find a more energetic; fruit based diet in adults due to higher daily energetic cost as a result of the high sexual dimorphism in gorillas (Breuer et al., 2007). Adult males need this extra energy to maintain their large body sizes and females need extra energy to meet the cost of reproduction (Bean, 2001).

METHODS

Study site

[See section 2.1]
Study species
[See section 2.2]

Study groups
[See section 2.3]

Data collection
[See section 2.4]

Statistical analysis
[See section 2.5]

The research complied with protocols approved by the American Society of Primatologists with ethical guidelines for the treatment of non-human primates, was approved by the appropriate animal care and use committees (i.e. Oxford Brookes University, UK) and followed Central African Republic’s laws for foreign research.

RESULTS

Food availability

There was no significant difference between the proportion of major gorilla food trees leafing in Bai Hokou (mean = 32.5 ± SD 10.2 %) and Mongambe (mean = 28.3 ± SD 8.7 %) during the six months of study (Wilcoxon signed-rank test: Z = 0.734, P = 0.463, N = 6, figure 8a). Also we found no significant difference between the proportion of major gorilla food trees fruiting in Bai Hokou (mean = 17.1 ± SD 7.3 %) and Mongambe (mean = 15.3 ± SD 10.0 %) throughout the study period (Wilcoxon signed-rank test: Z = 0.734, P = 0.463, N = 6, figure 8b). During the high frugivory (HF) season in Bai Hokou a mean of 19.9 ± SD 2.7 % trees were leafing and 23.8 ± SD 7.3 % trees were fruiting while during the low frugivory (LF) season a mean of 38.8 ± SD 1.0 % of trees were leafing.
and 13.1 ± SD 5.1 % of trees were fruiting (Figure 8). Similarly, during the HF season in Mongambe a mean of 26.4 ± SD 1.0 % of trees were leafing and 28.2 ±SD 0.2 % trees were fruiting while during the LF season a mean of 29.2 ± SD 11.0 % of trees were leafing and 8.9 ± SD 1.1 % trees were fruiting (Figure 8).

![Figure 8: Bar chart comparing the monthly percentage of trees leafing (a) and fruiting (b) in Bai Hokou (BH) and Mongambe (MG). Total number of trees monitored in Bai Hokou = 365 and Mongambe = 314](image)

**Diet composition**

With regards to the proportions of time spent consuming the different food types, the diet of both groups of western gorillas consisted mainly of fruits (35.7 ± SE 3.0 %), followed by stems (24.0 ± SE 2.1 %), leaves (21.4 ± SE 3.8 %), insects (14.2 ± SE 2.3 %) and bark (2.5 ± SE 0.9 %). Other food types (flowers, mushrooms) grouped together with items eaten so fast that could not be identified made up 3.1 ± SE 1.1 % of the diet (Figure 9).
Seasonality and group differences

Table IV) Effects of season and group on western gorilla feeding behavior and diet according to mixed model repeated measures analyses of variance (ANOVA)

<table>
<thead>
<tr>
<th>season</th>
<th>group</th>
<th>Season*group</th>
</tr>
</thead>
<tbody>
<tr>
<td>FR</td>
<td>17.924***</td>
<td>0.000</td>
</tr>
<tr>
<td>ST</td>
<td>0.008</td>
<td>0.929</td>
</tr>
<tr>
<td>LV</td>
<td>9.292**</td>
<td>0.010</td>
</tr>
<tr>
<td>BK</td>
<td>7.867*</td>
<td>0.016</td>
</tr>
<tr>
<td>INS</td>
<td>0.156</td>
<td>0.700</td>
</tr>
<tr>
<td>OF</td>
<td>4.202</td>
<td>0.063</td>
</tr>
<tr>
<td>DD</td>
<td>0.102</td>
<td>0.755</td>
</tr>
</tbody>
</table>

Results of separate mixed model repeated measures ANOVA with time spent feeding, proportion of feeding time dedicated to the consumption of fruits (FR), stems (ST), leaves (LV), insects (INS), bark (BK) and other food types (OF) and mean number of species consumed (DD) as dependent variables, and season and group as independent predictors. Values are F-values and significant values at P<0.05, P<0.01 and P<0.001 are represented by *, ** and *** respectively.

