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**Links between foraging strategies, feeding competition, and female agonistic relationships
in wild western gorillas (*Gorilla gorilla*)**

A Dissertation Presented

by

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Abstract of the Dissertation

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The links between female foraging strategies, feeding competition, and female social relationships in group-living primates have been a major focus of study for more than 35 years. Particular attention has been paid to the role of feeding competition, since differences in female competitive regimes have been hypothesized to explain much of the observed variation in female social relationships, dispersal patterns and reproductive success. Many of the tenets of the ensuing socioecological model have been tested, and in general the model has great explanatory power. However, some behavioral variation remains unexplained. The strength of contest competition, dependent on resource characteristics and some other modulating factors, is expected to vary across habitats within and between primate species along with the fraction of the diet composed of high quality monopolizable resources. Yet other factors may be equally or more important; in particular, the ability of females to avoid contest competition depends on group cohesion, which is related to risk of predation or infanticide either directly or indirectly

through their effects on group size, number of males per group, and sex-specific dispersal patterns. The relationships between resource characteristics and grouping patterns are of particular importance to socioecological models because they are thought to determine the monopolizability of resources from the primates' point of view. Some inconsistencies with the model can be attributed to the complexities of measuring and understanding variability in resource characteristics from a primate perspective including the quality, density, and spatial distribution of resources and the size and distance between alternative food sources in relation to primate preferences and group spread.

In this dissertation I examine the nutritional, social, and energetic consequences of increased fruit consumption in wild western lowland gorillas (*Gorilla gorilla*) with comparisons to mountain gorillas (*Gorilla beringei*). Specifically, I aim to determine whether dietary differences in western gorillas are associated with differences in the nutritional composition of the diet, and whether increased aggression over food can be linked to more consistent female dominance relationships and a linear and steep hierarchy and a positive correlation between female dominance rank and overall energy intake. I predict that the diet of western gorillas will be more diverse and varied in composition and will contain more fruit by wet weight and more total non-structural carbohydrates on a dry matter basis compared to that of mountain gorillas. Furthermore, I expect that increased reliance on fruit will be associated with higher rates of aggression over fruit in western compared to mountain gorillas and that increased aggression over fruit will be associated with a higher proportion of decided female dominance relationships and linear dominance hierarchies based on aggression. Based on expectations for increased within-group contest competition, I predict that female differences in overall individual energy acquisition will occur on the basis of rank and that aggression will be the primary mechanism by

which rank-based skew in overall energy intake occurs, although supplants or avoidance could promote this effect as well.

To address these predictions I studied a single one-male multi-female group of western gorillas in tropical lowland forest at the Mondika study site located along the boundaries of Central African Republic and Republic of Congo during August-November 2003, December 2004-October 2005, and June-August 2006. Feeding and behavioral data for four adult females were collected during full- and half-day focal follows. Nutritional analyses were conducted on gorilla food samples collected during follows to determine macronutrient, fiber, moisture, ash, and energy content of staple foods.

Results revealed that female western gorillas at Mondika consumed considerably more fruit by wet weight and that the nutritional composition of the diet contained more total non-structural carbohydrates than did that of mountain gorillas. This difference is likely related to the higher quality of western gorilla fruits compared to mountain gorilla fruits. As predicted, I found that female western gorillas directed higher rates of aggression toward other females over fruit. Dominance relationships were decided in many (60 %) though not all female dyads ($n = 15$ dyads) on the basis of aggression ($n = 551$ events) and stability was indicated in the directionality of decided relationships. Dominance hierarchies (for $n = 6$ females) were steep and linear in two of the four aggression data sets. Some females differed considerably from others in their overall competitive ability based on aggression while others differed little if at all. In addition, variation in female energy intake throughout the year was linked to the amount of time spent feeding and the proportion of feeding time spent on fruit, thus establishing the conditions for the occurrence of contest competition. However, contrary to predictions females did not differ in their overall rate of energy intake on the basis of rank, suggesting that contest competition is less strong or

more variable seasonally in western gorillas than expected on the basis of the relatively high percentage of fruit in the diet. This is a notable result considering that Wright and colleagues (2014) recently demonstrated rank-related variation in energy intake among female mountain gorillas at Bwindi. More research is needed to address the monopolizability of high quality fruits in western gorilla diets and to determine whether relaxed group cohesion allows low-ranking females to reduce within-group contest competition by avoiding high-ranking individuals while foraging on high quality resources during most of the year.

Dedication Page

To my parents,
for nurturing my appreciation for nature

Table of Contents

Abstract of the Dissertation	iii
Links between foraging strategies, feeding competition, and female agonistic relationships in wild western gorillas (<i>Gorilla gorilla</i>).....	iii
Dedication Page.....	vii
Table of Contents	viii
List of Figures.....	x
List of Tables	xi
Acknowledgments	xiii
CHAPTER ONE:	1
Introduction.....	1
Factors that might modulate within-group contest competition	8
Within-group feeding competition in apes and the potential for contest competition in western gorillas.....	9
Aims of this dissertation	11
Overview of study site, study periods, and research subjects.....	12
Overview of thesis chapters.....	13
CHAPTER TWO:.....	16
Differences in diet composition and nutrient intake between western lowland gorillas (<i>Gorilla gorilla</i>) at Mondika and mountain gorillas (<i>Gorilla beringei</i>) at Karisoke and Bwindi	16
Abstract.....	16
Introduction.....	17
Methods.....	22
Study site and subjects	22
Data collection	23
Chemical analysis of western gorilla foods	27
Data analysis	29
Cross-site comparison of the nutrient content of gorilla foods.....	31
Results	34
Overall diet diversity and composition	34
Nutrient composition of foods	34
Comparison of western and mountain gorilla diet and nutrient intake	36
Discussion.....	38

Western gorillas: measures of dietary composition	38
Dietary and nutritional differences between lowland and highland gorillas	39
Tables and Figures	46
CHAPTER THREE:	61
Female agonistic relationships, steepness of dominance hierarchies, and the role of the male in reinforcing within-group social relationships in wild western gorillas (<i>Gorilla gorilla</i>) ..	61
Abstract	61
Introduction	62
Methods	74
Study site	74
Study subjects and sampling protocol	75
Results	82
Type, frequency, and context of female aggression	82
Female rank, competitive ability, and steepness of hierarchies	84
Degree of directionality in dyads	85
Stability in female dominance relationships	87
Discussion	90
Assessments of rank, dominance relationships, and hierarchy characteristics	90
Tables and Figures	104
CHAPTER FOUR:	118
Dominance rank and energy intake in wild western gorilla females (<i>Gorilla gorilla</i>)	118
Introduction	118
Methods	126
Study site and study subjects	126
Data collection	127
Data analysis	128
Statistical methods	132
Results	136
Overall dietary pattern and energy intake	136
Rank and energy intake	138
Discussion	140
Tables and Figures	148
CHAPTER FIVE:	162
Summary and conclusions	162
Ecological flexibility in gorilla diet and nutrition	163
Effect of increased frugivory on female agonistic relationships	165
Dominance and energy intake in western gorillas	167
Benefits of high rank in western gorillas	170
Conclusions	171
References	173