As expected the proportion of feeding time dedicated to fruits consumption varied significantly between seasons (Table IV). Fruits consumption was higher during the HF season (mean Makumba = 47.0 ± SE 6.7 % and mean Mayele = 54.4 ± SE 7.8 %) than the LF season (mean Makumba = 27.3 ± SE 5.3 % and mean Mayele = 14.1 ± SE 6.2 %). However the effect of group difference on the proportion of time dedicated to fruit consumption was not significant (Table IV).
Figure 9: Diet composition of the Makumba and Mayele western gorilla groups during the high frugivory (a) and low frugivory season (b) as depicted by the percentages of time spent feeding on each food type.
The effect of season on leaves consumption was significant (Table IV). Both groups spent more time consuming leaves during the LF season (mean Makumba = 37.9 ± SE 9.4 %; mean Mayele = 29.7 ± SE 3.8 %) than the HF season (mean Makumba = 6.7 ± SE 4.4 %; mean Mayele = 11.1 ± SE 10.9 %). However the effect of group on overall leaf consumption time was not significant (Table IV). Leaves of *Whitfieldia elongata* were consumed regularly in both seasons. We found no seasonal differences in the percentage of time spent feeding on stems (Table IV). Makumba (mean HF = 26.5 ± SE 5.4 %, mean LF = 20.3 ± SE 5.1 %) and Mayele (mean HF = 21.0 ± SE 6.3 %, mean LF = 28.4 ± SE 9.9 %) did not differ significantly on the overall time spent feeding on stems (Table IV, Figure 9). Bark consumption was also significantly affected by season (Table IV). Bark consumption was minimal during the HF season but increased during the LF season especially for the Mayele group (Figure 9, Table IV).

Time spent feeding on insects did not differ between the two seasons (Table IV). Also both Makumba (mean HF = 16.8 ± SE 5.0 %, mean LF = 9.6 ± SE 3.1 %) and Mayele (mean HF = 13.2 ± SE 5.7 %, mean LF = 17.0 ± SE 3.6 %) did not differ significantly in time spent feeding on insects (Table IV). Termites (*Cubitermes* sp.) and different species of ants were the only two types of insects consumed. We found a trend in the time spent feeding on other food items between seasons (Table IV). Mayele tended to spent more time than Makumba feeding on other food types. Followed by flowers, the main “other food types” were wild mushrooms obtained from the soils of monodominant patches of *Gilbertiodendron dewevrei* by soil scratching. We observed dung consumption (gorilla dung) in both groups and noted identified food items consumed accordingly but unidentified items were recorded as “other food”.

The number of species consumed by the gorillas was not affected by season (Table IV) and the number of species consumed per day was not significantly different between Makumba (7.6 ± SE 1.4 species) and Mayele (8.6 ± SE 1.6 species).


**Seasonality and age class differences**

Adults (mean HF = 31.3 ± SE 5.4 %, mean LF=45.6 ± SE 5.9 %) and immatures (HF = 29.8 ± SE 4.7 %, LF = 48.8 ± SE 5.1 %) did not differ significantly in the percentage of time they spent feeding within the different seasons (table V). Also the effect of age class differences did not significantly affect the overall time the gorillas spent feeding (table V). We found no significant age class differences also in the time gorillas spent consuming fruits, leaves, stems, insects and other food types (Table V, Figure 10). However we found a trend in bark consumption time (table V). Adults tended to consume more bark than the immature (Figure 10).

We found no significant difference between the average number of species consumed by adults and immatures (Table V). However the effect of “season*age class” was significant (Table V). The immature consumed more species during the HF season but during the LF season the adults consumed more species (Table VI).

Table V) Effects of season and age class on western gorilla feeding behavior and diet composition according to mixed model repeated measures analyses of variance (ANOVA)

<table>
<thead>
<tr>
<th>season</th>
<th>Age class</th>
<th>Season*age class</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>feeding</td>
<td>7.085*</td>
<td>0.021</td>
</tr>
<tr>
<td>Fruit</td>
<td>13.642**</td>
<td>0.003</td>
</tr>
<tr>
<td>Bark</td>
<td>9.494*</td>
<td>0.010</td>
</tr>
<tr>
<td>Leaf</td>
<td>9.929**</td>
<td>0.008</td>
</tr>
<tr>
<td>Stem</td>
<td>0.026</td>
<td>0.874</td>
</tr>
<tr>
<td>Insects</td>
<td>0.296</td>
<td>0.596</td>
</tr>
<tr>
<td>Other</td>
<td>2.303</td>
<td>0.155</td>
</tr>
<tr>
<td>diversity</td>
<td>0.049</td>
<td>0.828</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>F</td>
<td>0.045</td>
<td>0.836</td>
</tr>
<tr>
<td>F</td>
<td>0.014</td>
<td>0.906</td>
</tr>
<tr>
<td>F</td>
<td>0.005</td>
<td>0.945</td>
</tr>
<tr>
<td>F</td>
<td>0.017</td>
<td>0.784</td>
</tr>
<tr>
<td>F</td>
<td>14.283**</td>
<td>0.003</td>
</tr>
<tr>
<td>P</td>
<td>0.139</td>
<td>0.716</td>
</tr>
<tr>
<td>P</td>
<td>0.032</td>
<td>0.862</td>
</tr>
<tr>
<td>P</td>
<td>3.671</td>
<td>0.079</td>
</tr>
<tr>
<td>P</td>
<td>0.130</td>
<td>0.725</td>
</tr>
<tr>
<td>P</td>
<td>0.645</td>
<td>0.438</td>
</tr>
<tr>
<td>P</td>
<td>0.000</td>
<td>0.987</td>
</tr>
<tr>
<td>P</td>
<td>0.005</td>
<td>0.945</td>
</tr>
</tbody>
</table>

Results of separate mixed model repeated measures ANOVA with proportion of feeding time dedicated to the consumption of fruits, stems, leaves, insects, bark and other food types as dependent variables, and season and age class as independent predictors. Values are F-values and P significance. Significance level at P<0.05 and P<0.01 are indicated by * and **.
Figure 10: Diet composition of the adult and immature western gorilla during the high frugivory (a) and low frugivory season (b) as depicted by the percentages of time spent feeding on each food type.
Table VI) Adult and immature western gorilla diet composition as depicted by the percentage of time spent feeding on different food types.

<table>
<thead>
<tr>
<th>Food type/season</th>
<th>Mean % time ± SE</th>
<th>adults</th>
<th>immatures</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit HF</td>
<td>48.9±7.9</td>
<td>51.2±6.8</td>
<td></td>
</tr>
<tr>
<td>Fruit LF</td>
<td>21.8± 6.8</td>
<td>21.4±5.9</td>
<td></td>
</tr>
<tr>
<td>Bark HF</td>
<td>0</td>
<td>0.03±0.01</td>
<td></td>
</tr>
<tr>
<td>Bark LF</td>
<td>8.4±2.6</td>
<td>2.0±2.2</td>
<td></td>
</tr>
<tr>
<td>Leaf HF</td>
<td>7.4±5.1</td>
<td>9.5±4.4</td>
<td></td>
</tr>
<tr>
<td>Leaf LF</td>
<td>36.6±11.0</td>
<td>32.7±9.5</td>
<td></td>
</tr>
<tr>
<td>Stem HF</td>
<td>26.0±6.3</td>
<td>22.7±5.5</td>
<td></td>
</tr>
<tr>
<td>Stem LF</td>
<td>19.2±5.9</td>
<td>27.2±5.2</td>
<td></td>
</tr>
<tr>
<td>Insect HF</td>
<td>15.5±5.8</td>
<td>15.1±5.0</td>
<td></td>
</tr>
<tr>
<td>Insect LF</td>
<td>12.9±3.9</td>
<td>12.7±3.4</td>
<td></td>
</tr>
<tr>
<td>Other HF</td>
<td>1.4±1.5</td>
<td>1.9±1.3</td>
<td></td>
</tr>
<tr>
<td>Other LF</td>
<td>4.2±2.5</td>
<td>4.4±2.2</td>
<td></td>
</tr>
</tbody>
</table>

Percentages of time that adult and immature western gorillas spent feeding on different food types and the average number of species consumed (diversity) during the high frugivory (HF) and low frugivory (LF) seasons

In summary, contrary to our predictions there was no difference in food availability between the two sites. Also we found no significant differences between the diet compositions of the two groups. Both age classes also had the same diet composition.

DISCUSSIONS

Food availability

We found no significant difference between the leafing and fruiting patterns of major gorilla food trees in Bai Hokou and Mongambe. This means both western gorilla groups were exposed to similar food availability conditions during the study period. However, western gorillas also consume fruits and leaves of lianas, piths and leaves of terrestrial vegetation and insects which are not measured in this study. Therefore, the aim of our study is not to quantify the overall food availability
for gorillas but simply, show fruiting and leafing patterns of the most important western gorilla food (Masi, 2008). A similar phenological study by Remis (1997) in Bai Hokou found a lower proportion of trees with young leaves (monthly percentages ranging from 1-36 %) and fruits (monthly percentage ranging from 1-24 %). The study however covered a longer period (March 1990-August 1992). Our study is limited to just six months and does not depict complete leafing and fruiting cycles, and possible inter-annual variations in food availability shown in other phenological studies (Van Schaik et al., 1993; Remis, 1997; Chapman et al, 1999; Morellato et al., 2000; Brugiere et al., 2002; Bollen & Donati, 2005).

**Diet composition, seasonality and group differences**

As expected on the bases of previous study (Masi et al., 2009) both groups spent more time feeding during the LF than the HF season. Reduced feeding time in the HF season could be explained by increased consumption of ripe fruits which are higher in sugar and energy (Remis et al., 2001; Masi, 2008; Doran-Sheehy et al., 2009; Masi et al., 2009) thereby requiring less time to meet the energy requirement of the groups (Altmann, 1998). Foliage on the other hand is lower in energy content (Altmann, 1998; Remis et al., 2001; Doran-Sheehy et al., 2009) and requires greater quantity to meet the energy requirements of the group. Thus during the LF season when ripe fruits are scarce and western gorillas depend on foliage, they require more to ingest larger quantities of food, thus longer feeding time, to meet their energy requirements.