List of Figures

Figure 2.1. Mean percentage (wet weight based on staple foods scaled up to 100 %) of fruit, herb, and leaf in gorilla diets at Mondika, Bwindi, and Karisoke.....	59
Figure 2.2. Total non-structural carbohydrate (TNC), crude protein (CP), and neutral detergent fiber (NDF) content (% dry matter) of preferred (Pref: n = 5) and non-preferred (Fall: n = 4) fruits in the staple diet at Mondika compared to staple fruits (n = 3) at Bwindi.....	60
Figure 3.1. Female competitive ability and steepness of dominance hierarchies based on normalized David's scores (Norm DS) for A) aggression (n = 551 events), B) decided aggression (n = 263 events), C) aggressive signals (n = 484 events), and D) decided aggressive signals (n = 222 events).....	112
Figure 3.2. Stability of female dominance relationships in A) focal and B) non-focal dyads based on initiation of aggressive signals within four time periods.....	113
Figure 3.3 Stability of female rank and steepness of dominance hierarchies based on normalized David's scores (Norm DS) for all aggressive signals initiated within each of the four periods from Figure 3.2, including A) Period 1: n = 29 signals, B) Period 2: n = 74 signals, C) Period 3: n = 157 signals, and D) Period 4: n = 120 signals.....	115
Supplementary Figure 3.1. A comparison of female competitive ability in four datasets.....	117
Figure 4.1. Mean monthly proportion (+ SE) of feeding time spent on fruit and leaf.....	152
Figure 4.2. Mean monthly energy intake rate (kcal / hr + SE).....	153
Figure 4.3. Comparing models of female energy intake rate with model selection statistics and parameter estimates for best-fitting model.....	154
Figure 4.4. Correlation between rank and energy intake rate within months.....	155
Figure 4.5. Mean monthly rate of alpha female aggression (N of events / hr + SE) toward other females while feeding on fruit.....	156
Supplementary Figure 4.1. Histogram of follow duration and scatter-plot of relationship between follow duration and proportion of time spent feeding. Loess smoothing line (right panel) is for demonstration purposes.....	161

List of Tables

Table 2.1. Diet of adult female western gorillas ranked by percent intake by wet weight averaged across 11 months.....	46
Table 2.2. Macronutrient, fiber, energy, and moisture content of western gorilla fruits, leaves, and herbs at Mondika.....	52
Table 2.3. Mean nutrient content (% dry matter) of preferred and non-preferred fruit and herb species in the diet of western gorillas at Mondika.....	53
Table 2.4. Inventory of staple gorilla food types at Mondika, Bwindi, and Karisoke.....	54
Table 2.5. Mean (SD) nutrient content (% dry matter) of fruit and herb species in the staple diet of western (Mondika) and mountain (Bwindi; Karisoke) gorillas.....	55
Table 2.6. Nutrient contributions (percentage of dry matter intake) to gorilla diets at Mondika (in bold), Bwindi, and Karisoke with comparisons to chimpanzees, bonobos, and three species of African monkey with non-specialized guts.....	56
Supplemental Table 2.1. Nutrient content (% dry matter) of staple gorilla foods at Mondika, in descending order of wet weight contribution.....	57
Table 3.1. Testing the links between increased percentage of potentially monopolizable food items (percent frugivory) in the diet, context of aggression, and female agonistic relationships in three populations of gorillas.....	105
Table 3.2. Monthly distribution of full- and half-day focal follows for four adult female western gorillas (MA; ME; BE; EB).....	106
Table 3.3. Minimum number of aggressive events (Min N) required within a dyad to detect decided dominance relationships at $p < 0.05$, according to the degree of skew (Win ratio) in the percent of events won by each dyad member (F1; F2).....	107
Table 3.4. Summary of MatMan female dominance hierarchies using four data sets.....	108
Table 3.5. Summary of decided dominance relationships based on four data sets (A-D) using G-tests.....	109
Table 3.6. Percentage of aggression initiated or won by the dominant female in dyads.....	111
Supplemental Table 3.1. Calculation of David's scores using decided aggressive signals ($n = 222$ signals).....	116

Table 4.1. Number and duration of follows used to examine rank and energy intake and variation in feeding behavior.....	148
Table 4.2. Monthly variation in female feeding strategies, including time spent feeding, feeding time spent on fruit and leaf, and effects of fruit and leaf feeding on time spent feeding.....	149
Table 4.3. Comparing models of female energy intake rate with model selection statistics and parameter estimates for best-fitting model.....	150
Table 4.4. Correlation between rank and energy intake rate within months.....	151
Supplemental Table 4.1. Distribution of 212 half-day follows by month (M; December-October) and focal female (MA, ME, BE, EB), including sample sizes (N), mean duration (Hrs), and mean start (Start), and stop (Stop) times of morning (M) and afternoon (A) follows (F).....	157
Supplemental Table 4.2. Short-duration follows (< 4.5 hrs) excluded from feeding and energy intake analysis.....	158
Supplemental Table 4.3. Energy content (kcal/ 100 g organic matter) and intake rates (mean wet g / min) of fruits (FR = pulp; SE = seed), herbs (ST = stem; SH = shoot), termites (TE), and leaves (LE= leaf; BK = young bark) consumed by female western gorillas and sorted in descending order of caloric value by food type.....	159

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CHAPTER ONE: Introduction

Energy intake and expenditure limits female fitness in mammals, birds, and in other animals in which maternal investment in the production and rearing of offspring is energetically costly and depends critically on a female's ability to acquire enough high quality food to meet energetic demands (Williams 1966; Trivers 1972; Bradbury and Vehrencamp 1977; Wrangham 1980; Clutton-Brock et al. 1982; Wade and Schneider 1992). Accordingly, females provisioned with high quality food reach age of first reproduction earlier, have shorter inter-birth intervals, and wean infants earlier compared to non-provisioned females (Sadleir 1969; Gilmore and Cook 1981; Lunn et al. 1984; Asquith 1989; Hendrickx and Dukelow 1995; Gomendio et al. 1995; Takahata et al. 1998; Borries et al. 2001; Altmann and Alberts 2003a; Altmann and Alberts 2003b; Altmann and Alberts 2005). Female reproductive success also depends on maternal and offspring survival, however, and local predation pressure is thought to be an important factor shaping individual mortality risk and grouping behavior in the wild (Struhsaker and Leakey 1990; Isbell 1994; Hill and Dunbar 1998; Janson 1998; Wright 1998; Boinski et al. 2000; Hass and Valenzuela 2002; Boinski and Chapman 2005). Female foraging strategies have thus evolved to reflect the basic tradeoff between minimizing predation risk and maximizing foraging efficiency (Janson 1990; Kotler et al. 1991; Isbell 1994; Janson and Goldsmith 1995).

van Schaik and colleagues (van Schaik 1983; Janson and van Schaik 1988; van Schaik 1989) hypothesized that female primates form groups to reduce the risk of predation but subsequently incur costs as a result of increased feeding competition with increased group size and cohesion. Differences in the quality, size, and distribution of food resources are thought to

determine the mode(s) of feeding competition within and between primate groups, and this in turn has been hypothesized to explain much of the intra- and inter-specific variation in female social relationships, dispersal patterns, and reproductive success seen in primates (Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Koenig 2002).

Two modes of feeding competition are recognized in the feeding ecology literature, contest and scramble (Nicholson 1954). Contest competition is predicted to occur when high quality resources can be monopolized or usurped so that priority of access is based on fighting ability or rank (Janson and van Schaik 1988). Within-group contest competition occurs in some species when high-ranking females direct aggression toward (or supplant) low-ranking females over access to monopolizable resources, whereas in other species low-ranking females systematically avoid dominant females with the same net result of reduced food acquisition in subordinates (Janson and van Schaik 1988). Repeated aggression or supplants are hypothesized to lead to unidirectional dominance relations and a linear dominance hierarchy (van Schaik 1989; Sterck et al. 1997). In this situation kin-based coalitions could provide females and their relatives with greater access to monopolizable resources and consequently higher fitness, and so females should benefit from remaining in, rather than dispersing from, their natal group (Wrangham 1980; van Schaik 1989).

In contrast, scramble competition occurs when resources are evenly and abundantly distributed in very large patches or concentrated in very small patches with short depletion times (van Schaik 1989; Boinski 1999; Boinski et al. 2002) such that any attempts to monopolize a patch or usurp resources from another individual would not be worthwhile regardless of size or rank. Thus all females within a group have equal access to resources and should not be expected to differ in resource acquisition or reproductive success (van Schaik 1989; Sterck et al. 1997).

Scramble competition is indicated when individual energy intake within a group decreases with increasing group size, because group size is the main factor influencing individual access to resources (van Schaik and van Noordwijk 1988; Janson 1988; Janson and van Schaik 1988; van Schaik 1989) and reproductive success. Since resources cannot be monopolized under these ecological conditions, unidirectional female dominance relationships and linear dominance hierarchies based on aggression or supplants over food would not be expected to occur within groups and kin-based coalitions should be uncommon among females (van Schaik 1989). If risk of predation is low, females may move freely between groups and particularly to smaller groups (if other factors allow) to reduce scramble feeding competition by maximizing foraging efficiency (Wrangham 1980; van Schaik 1989; Sterck et al. 1997).

The presence of scramble and contest competition within and between primate groups is thought to have a predictable influence on female agonistic relationships, dispersal, and individual feeding success (van Schaik 1989; van Schaik 1996; Sterck et al. 1997). The basic premises of the current socioecological model (Sterck et al. 1997) and the empirical data available to test each premise have been reviewed (Koenig 2002). Much of the current socioecological model is supported, although much still remains to be tested and some behavioral variation remains unexplained by the model (Koenig and Borries 2006; Thierry 2007; Broom et al. 2009; Koenig and Borries 2009). Several of these inconsistencies with the model will be described in Chapter 3. Some refinements to the current socioecological model are presumably needed to accommodate behavioral variation not accounted for by ecological, demographic, or anthropogenic (e.g. habitat disturbance) explanations (van Schaik 1996; Sterck et al. 1997; Sterck 1998). However, a group of leading researchers agree that primates show remarkable ecological flexibility in the composition of their diets, nature of female social

relationships, dispersal patterns, and rates of reproduction within and between closely related species living in different environments (Sterck et al. 1997; Boinski et al. 2002; e.g. see Koenig and Borries 2006; Koenig and Borries 2006). The most extensive and robust evidence for this flexibility comes from comparative studies of squirrel monkeys (Mitchell et al. 1991; Boinski 1999), baboons (Byrne et al. 1990; Barton and Whiten 1993; Barton et al. 1996), and Hanuman langurs (Borries et al. 1991; Borries 1993; Koenig 2000; Borries et al. 2001) occupying different habitats with varying resource characteristics.

One of the best empirical demonstrations of behavioral responses to different habitat types comes from baboons studied in two contrasting environments, *Papio anubis* at the savanna site of Laikipia (Kenya) and *Papio ursinus* at the montane site of Drakensberg (South Africa). At Laikipia, the baboons spent a considerably higher percentage of feeding time on clumped foods and experienced higher predation pressure compared to baboons at Drakensberg (Barton et al. 1996). These conditions at Laikipia were also associated with higher rates of agonism overall and in the context of feeding, increased group cohesion when foraging, higher rates of female coalition formation and female-female grooming, a significant positive correlation between rank and food intake, and much lower incidence of female dispersal compared to baboons at Drakensberg (Barton et al. 1996).

Baboons at different sites have long been noted for their pronounced intra- and inter-specific differences in the composition of the diet (Altmann et al. 1987; Byrne et al. 1993; Barton et al. 1996; Altmann 1998; Codron et al. 2006; Johnson et al. 2012), which is hypothesized to result from variation between sites in the quality and availability of resources. Baboons inhabit a broad geographic range, and although baboon diets are nearly always eclectic, at some sites there is little overlap in the types of foods consumed (Barton et al. 1993; Byrne et al. 1993; Codron et

al. 2006; Johnson et al. 2012). Such dramatic differences in dietary composition are reflected in the percentage of fruits and seeds, underground plant parts, leaves, flowers, and animal prey in the overall diet. For example, at some sites underground plant parts account for more than 50% of the baboon diet by percent feeding time, whereas at other sites fruits and seeds exceed more than 50 % of baboon feeding time and underground plant parts are a much less important component of the overall diet (Altmann 1998; Kamilar 2006).

Nutritional differences in the composition of primate diets can result from major differences in the percentage of various food types consumed but also based on differences in the nutrient makeup of a given food type across sites. In baboons, the nutrient makeup of foods was broadly similar between sites in close geographic proximity to one another with similar habitat types (Altmann et al. 1987; Barton et al. 1993). However, for sites separated by wide geographic distance with very different habitat types (i.e. forest vs savanna) some differences in the nutrient content of baboon foods were indicated between sites when comparing among shared food types (Barton et al. 1993; Johnson et al. 2012), suggesting that the nutrient profiles of baboon diets in different environments have the capacity to differ.