Overall fruits were the most consumed food type by the western gorilla groups, followed by stems, leaves, insects and then bark. Both groups spent more time consuming fruits during the HF season than the LF season. This increased fruits consumption with increased availability has been shown by both indirect studies based on feeding signs and analyses of fecal samples (Calvert, 1985; Rogers et al., 1990; Williamson et al., 1990; Nishihara, 1995; Kuroda et al., 1996; Remis, 1997; Goldsmith, 1999; Doran et al., 2000) and direct observation (Doran-sheehy et al., 2009; Masi et al.) 2009). However contrary to our prediction we found no significant difference between the proportions of
fruits in the diet of the two groups. This means that group size does not affect frugivory in western gorillas. In Sulawesi crested black macaques larger groups have been shown to consume less fruit in comparison to smaller groups (O’Brien & Kinnaird, 1997). Our study emphasizes the importance of fruits in the diet of western gorillas. Western gorillas remain ripe fruit opportunists and will track ripe fruits when available no matter the group size (Rogers et al., 1990; Doran-Sheehy et al., 2009). However just a few more individuals might not really make a difference, hence more studies need to carried out on much larger groups before making a concrete conclusion.

Stems of terrestrial herbal vegetation were consumed in equal proportion throughout the study. Stems are richer in proteins than fruits; provide more minerals than leaves and are readily available all year round (Altmann, 1998; Doran-Sheehy et al., 2009). This explains why we found no significant difference between the time spent for stems consumption in both groups and seasons. Stems are therefore staple western gorilla food (Doran et al., 2002; Doran-Sheehy et al., 2009) and can act as a buffer in the diet of most frugivorous primates in areas of lower density of fruit patches (Bean, 2001).

Leaves consumption was affected by seasons since both groups spent significantly more time consuming them in the LF season than the HF season. Similar to the gorillas in Mondika, Republic of Congo, the main leaf types consumed were *Whitfieldia elongate* and *Celtis mildbraedii* possibly because of their high protein content (Doran-Sheehy et al., 2009). Leaves contain more proteins but less energy than fruits and are more fibrous (Altmann, 1998; Remis et al., 2001; Doran-Sheehy et al., 2009) so are consumed in great quantities only in the absence of fruits. Leaves are therefore a major fallback resource for western gorillas (Doran et al., 2002; Doran-Sheehy et al., 2009). Contrary to our predictions the two groups did not differ in the proportion of leaves in their diet. So both groups met their energy requirements without necessarily changing the diet composition. This is as a consequence of having the same proportion of fruits in their diet. Both groups consumed more fruits
during high fruit availability (in similar amounts) and so should have similar amounts of the fallback resource in the season of fruit scarcity.

Bark consumption was also very seasonal ranging from almost zero consumption in the HF season to a higher consumption in the LF season. Bark was the least consumed of all the food types and it seems to be really a fallback food for western gorillas. Insects (mainly termites) were present in the diet and consumed in similar quantities by both groups and in both seasons. A similar proportion of termite has been observed in a previous study on western gorillas of Bai Hokou (CAR) that included also a third group (Cipolletta et al., 2007). Termites are a rich source of protein thus required in almost equal amounts all year round.

Seasonal and group differences had no effect on the number of species consumed. This means diet diversity (number of species consumed) is not affected by group size or food availability. These results confirm that western gorilla diet may be very varied yet selective (Rogers et al., 2004). They are very flexible and consume succulent ripe fruits when available and switch to fallback foods in times of fruit scarcity, allowing them to maintain the diversity of species consumed. However, further studies on the number of food items (food type per each species) consumed needs to be done since a diet switch can always result to an increase or decrease in dietary breadth (Wrangham, 1977; Bean, 2001; Hemingway & Brynum, 2005). Moreover, data were collected during half day observations so might not represent the complete daily diet of the individual gorillas. For example on very wet mornings the gorillas constructed day nests and rested for many hours and fed more towards the afternoon so if data were collected in the first half of the day, it could be under representative of the daily diet.

**Age class and diet differences**

The proportion of time that adults spent feeding was not different from that of immature. Also there was no significant difference in the proportion of time that both age classes spent feeding on fruits, stems, leaves and insects. Therefore as contrary to our predictions we found no significant
difference between the diet composition of adult and immature western gorillas. Bark consumption however tended to be higher in adults than immature. This could be explained by the fact that young primates are weaker and find it difficult to strip off the bark of trees (Bean, 2001). Generally adult great apes have energy constrains as a result of the high sexual dimorphism and cost of reproduction (Bean, 2001) but the large body size of males my restrict them from accessing some areas of food patches (such as outer tree branches) while the young might not be strong enough to exploit some resources (such as stripping of bark and breaking of termite mounts). Also smaller animals (females and immature) can be displaced from food sources (Bean, 2001). However more detailed studies are required to give a concrete comparison of adult and immature western gorilla diet.

The immature consumed significantly more food species in the HF season than the adults. This could be explained by hierarchy in feeding whereby adults monopolize resources and displace younger ones (Bean, 2001) so that they search alternative food sources. This could also be as a result of lower neophobia in trying out different food items in immature western gorillas (Masi et al., 2012).

In conclusion, seasonal variation in fruit availability is more significant in the feeding behavior of western gorillas than the effect of group size. Western gorillas remain selective ripe fruit opportunist and will track fruits when available irrespective of group size or age class. Insects and stems of terrestrial herbal vegetation are staple western gorilla food and their consumption is not affected by seasons, group size or age class. Leaves and bark act as major western gorilla fallback resources, however leaves are consumed in higher proportions than bark. These two resources are consumed more during periods of food scarcity and are ingested in greater quantities than fruits; as a result western gorillas spend more time feeding during periods of fruit scarcity. Other ape species also show seasonality in diet. The diet of orangutans may vary from 100 % fruits during months of high fruit availability to about 27 % fruits and 37 % bark when fruits are scarce (Galdikas, 1988; knott, 1998). However contrary to western gorillas, male orangutans ingest more calories than females.
during seasons of fruit scarcity. Even though chimpanzees maintain a more selective ripe fruits diet than western gorillas (Head et al., 2011) they also respond to fruit scarcity by incorporating herbs, bark and pith in their diet (Wrangham et al., 1998; Head et al., 2011). Contrary to western gorillas and other great apes, the diet of Old World monkeys are not affected in great magnitudes by seasonal changes (see review by Doran-Sheehy et al., 2009). More studies with larger gorilla groups and different ages well represented are required make concrete comments on the effect of group size on diet.

ACKNOWLEDGEMENTS

We would like to thank the government of the Central African Republic, namely the Ministre de l’Education Nationale, de l’Alphabetisation, de l’Enseignement Superieur, et de la Recherche for providing research permits to conduct our work in the Central African Republic; World Wildlife Fund and the administration of DSPA for granting research approval and assistance with obtaining permits; and the Primate Habituation Programme for providing logistical support in the field. This study complied with animal care regulations and national protocols. We greatly thank the Oxford Brookes University and Muséum National d’Histoire Naturelle (MNHN) for institutional support. Many thanks to WWF for continued support and logistical assistance and the PHP guides, Nganare Guy and Franck Dodonou for phenological data collection. We gratefully acknowledge Dr Anna Feistner for logistical help, profound encouragements and very valuable comments on this manuscript. Very special thanks go to the Ba’Aka trackers for their incredible help and invaluable involvement.
Chapter 5 – General Conclusions

Contrary to my predictions Bai Hokou and Mongambe do not significantly differ in availability of major western lowland gorilla (WLG) food showing that both groups even though spaced about 10 km apart are exposed to similar conditions of varying food availability between seasons. Both groups spend majority of their time feeding (38.8 %), followed by resting (33.1 %), traveling (19.1 %) and a small proportion for social activities (5.3 %). Some aspects of their activity budgets vary between seasons but contrary to my prediction both small and large groups respond similarly. Irrespective of group size, WLGs feed less, travel more and socialize more during seasons of high frugivory in comparison to the low frugivory seasons but the time spent resting does not vary between seasons or groups. Therefore WLGs respond more to changes in food availability than group and age differences. Apart from social behaviour, activity budgets and diet of adults are similar to those of immatures showing that in western gorillas the energy requirements for the large bodied silverbacks, reproducing females and growing immatures may reach the same level. As previously shown (Masi et al., 2009), my results show that WLG dedicate only little time to intra-group social interactions, particularly adults. Immatures dedicate a significantly higher proportion of time to social activities (mainly play) than adults. This result highlights that the main strong social bond in WLG groups is mainly between females and their offsprings, or among youngsters (Masi et al., 2012), no real special bonds are found among adults (Personal observation).

Based on the proportion of time spent feeding on different food items, fruits (35.7 %) constitute the greatest proportion of western gorilla diet, followed by stems (24 %), leaves (21 %) insects (14 %), and a very small proportion by bark (2.5 %). The high proportion of fruit in diet shows that WLGs track fruit when available therefore cutting down these fruit trees will greatly affect their diet. Irrespective of group size and age class, WLGs cope in the face of changing food availability by adapting their diet to suit seasons. Typical diet composition of the high frugivory season includes more fruits, less leaves and bark in comparison to the low frugivory season when less fruits, more
leaves and bark are consumed. Stems of terrestrial vegetation and insects are staple WLG food and their proportion in the diet does not show any seasonality. WLGs may therefore be more resilient to the effects of logging than sympatric chimpanzees.