The nutrient composition of primate diets may, however, retain similarities among populations of a species occupying environments in relatively close geographic proximity to each other. One example in support of this notion comes from dietary comparisons of blue monkeys (*Cercopithecus mitis*) and mountain gorillas (*Gorilla beringei*) inhabiting moderate-to-high elevation sites in east Africa, including the Virunga Volcanoes of Rwanda, Democratic Republic of Congo, and Uganda (*C. mitus*; *G. beringei*), Kibale National Park in Uganda (*C. mitus*), and Bwindi Impenetrable Forest in Uganda (*G. beringei*). A comparison of blue monkeys in the Virunga Volcanoes with those at Kibale and mountain gorillas in the Virunga

Volcanoes with those at Bwindi revealed that for each species the nutrient profiles did not differ between sites (Twinomugisha et al. 2006; Rothman et al. 2007) despite differences in the number and diversity of staple foods. This raises the question of whether primates inhabiting a wide range of habitat types at different altitudes like blue monkeys, gorillas, and baboons adjust their diets to achieve a species-specific optimal arrangement of nutrients and whether environmental differences need be more extreme to reflect nutritional differences. I hypothesize that the quality and availability of staple foods will determine the nutrient composition of the diet at different locations, and that there is no fixed nutrient profile for diets of a species or closely related species.

Fruit is a high quality and preferred food type for all great apes, including chimpanzees, gorillas, bonobos, and orangutans. For gorillas, some species of fruits are, in addition, relatively rare in the environment, concentrated in their spatial distribution, and limited in their seasonal availability (Rogers et al. 1990; Williamson et al. 1990; Tutin and Fernandez 1993; Remis 1997; Remis et al. 2001; Doran et al. 2002). If fruits are more desirable than other food types, then the percentage of fruit in the diet may serve as a simple and reliable indicator of contest competition in the absence of data on patch monopolizability (e.g. resource characteristics; feeding party size; exclusion of individuals from the patch), although this can also work with flowers and high quality leaves as seen in folivorous primates (Koenig et al. 1997; Koenig et al. 1998; Koenig 2000).

In this dissertation, I aim to explore whether a considerable increase in the percentage of fruit in the diet of western lowland gorillas (*Gorilla gorilla*) is associated with i) differences in the overall nutrient composition of the diet compared to that of mountain gorillas (Watts 1984; Watts 1996; Doran and McNeilage 2001; Rothman et al. 2007; Doran-Sheehy et al. 2009a; Masi

et al. 2009) as well as b) a host of different social and energetic aspects of female group life based on predictions for increased contest competition in the socioecological model, if fruit were an indicator of contest competition (van Schaik 1989; Sterck et al. 1997). Gorillas have been studied for the composition of their diets and nutrient content of foods at several sites, and differences in diet have been revealed for western gorilla populations as compared mountain gorillas on the basis of indirect sampling methods and direct feeding observations (Waterman et al. 1983; Watts 1984; Calvert 1985; Rogers et al. 1990; Williamson et al. 1990; Tutin and Fernandez 1993; Nishihara 1995; Kuroda et al. 1996; Remis 1997; Rogers et al. 2004; Rothman et al. 2007; Ganas et al. 2009). The present study will expand on these past studies to examine whether such dietary differences are associated with fundamental shifts in the nutrient profile of the diet, the nature of female agonistic relationships, and whether female dominance rank is correlated with individual energy intake within the group.

Here, I use behavioral data collected from a group of habituated western gorillas inhabiting tropical lowland forest in west-Central Africa over eighteen months from 2003 to 2006 to examine whether a more frugivorous population of gorillas relative to those of mountain gorillas, which are largely herbivorous (Watts 1984; Watts 1996; Rothman et al. 2007), differ fundamentally in the nutrient composition of their diets, patterns of aggression, consistency of female dominance relationships, linearity of the female dominance hierarchy, and frequency of female coalitions. To test whether western gorillas face considerable within-group contest competition as a consequence of increased frugivory, I describe the wet weight diet of female western gorillas and use estimates of the energy content of dietary items to test whether females differ in the overall rate of energy intake on the basis of dominance rank as predicted by the socioecological model.

Factors that might modulate within-group contest competition

The degree to which contest competition, indicated by rank-related differences in resource acquisition, is expressed across primate populations should vary considerably based on continuous variation in resource characteristics and other modulating factors. First, if group cohesion is high such as in cases of high predation pressure (van Schaik 1989; Barton et al. 1996), then low-ranking females must be in frequent association with high-ranking females and may suffer feeding costs as a result. However, if group cohesion is reduced through reduced risk of predation or infanticide (van Schaik and Kappeler 1997), individuals can forage more independently, and low ranking females may be able to compensate for reduced access to high quality patches.

Patterns of sex-biased dispersal and the number of males in a group may also influence the expression of within-group contest competition. For example in one-male multi-female social organizations in which female secondary transfer commonly occurs the male may benefit from egalitarian relationships among females, because females that lose too many contests may transfer (Watts 1994; Watts 2003). If so, then the male would be expected to reduce a high-ranking female's ability to exert her power by punishing females that initiate aggression (Watts et al. 2000; Watts 2003). In this case, the frequency of feeding contests would depend on how frequently females foraged separately from the male. If the male is frequently present in the same feeding party as females he may act to reduce individual variation in female energy intake in monopolizable food patches. However, rank-related differences in resource acquisition could occur in the male's absence.

Within-group feeding competition in apes and the potential for contest competition in western gorillas

Understanding the role of feeding competition in great apes compared to smaller primates has long been a challenge because their larger body sizes lead to reduced predation pressure (Doran and McNeilage 2001) and therefore the primary benefit attributed to cohesive grouping is lacking (but see: Harcourt and Stewart 2007). It has been suggested that due to lower predation risk great apes may reduce the effects of feeding competition by increasing group spread, as evidenced by frequent solitary foraging or fission-fusion in all species (van Schaik and van Hoof 1996; White 1996; Wrangham et al. 1996; Doran and McNeilage 2001) but mountain gorillas (Watts 1996). However, although within-group contest competition may be minimized through compensatory mechanisms, it does not preclude the presence of some contest competition. Linear dominance hierarchies have been described for female chimpanzees in the Tai Forest (Wittig and Boesch 2003) and higher-ranking female chimpanzees at Gombe have faster maturing daughters and higher infant survival than lower-ranking females (Pusey et al. 1997). Thus, either the relationship between feeding competition, rank and energy gain, and reproductive success does not explain the presence of female dominance hierarchies in all primates or significant contest competition might occur in societies with reduced cohesion of group members and female transfer.

Feeding competition and its consequences are well studied in mountain gorillas. They feed on resources that are abundant and evenly distributed throughout the year (Watts 1984; Watts 1998; Rothman et al. 2007), with the exception of fruits at Bwindi (Rothman et al. 2006a;

Rothman et al. 2007; Robbins 2008; Rothman et al. 2011) and seasonal bamboo shoots at Karisoke (Watts 1998; Harcourt and Stewart 2007), and the importance of feeding competition is limited in terms of contest and scramble effects on female reproductive success (Watts 1985; Watts 1996; Watts 2003; Robbins et al. 2007). Consequently, most contests over food in mountain gorillas do not interrupt feeding (Watts 1994; Watts 2003), females do not form linear dominance hierarchies on the basis of aggression (Watts 1994; but see: Robbins 2008) because most aggression is bidirectional and undecided in outcome (Watts 1994; Robbins 2008), although a linear hierarchy is supported for the Karisoke population based on displacements (Watts 1994; Robbins et al. 2005), and females disperse from their natal groups (Watts 1996).