However not all individuals of the larger group were sampled (just six out of 15) so it might be under represented. Furthermore comparing a group of nine to that of 15 individuals might not make a suitable comparison for effects of group size and pooling large body-sized and heavy weighted silverback and females into one category for analyses might have masked the differences between the different ages. Future studies aimed at investigating the effects of group size and age class on gorilla diet and activity budgets should involve groups with a larger difference in group size.
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Appendices

Appendix I: Ethics clearance

Faculty of Humanities and Social Sciences

Application for ethics approval for a research project involving human participants

Undergraduates and Foundation Degree Students:
Before completing this form, the ethics review checklist (School form HSS.E1) should have been completed to establish whether an additional application for ethics approval is required. If ethics approval is required, you should complete this form, sign it and submit it to the Faculty Research Ethics Officer, Maggie Wilson at mwilson@brookes.ac.uk. A decision form, E3 will then be returned to you by e-mail.

Master’s Students:
You should complete this form before you start your project and submit it to your supervisor. If he or she is unable to sign it at this stage, the form will be referred to the Faculty Research Ethics Officer, as above, who may seek further information and clarification from you. A decision form, E3, will then be returned to you by e-mail.

All students should refer to the University Code of Practice on Ethical Standards for Research involving Human Participants, available at www.brookes.ac.uk/es/ethics and Faculty guidelines, which are included in the relevant on-line module or course handbook. You should bind a copy of the approved form in your final project or dissertation submission.

1. Name of Principal Investigator (Student):
   Terence Fuh Neba
   E-mail address: terencefuh@yahoo.com

2. Name of Supervisor and e-mail address:
   Dr Giuseppe Donati
   E-mail address: gdonati@brookes.ac.uk

3. Working Project Title:
   The role of food availability and group size on the diet and activity pattern of western lowland gorillas in Dzanga-Sangha, Central African Republic.

4. Project Type (please specify course and give module number):
   Master’s project: MSc Primate Conservation P20107
   Master’s dissertation: MSc Primate Conservation P20107
   Undergraduate project:
   Undergraduate dissertation:
   Foundation degree project:
7. Participants involved in the research:

Two well-established gorilla groups, Matutu (9 individuals) and Mabinti (16 individuals) will be followed as part of the behavioral data. Every day a team of researchers will observe the groups. During this activity, the abundance, type, and feeding behavior of leaf and fruit will be monitored as well as the animal's activity. This information will be used to gain an understanding of the general knowledge on their ecology and conservation strategies to ensure long-term viability.

6. Methods of data collection:

6.1 a) Number of hours per day: 4 hours.

6.1 b) Observation schedule:

Two well-established gorilla groups, Matutu (9 individuals) and Mabinti (16 individuals), will be followed as part of the behavioral data. Every day a team of researchers will observe the groups. During this activity, the abundance, type, and feeding behavior of leaf and fruit will be monitored as well as the animal's activity. This information will be used to gain an understanding of the general knowledge on their ecology and conservation strategies to ensure long-term viability.

5. Background and rationale of proposed research:

The proposed research aims to examine the diet, activity patterns, and behavioral ecology of western lowland gorillas. A significant reduction in numbers due to habitat loss and poaching has led to the species being critically endangered. Western lowland gorillas are found in forests that remain unharmed. The Regional Action Plan for the Conservation of Chimpanzees and Gorillas in Western Equatorial Africa and the general knowledge on their ecology and conservation strategies will be used to ensure long-term viability.
8. Potential benefits of the proposed research:

9. Potential adverse effects of the proposed research and steps to be taken to deal with them:

(These could include possible psychological stress or anxiety)

10. Plan for obtaining informed consent:

(Please attach copy of information sheet and consent form)

Note: consent forms are not needed for questionnaires

11. Steps to be taken to ensure confidentiality of data:

(Please outline steps to be taken to ensure confidentiality, privacy and anonymity of data during collection, storage and publication of data)

N/A

All materials submitted will be treated confidentially.

I have read and understood the University’s Code of Practice on Ethical Standards for Research involving Human Participants

Signed: ________________________________

Principal Investigator
/Student

Signed: ________________________________

Supervisor

Date: 5/3/2013

everyday gorilla tracking will be led by two trackers. All these people are staff of the Primate
Habituation Program and it is their job to assist all researchers.

Much remains to be learned about the ecology and behaviour of western lowland gorillas. Also, the immediate and long term response of gorillas to logging remains unresolved. This project will provide rich knowledge to add on to the available information on this species necessary for the formulation of conservation strategies to ensure long term viability.

Following habituated gorillas at close range can expose them to diseases and stress. We will maintain the 7m rule of gorilla tracking and keep the team at a minimum number. We will also follow all protocols of working with gorillas. All sick staff will be exempted from going close to the gorillas.

N/A (No consent is required since no one will be interviewed).
## Appendix II: Gorilla food list

<table>
<thead>
<tr>
<th>Ba’aka name</th>
<th>Scientific name</th>
<th>Kind</th>
<th>Part eaten by gorilla</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apa</td>
<td>Vapaca guineensis</td>
<td>tree</td>
<td>bark - leaf</td>
</tr>
<tr>
<td>Babango</td>
<td>Diospyros iturensis</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Bambu</td>
<td>Gambeya lacourtiana</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Bemba ( malapa )</td>
<td>Gilbertiodendron deweuvrei</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Beti ( mbeti )</td>
<td>Uvariastrum pierreanum</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Bokoko</td>
<td>Ataenidia conferata</td>
<td>tree</td>
<td>leaf - fruit</td>
</tr>
<tr>
<td>Boko</td>
<td>Grewia</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Bokoko</td>
<td>Klainedoxa gabonensis</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Boto</td>
<td>Mammee africana</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Doto</td>
<td>Palisota ambiqua</td>
<td>thv</td>
<td>stem</td>
</tr>
<tr>
<td>Djele</td>
<td>Tetraptera tetraptera</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Ekoule</td>
<td>Dioscorea</td>
<td>liana</td>
<td>leaf</td>
</tr>
<tr>
<td>Ekoule akoumba )</td>
<td>Anchomanes diffamis</td>
<td>liana</td>
<td>leaf - stem</td>
</tr>
<tr>
<td>Ekoumbe</td>
<td>Anchomanes diffamis</td>
<td>liana</td>
<td>leaf - stem</td>
</tr>
<tr>
<td>Embema</td>
<td>Pterocarpus soyauxir</td>
<td>tree</td>
<td>fruit - leaf - bark - flower - stem</td>
</tr>
<tr>
<td>Embongo</td>
<td>Srombosia postulata</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Epopolo</td>
<td>Berlinia</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Etebele( Eboto fruit )</td>
<td>Detarium macrocarpia</td>
<td>tree</td>
<td>fruit - leaf - bark</td>
</tr>
<tr>
<td>Etokoloko</td>
<td>Tabernaemontana</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Etokobola</td>
<td>Tridisia Macrophilla</td>
<td>liana</td>
<td></td>
</tr>
<tr>
<td>Gao</td>
<td>Laccospenna Secundiflora</td>
<td>palm</td>
<td>stem - leaf</td>
</tr>
<tr>
<td>Genye</td>
<td>Aframomum lemon</td>
<td>thv</td>
<td>stem - fruit</td>
</tr>
<tr>
<td>Indjombo(Toundou=fruit)</td>
<td>Aframomum sp</td>
<td>thv</td>
<td>stem - fruit</td>
</tr>
<tr>
<td>Indolou</td>
<td>Whitfiela elongata ?</td>
<td>liana</td>
<td>leaf</td>
</tr>
<tr>
<td>Indoya</td>
<td>Whitfiela elongata ?</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Inganda(molopo)</td>
<td>Milletia sp</td>
<td>tree</td>
<td>leaf</td>
</tr>
<tr>
<td>Ingoka</td>
<td>Thomadesia laurifolia</td>
<td>tree</td>
<td>fruit - leaf - stem</td>
</tr>
<tr>
<td>Ingoyo</td>
<td>Pancovia laurentii</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Kakala</td>
<td>Celtis adolfi-fridenci</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Kaya (ngwasa )</td>
<td>thv</td>
<td>fruit - leaf</td>
<td></td>
</tr>
<tr>
<td>Kiyeye(in the clearing)</td>
<td>Scleria sp</td>
<td>thv</td>
<td>stem</td>
</tr>
<tr>
<td>Koko</td>
<td>Gnetum</td>
<td>vine</td>
<td>leaf</td>
</tr>
<tr>
<td>Kusa</td>
<td>Manniofriton fuluum</td>
<td>vine</td>
<td>stem</td>
</tr>
<tr>
<td>Landa ( ndembo )</td>
<td>Futumia elasrica</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Lembe(ita ti babango na)</td>
<td>Diospyros Crassiflora</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Molombo</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Liamba</td>
<td>Ficus moscoso</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Madjembe</td>
<td>Urera</td>
<td>liana</td>
<td>leaf</td>
</tr>
<tr>
<td>Maimbo</td>
<td>Trichilia</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Mangabo ( ita ti doto )</td>
<td>Palisota brachithyrsa</td>
<td>thv</td>
<td>stem</td>
</tr>
<tr>
<td>Name</td>
<td>Scientific Name</td>
<td>Category</td>
<td>Notes</td>
</tr>
<tr>
<td>-----------------------</td>
<td>-----------------------------</td>
<td>------------</td>
<td>------------------------------</td>
</tr>
<tr>
<td>Matokodi</td>
<td>Augicocalix pinaertii</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Madjome</td>
<td>Dialium guineense</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Mbango</td>
<td>Pacchyphyllum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mbindjo</td>
<td>Dalhousiea africana</td>
<td>vine</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Mbongo (embongo)</td>
<td>Fernandoa Adolfi fradericii</td>
<td>tree+liana</td>
<td>leaf - flower</td>
</tr>
<tr>
<td>Moadjali</td>
<td>Antrocaryou micrastes</td>
<td>tree</td>
<td></td>
</tr>
<tr>
<td>Mobéi</td>
<td>Anonidium mannii</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Mokata</td>
<td>Symphonia Globulifera or</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Mokenjenje</td>
<td>Synsepalum stipatum</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Mosse</td>
<td>Nauclea diderrichii</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Mokombe</td>
<td>Dialium</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Molombo</td>
<td>Dyaspiros sp</td>
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<td></td>
</tr>
<tr>
<td>Mongendja</td>
<td>Manilkara letouzeyi</td>
<td>tree</td>
<td>fruit - leaf - bark</td>
</tr>
<tr>
<td>Mongwangwa</td>
<td>Vitex grandifolia</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Mosombo</td>
<td>Irvingia grandifolia</td>
<td>tree</td>
<td>leaf</td>
</tr>
<tr>
<td>Motunga</td>
<td>Poliaithia swerc lens</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Ndembo</td>
<td>Landolphia</td>
<td>liana</td>
<td>fruit - stem</td>
</tr>
<tr>
<td>Njobe</td>
<td>Strombosia grandifelia</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Ngata</td>
<td>Myriathus arboreus</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Ngomangoma</td>
<td>Barteria fistulosa</td>
<td>tree</td>
<td>leaf - bark</td>
</tr>
<tr>
<td>Ngombe</td>
<td>Celtis mildbraedii</td>
<td>tree</td>
<td>fruit -leaf - bark -flower - stem</td>
</tr>
<tr>
<td>Ngoumou</td>
<td>Ficus sp</td>
<td>liana</td>
<td>fruit -leaf - bark</td>
</tr>
<tr>
<td>Ngouluma</td>
<td>Duboscia macrocarpa</td>
<td>tree</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Payo</td>
<td>Irvingia excelsa</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Pembe</td>
<td>Landolphia</td>
<td></td>
<td>fruit - bark</td>
</tr>
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<td>Pota</td>
<td>Hexabolus crispiflorus</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Tembo</td>
<td>Drypetes</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Tondo</td>
<td></td>
<td>liana</td>
<td>fruit - leaf</td>
</tr>
<tr>
<td>Toundou (fruit of Injombo)</td>
<td>Aframonum</td>
<td>fruit</td>
<td>fruit</td>
</tr>
<tr>
<td>Touba</td>
<td>Donella ubeguensis</td>
<td>tree</td>
<td>fruit</td>
</tr>
<tr>
<td>Wusa</td>
<td>Treculia africana</td>
<td>tree</td>
<td>fruit</td>
</tr>
</tbody>
</table>
Appendix III: Cover Letters for Article Submission