Western gorillas differ from mountain gorillas in several aspects of their feeding ecology, including having a more variable and diverse diet consisting of much more fruit (Tutin et al. 1991; Watts 1996; Remis 1997; Rogers et al. 2004; Doran-Sheehy et al. 2009a; Masi et al. 2009) and showing decreased group cohesion (Doran and McNeilage 2001; Salmi 2013). Although western gorilla diets include relatively abundant and evenly distributed foods such as herbs and leaves as in mountain gorillas (Rogers et al. 2004), other components of the diet such as fruits and seeds are more patchily distributed and seasonal (Williamson et al. 1990; Remis 1997; Doran et al. 2002). Thus, increased reliance on fruit in western gorillas might be associated with increased within-group contest competition compared to mountain gorillas ("but see:" Wheeler et al. 2013). On the other hand, reduced group cohesion may reduce contest competition within groups by allowing low-ranking females to spread out while foraging and avoid higher-ranking females at monopolizable fruit patches. Indeed, group spread is estimated to be large in western gorillas, with females sometimes foraging hundreds of meters from other group members (Doran and McNeilage 2001; Salmi 2013). In addition, demographic studies indicate that reproductive

groups of western gorillas contain only one male (Parnell 2002; Stokes et al. 2003; Robbins et al. 2004) in contrast to more frequent multi-male groups in mountain gorillas (Robbins et al. 2001). The presence of one silverback male may explain additional variation in the dynamics of aggression among females depending on whether the male intervenes in female aggressive conflicts and in what direction his support is given. Based on these differences in dietary composition, group cohesion, and presence of only one silverback male in western gorillas as compared to mountain gorillas, I seek to test whether these differences are associated with greater within-group contest competition, a divergent nutritional profile, and more clearly differentiated female agonistic relationships in western as compared to mountain gorillas.

Aims of this dissertation

In this dissertation, I examine the nutritional, social, and energetic consequences of increased frugivory (if fruit were an indicator of contest competition) in wild female western gorillas with comparisons to mountain gorillas as a test of the socioecological model's (van Schaik 1989) predictions for within-group contest competition. First, I describe the wet weight and nutrient composition of the female western gorilla diet at a lowland mixed species forest site (Mondika) and explore whether differing ecological conditions between western and mountain gorilla habitats are associated with differences in the nutritional composition of gorilla diets. Second, I examine the context, rate, and outcomes of female aggression in a group of western gorillas for which fruit comprises more than a third of the overall female diet based on feeding time (Doran-Sheehy et al. 2009a) and determine whether increased feeding aggression (over fruit) is associated with a greater proportion of decided dominance relationships compared to

mountain gorillas and a steep and linear dominance hierarchy based on aggression. Third, I test whether females differ in their overall rate of individual energy intake on the basis of dominance rank in western gorillas, which is an indicator of contest competition, and further characterize what factors influence variation in female energy intake throughout the year.

Overview of study site, study periods, and research subjects

Research was conducted at the Mondika Research Center (02° 21' 859'' N, 016° 16' 465'' E) site established in 1995 by Diane Doran (Doran and McNeilage 1998) along the border of the Central African Republic (Dzanga-Sangha National Park) and the Republic of Congo (bordering Nouabale-Ndoki National Park). The study area encompasses 50 km² of tropical lowland mixed-species forest (altitude: < 400 m) including strips of monodominant *Gilbertiodendron dewevrei* (Caesalpiniaceae) forest along streams, swamp forest bordering the Ndoki River, and light gaps (Mehlman and Doran 2002). There is little topographic relief within the study area. There is no evidence of recent human disturbance or logging at the site and the study area is home to 10 species of diurnal primates (Doran et al. 2002), including guenons, mangabeys, red colobus monkeys, black and white colobus monkeys, chimpanzees, and gorillas. Annual rainfall averages 1600 mm (8 years of rainfall data, Doran-Sheehy et al. 2009a) and is seasonal in distribution, with a two-to-three month annual dry season (of less than 50 mm of rainfall per month: December-March) and a two-month period of higher than average rainfall (> 200 mm per month: August-September). Daily temperatures ranged from a mean minimum of 21.0 C to a mean maximum of 28.2 C (5 years of temperature data, Doran et al. 2002).

Data were collected in August-November 2003 (during a pilot study), December 2004-October 2005 (during the main study period), and June-August 2006 (during a supplementary

study period). A single study group known as the Kingo group, which had been followed on a near-daily basis since 2001, was the focus of this study. The group was composed of one silverback male, 5-6 adult females, and their offspring. Although the silverback had been the subject of focal follows since 2001, females were slower to habituate. Prior to the start of the main study period in November 2004 four of six adult females permitted close following and became the subjects of focal follows.

Overview of thesis chapters

In chapter two I assess whether the nutritional composition of the diet in western gorillas differs from that described for mountain gorillas at two sites. In this chapter, I describe the wet weight diet of female western gorillas, identify staple foods, compare nutrient content of major food types (fruits, leaves, herbs) based on chemical analysis, and compute overall nutrient consumption in western gorillas on a dry matter basis. Direct comparisons of western gorilla dietary composition, nutrient content of fruits and herbs, and nutrient consumption are made with published mountain gorilla data from Bwindi and Karisoke (Watts 1984; Rothman et al. 2007). I hypothesize that western gorillas will consume more fruit by wet weight, have a more diverse staple diet including more fruit species, and that their diet will contain more total non-structural carbohydrates compared to mountain gorillas in both populations. I interpret results within the comparative framework of broad-scale ecological differences between habitats occupied by western and mountain gorillas to explain apparent differences in diet and nutrient intake.

Chapter three addresses four major premises of the socioecological model concerning increased reliance on monopolizable foods (using fruit as a rough proxy) in western compared to mountain gorillas and its predicted social consequences on rates of female aggression,

consistency of female dominance relationships, linearity and steepness of hierarchies, and frequency of female coalitions. To test these predictions, I compiled data from published studies of female agonistic relationships in Karisoke and Bwindi mountain gorillas. Specifically, I predict that increased fruit in the western gorilla diet will be associated with increased feeding aggression and a greater proportion of decided aggression relative to that seen in mountain gorillas. Accordingly, I predict that more decided aggression will be associated with a higher proportion of decided dominance relationships and a steep (de Vries et al. 2006) and linear (de Vries 1998) dominance hierarchy, despite little involvement from female coalitions. I conclude by examining whether the dominant male plays an important role in buffering female aggression by intervening in female conflicts as seen in mountain gorilla groups (Watts 1994; Watts 1997).