1. International Journal of Primatology

Terence Fuh,
Avenue des Matyrs,
B.P. 1053, Bangui,
Central African Republic.
Tel: (236) 75 14 25 42
Email: terencefuh@yahoo.com

Editorial Board,
International Journal of Primatology

6th September 2013

Dear Sirs,

Please find accompanying this letter submission of manuscript titled:

‘The role of food availability and group size on activity budgets of western lowland gorillas (Gorilla gorilla gorilla) in the Dzanga-Sangha National Park of Central African Republic’.

Variation in food availability, group size, body size, climate and anthropogenic activities in the habitat of western lowland gorillas could influence their behaviour and diet. Not much is known about the ecology and behaviour of this species since habituating them to human presence has been a great challenge. We report how food availability, group size and age/sex differences may influence feeding behaviour of western lowland gorillas.

Word Count:
I declare that the work described has not been published previously and that it is not under consideration for publication elsewhere. I confirm that all co-authors acknowledge their participation in conducting the research leading to this manuscript and agree to its submission to be considered for publication. The manuscript has been approved tacitly or explicitly authorities of the Primate habituation Program, Dzanga-Sangha Protected Areas.

I look forward to hearing from you,

Yours sincerely,

Terence Fuh

[Signature]

[Logos: WWF, Oxford Brookes University]
2. American Journal of Primatology

Terence Fuh,
Avenue des Matyrs,
B.P. 1053, Bangui,
Central African Republic.
Tel: (236) 75 14 25 42
Email: terencefuh@yahoo.com

Editorial Board,
American Journal of Primatology

6th September 2013

Dear Sirs,

Please find accompanying this letter submission of manuscript titled:

‘The role of food availability and group size on the diet of western lowland gorillas: case study of Bai Hokou and Mongambe in Central African Republic’.

Variation in food availability, group size, body size, climate and anthropogenic activities in the habitat of western lowland gorillas could influence their diet and activity patterns. Yet much remains to be learned about the ecology and behaviour of this species since habituating them to human presence has been a great challenge. We report how food availability, group size and age/sex differences may shape the diet and activity pattern of western lowland gorillas.

Word Count:
I declare that this is original work submitted solely to AJP and that it has not been published elsewhere and also all co-authors acknowledge their participation in the research and agree to its submission to be considered for publication. All appropriate ethics and other approvals were obtained for the research.

I look forward to hearing from you,

Yours sincerely,

Terence Fuh