In chapter four I explore whether western gorillas face considerable within-group contest competition by determining whether females differ in overall energy intake on the basis of rank. I predict that high-ranking females will achieve higher overall energy intake compared with low-ranking females; dominants should direct aggression toward other females in the context of feeding on fruit, and as a result should acquire more fruit overall. To gain a better understanding of how variation in fruit consumption and feeding time might influence variation in female energy throughout the year I test whether feeding time on fruit and time spent feeding positively predict variance in female energy intake. In addition, I evaluate whether the frequency of fruit-based feeding aggression varies throughout the year and whether fruit aggression is higher or lower during the peak fruiting period as might be expected if fruits provoke contest competition.

In chapter five I summarize the major findings of this dissertation and discuss the links between female foraging strategies (diet; nutrition), feeding competition (energetic consequences), and female social relationships (dominance relationships; linearity and steepness

of hierarchy based on aggression) in wild western gorillas. Implications of the unique arrangement of associations between foraging outcomes and female agonistic relationships in western gorillas, a large-bodied primate with a variable diet and relaxed group cohesion, are discussed with relevance to the socioecological model and possible refinements for predictions based on individualistic primate societies with low predation pressure.

CHAPTER TWO:
Differences in diet composition and nutrient intake between western lowland gorillas (*Gorilla gorilla*) at Mondika and mountain gorillas (*Gorilla beringei*) at Karisoke and Bwindi

Abstract

Western gorillas (*Gorilla gorilla*) inhabit lowland forests that contain a greater prevalence and diversity of fruiting trees compared to highland and afro-alpine habitats occupied by mountain gorillas (*Gorilla beringei*). Ecological differences between gorilla habitats have presumably led to dietary differences and variation in life history strategies. Whether dietary differences translate into clear nutritional differences between western and mountain gorillas remains unclear, especially since similar nutrient intake was observed between mountain gorilla groups at Bwindi and Virunga despite differences in diet. To examine whether western gorilla diets differ in nutritional composition compared to mountain gorillas, I conducted focal follows of adult female western gorillas during an 11-month period at the Mondika Research Center (CAR; Republic of Congo). During follows, I recorded focal feeding observations (food species and part) instantaneously at one-minute intervals and sampled focal feeding rates opportunistically. Gorilla food samples were taken, weighed, and used to calculate overall wet weight intake. Macronutrient content of 41 western gorilla foods was determined from chemical analysis, and results were compared with published reports from Bwindi and Virunga. Results indicate that Mondika gorillas consumed considerably more fruit and leaf and less herb by wet weight than Bwindi and Virunga gorillas. Fruits at Mondika also contained significantly higher concentrations of non-structural carbohydrates compared to fruits at Bwindi, resulting in a diet much richer in total non-structural carbohydrates than seen in mountain gorillas. Comparison of

nutritional composition of diets between sites also indicated that western gorilla diets, compared to mountain gorillas, contained more fiber and less protein, which may have implications for energetic constraints on gorilla life history strategies.

Introduction

When the geographical distribution of a species is large, environments may vary widely in altitude, rainfall, and resource availability. Accordingly, intra-specific variation in diet can be considerable (Watts 1996; Yamagiwa et al. 1996; Altmann 1998; Koenig et al. 1998; Chapman and Chapman 1999; Davies et al. 1999; Chapman et al. 2002; Remis 2003; Wich et al. 2006; Potts et al. 2011), and populations of a species (or closely related species) studied in different environments may differ in sociality, dispersal strategies, and/or rates of reproduction (Mitchell et al. 1991; Newton and Dunbar 1994; Barton et al. 1996; Boinski 1999; Borries et al. 2001).

Among primates there is broad empirical support that prevailing local ecological conditions shape variability in dietary composition, dispersal strategies, and female social relationships (Sterck et al. 1997), particularly from comparative studies of baboons (Barton et al. 1996), Hanuman langurs (Koenig and Borries 2001), and squirrel monkeys (Boinski et al. 2002) living in different environments. Baboons (*Papio spp.*) studied in different habitats and regions, which differ in altitude, climate, vegetation types, food distribution, and predation risk, have widely varying diets (Byrne et al. 1993; Barton et al. 1996; Altmann 1998). For example, in some locations fruits and seeds account for greater than 50% of the baboon diet by feeding time, whereas in others underground plant parts comprise the bulk of the baboon diet by feeding time (Table 9.7, p. 541, Altmann 1998).

Dramatic differences in dietary composition may or may not translate into nutritional differences, however, depending on variation in the nutrient content of food types. For baboons inhabiting two savanna sites in relatively close geographic proximity to each other in Kenya, the nutritional chemistry of food types at the first site, Laikipia (Barton et al. 1993), was similar to that at the second site, Amboseli (Altmann et al. 1987). However, when comparing baboon foods from the two savanna sites in Kenya to baboon foods from a forest site, Kibale, in Uganda (Johnson et al. 2012) the fiber (ADF) content of food types common to each site was highest at the forest site, suggesting that the nutrient content of foods may diverge when comparing sites separated by greater geographic distances and differing habitats.

Similar to baboons, gorillas occupy diverse habitats at varying altitudes and their diets and life history schedules also vary (Watts 1996; Doran and McNeilage 1998; Rogers et al. 2004; Stoinski et al. 2013). Presently, two species of *Gorilla*, the eastern mountain gorilla (*G. beringei*) and the western lowland gorilla (*G. gorilla*), are recognized on genetic (Ruvolo et al. 1994; Garner 1996) and morphological grounds (Groves 2003). It is estimated that the eastern and western gorilla species diverged from one another somewhat recently, around 1.75 million years ago, based on new molecular sequencing data (Scally et al. 2012).

Mountain gorillas live at high altitudes (2500-3700 m) in the Virunga Volcanoes of Rwanda, Democratic Republic of Congo, and Uganda (Watts 1984; Harcourt and Stewart 2007; Rothman et al. 2007) and at intermediate altitudes (2100-2500 m) in Bwindi Impenetrable National Park of Uganda (Goldsmith 2003; Rothman et al. 2006a; Rothman et al. 2007; Ganas et al. 2009). A third population of eastern gorillas with unique sub-specific designation (*G. b. graueri*) lives at intermediate altitudes (2050-2350 m) in Kahuzi-Biega National Park of DRC (Yamagiwa et al. 2005), but will not be considered further here. Surprisingly, despite dietary

differences between mountain gorillas at Virunga and Bwindi the nutrient composition of their diets did not differ (Rothman et al. 2007).

More specifically, mountain gorilla diets at Karisoke in the Virunga Volcanoes and at Bwindi in Uganda consist primarily of protein-rich leaves from a few species of abundant terrestrial herbs based on wet weight intake (Watts 1984; Watts 1996). At Bwindi the diet includes more fruit (15 % by wet weight: Rothman et al. 2007), which is largely absent in the Virunga diet (Watts 1984). Because gorilla fruits are typically higher in sugar and lower in protein than leaves or herbs (Rothman et al. 2006b), a reasonable expectation would be that overall dietary nutritional composition would also differ between Bwindi and Virunga. However, Rothman et al. (2007) found that the overall nutrient composition of the diets was nearly identical at the two sites and included relatively high crude protein (17 - 18 % by dry weight) and neutral detergent fiber (41 - 43 %) and relatively low total non-structural carbohydrate (18 - 19 %) content. Thus, despite differences in environment and diet, gorillas in each habitat seem to adjust their diets to maintain similar nutrient intake. However, this comparison was based on two populations of mountain gorillas separated by only 30 km, raising the question of whether gorillas living in a much different ecological landscape, with greater plant species diversity, would also have a diet similar to that of mountain gorillas in their overall nutrient consumption. I address this question by comparing western gorillas to mountain gorillas, which do not have a particularly deep divergence time and until recently were considered the same species (*G. gorilla*) with sub-specific designations (Doran and McNeilage 1998).

Western gorillas live primarily in lowland rainforests of western Central Africa (Doran and McNeilage 1998) although some populations occupy disturbed habitats (Calvert 1985; Oates et al. 2003). Lowland forests tend to have taller canopies, higher densities of fruiting trees,

greater plant diversity, and reduced evenness and abundance of preferred terrestrial herbs than montane forests (White et al. 1995; Kuroda et al. 1996; Goldsmith 2003; Yamagiwa et al. 2003; Ganas et al. 2009). Data on western gorillas from six sites showed that their diets include an average of 148 plant species and that they fed on a mixture of herbs, seasonally available sugary fruits, and leaves (Rogers et al. 2004). Diets have been studied most extensively at two sites (Bai Hokou and Mondika) separated by about 50 km. Based on the percent of feeding time, gorillas at both sites ate roughly equal proportions of fruit, leaf, and herb, with the relative proportions of these food types shifting throughout the year (Remis 1997; Remis 2003; Mongo 2006; Doran-Sheehy et al. 2009a; Masi et al. 2009). During periods of high fruit availability, ripe fruit accounted for up to 70 % of feeding time (Doran-Sheehy et al. 2009a; Masi et al. 2009) with much less time feeding on leaves and herbs. During periods of fruit scarcity, leaf and herb consumption increased dramatically (Doran-Sheehy et al. 2009a). However, data on wet weight intake comparable to those reported for mountain gorillas (Watts 1984; Rothman et al. 2007), rather than those based just on time spent feeding, were so far not yet available. Wet weight data are needed to confirm previous food intake percentages because feeding time is sometimes a poor approximation of actual intake (Chivers 1998; Zinner 1999).

Here I present the first data on western gorilla diet based on wet weight intake and food nutrient composition. If measures of diet composition based on wet weight intake are consistent with those based on feeding time, then I expect that western gorillas eat considerably more fruit, seed, and dicotyledonous leaf and less herb than mountain gorillas (Calvert 1985; Williamson et al. 1990; Tutin et al. 1991; Tutin and Fernandez 1993; Nishihara 1995; Kuroda et al. 1996; Remis 1997; Doran et al. 2002; Goldsmith 2003; Rogers et al. 2004; Mongo 2006; Cipolletta et al. 2007; Doran-Sheehy et al. 2009a; Masi et al. 2009). Furthermore, because fruits are usually

higher in soluble sugars and non-structural carbohydrate compared to leaves or herb stems (Hladik 1977; Herrera 1987; Rogers et al. 1990; Wrangham et al. 1991; Kunz and Diaz 1995; Corlett 1996; Ruby et al. 2000), I expect that the gorilla diet at Mondika would be higher in total non-structural (or “simple”) carbohydrates and easily-assimilable energy than mountain gorilla diets. Because major food types may vary in sugar, protein, and fiber content both within and between sites (Ganzhorn 1992; Ganzhorn 1995; Chapman et al. 2003), I examine the average nutrient content of plant foods at Mondika and compare these to those published previously for the two mountain gorilla sites to assess whether the nutritional quality of foods vary across sites.

In a previous study of gorilla diet at Mondika, Doran-Sheehy and colleagues (2009a) categorized fruit and herb foods as preferred or fallback food species based on whether gorillas consumed each species to a greater (preferred) or lesser (fallback) degree than would be expected based on availability. If gorillas make foraging decisions based on the relative quality of available alternatives, I would expect their fruit and herb preferences to have a clear nutritional basis. Furthermore, because carbohydrate content is an important factor influencing fruit and pith selection in gorillas (Rogers et al. 1990; Ganas et al. 2009), I predict that preferred food species will contain higher sugar and total non-structural carbohydrate content compared to fallback food species.

The staple diets of mountain gorillas have been described (as defined by the collection of foods that contribute a minimum of 1 % to wet weight intake) as mainly containing herbaceous leaf species, although this varies between sites (Rothman et al. 2007). To make meaningful dietary comparisons between sites, I similarly describe the staple diet of western gorillas at Mondika based on wet weight intake and subsequently limit all cross-site comparisons to consideration of staple foods including the nutrient content of foods (as well as preferred and

fallback species) and nutrient composition of gorilla diets. I conclude by assessing how our understanding of the flexibility of gorilla diets and their nutrient composition shifts when extending comparisons based on montane habitats to include those of lowland rain forest.

Methods

Study site and subjects

Research was conducted on one group of habituated western gorillas (*Gorilla gorilla*) at the Mondika Research Center (02° 21' 859'' N, 016° 16' 465'' E) located on the border of Republic of Congo and Central African Republic (Doran et al. 2002). The study area was established in 1995 (Doran and McNeilage 1998). There is no history of commercial logging or recent human disturbance at the site apart from researcher presence. The study area (50 km²) is low elevation (altitude: < 400 m) and has little topographic relief (Doran-Sheehy et al. 2009a). The forest consists of mixed species tropical lowland forest, monodominant *Gilbertiodendron dewevrei* (Caesalpiniaceae) forest, light gaps, and swamp forest (Doran et al. 2002; Doran-Sheehy et al. 2009a). Annual mean rainfall averages 1600 mm (8 years of rainfall data, Doran-Sheehy et al. 2009a) and varies seasonally, with an annual two-to-three month dry season (December-February) with less than 50 mm of rainfall per month (Doran et al. 2002; Doran-Sheehy et al. 2009a) and a two-month period of higher than average rainfall (> 200 mm; September-October). Fruit availability is seasonal (Doran-Sheehy et al. 2009a), with an annual two-to-three-month fruit peak occurring between June and September. The timing of the fruit peak is consistent across years at Mondika and at other research sites in the area although there is inter-annual variation in the quantity of fruit produced (Doran-Sheehy et al. 2009a).

A single habituated gorilla group was monitored most days between April 2001 and 2010 as part of a long-term study. Gorilla diet, resource availability, and nutrient content of foods have been studied previously at the site (Doran et al. 2002; Doran-Sheehy et al. 2006; Doran-Sheehy et al. 2009a). Research for this study was conducted between December 2004 and October 2005, during which time the study group comprised one adult silverback male and 5-6 adult females and their immature offspring. Research subjects included four habituated adult females (F1-F4). Female reproductive states varied within and between subjects throughout the study, with more than one reproductive state represented in at least half of the subjects. In summary, F1 was initially pregnant (December 2004 to March 2005), gave birth in March, and lactated for the rest of study (March to October 2005). F2 was inferred to be cycling or in lactational amenorrhea at the start of study (December 2004 to January 2005), however, upon the death of her 2-yr old offspring (in January) she quickly conceived (in February 2005), and gestated for the rest of study (March to October 2005). F3 was also inferred to be cycling or in late-stage lactational amenorrhea (December 2004 to August 2005) for the majority of the study, however, following the death of her 2-yr old offspring (in August) her reproductive status was considered unknown (non-cycling?; August to October 2005). F4 had no dependent offspring, and her reproductive status was unclear throughout the study.

Data collection

All-day (n = 59; mean duration = 6.1 ± 0.5 activity hrs) or half-day (n = 95; mean duration = 3.2 ± 0.4 activity hrs) focal follows were conducted, rotating among females. Every focal hour consisted of four 10-min sampling periods (00-09; 15-24; 30-39; 45-54) for a total of

40 min, otherwise called an activity hour. During each 10-min period, I conducted instantaneous sampling of activity states (feeding; resting; traveling; playing/socializing) at one-min intervals. If the subjects were feeding, I recorded the species and food category. Feeding time included time spent preparing, processing, chewing, and ingesting foods, following similar operational definitions of feeding behavior (i.e. food preparation and ingestion) used in the Karisoke (Watts 1984) and Bwindi (Rothman et al. 2007) studies. Food categories included: 1) fruit (i.e. pulp; seeds; skin), 2) herb (i.e. piths; shoots; roots), 3) leaf (i.e. leaves from dicotyledonous trees, shrubs, and lianas and including young bark from *Celtis* when consumed simultaneously with leaves), 4) insects, 5) flowers, 6) other (i.e. soil scratch; gorilla feces), and 7) unknown (i.e. assorted unidentified leaf and insect species).

Feeding behavior differed slightly between morning (7:00-12:00) and afternoon (12:00-17:00) follows and varied with time of year. To avoid sampling bias, I divided each all-day follow into two half-day follows, which when combined with the other half day follows yielded a total of 213 half-day follows. From these I randomly selected 3 morning and 3 afternoon samples in each of 11 months using the sample function in R (R Development Core Team 2011), yielding a total of 66 half-day follows and 201 focal activity hours. There was no significant individual or monthly variation in focal follow duration (ANOVA, female ID: $F_{3,62} = 0.86$, $p = 0.47$; ANOVA, month: $F_{10,55} = 1.63$, $p = 0.12$), percent feeding time (ANOVA, female ID: $F_{3,62} = 0.64$, $p = 0.59$; ANOVA, month: $F_{10,55} = 0.66$, $p = 0.76$), or total feeding min per follow (ANOVA, female ID: $F_{3,62} = 1.13$, $p = 0.34$; ANOVA, month: $F_{10,55} = 0.96$, $p = 0.49$).

Feeding rates

Feeding rates were measured opportunistically during focal follows for 34 commonly eaten foods, including 14 fruit species, 12 leaf species, 7 herb species, and 1 insect species (Table 2.1), as the number of whole items (fruits, herbs) or handfuls (leaves, termites) consumed during one-min intervals. An average of 25 (SD = 24; range = 2 - 108; n = 34 food items) feeding rates were measured per food item. I collected food samples while following focal subjects (for fruits and tree leaves) and when conducting morning re-visitations to feeding locations used during the previous day (for fruits, herbs and leaves). One collection, consisting of at least 10 specimens (except for the largest fruit species), was made once per food species because of constraints on project personnel and financial considerations. From each collection, I measured the wet weight (in grams) per item or handful following Koenig et al. (1997) and used the mean unit weight of items to calculate an average rate of ingestion (i.e. number of grams of wet weight consumed per minute of feeding time). Focal feeding rates were unavailable for many food items. Thus, feeding rates for an additional 4 food items (3 fruit species; 1 leaf species; see Table 2.1) were recorded opportunistically at food patches in which a minimum of two adult group members were feeding. For an additional 30 foods (2 fruit species; 1 seed species; 25 leaf species; 2 flower species), I substituted the average focal feeding rate on food species of similar size and construction within the same food category since food items within the same food category show similar rates of ingestion (Schülke et al. 2006). For fruits, species could be matched to one of the following size-construction categories, 1) small and juicy, 2) medium and dry, or 3) large and juicy. Seeds were treated as a separate category. In one case (i.e. for *Landolphia*- a large and juicy fruit), the ingestion rate of another species of the same genus was substituted. Leaves varied little in feeding rates as expected for food species within the same

food category (Schülke et al. 2006), and therefore the average ingestion rate of 20.9 g / min was substituted for all leaf species with missing feeding rate data. Together, this yielded 68 food items for which I measured or estimated feeding rates (with the estimated foods accounting for less than 10 % of annual feeding time). The remaining fruit, insect, and herb species that were unaccounted for in the present study (n = 37 food items) were rarely eaten, each contributing less than 1 % (range: 0.1 - 0.9 %) of total feeding time (with the exception of two insect species with long preparation times: soil scratch = 1.5 %; weaver ants = 1.0 %) and were excluded from all wet weight calculations of diet.

Plant sample collection

I collected plant samples of 26 gorilla food species during this study using standard methods described previously (Doran-Sheehy et al. 2009a). To increase sample sizes I collected an additional 15 food items in 2006 bringing the total sample to 41 food items, including 18 fruits, 7 herbs, 15 leaves, and termites. Together, these items accounted for 87 % of the diet by wet weight. Three fruit species that were not included in the diet during this study but were important in previous years were also included in nutritional analysis (Table 2.1). In brief, the part of the food item that was typically consumed by gorillas was preserved in 90 % unboiled ethanol (fruits and insects) and shaken for 30-sec to mix constituents or field dried at < 60° C (leaves and herbs) and stored with desiccant until transported for chemical analysis. The amount (mL) of ethanol used to preserve each food sample was measured prior to mixing to estimate the ratio of ethanol to food for each sample, however a consistent ratio across samples of ethanol:food preserved could not always be achieved or assured.

Chemical analysis of western gorilla foods

Nutritional analyses were carried out by Jessica Lodwick and Patrice Mongo in the nutritional ecology laboratory in the Department of Human Evolutionary Biology at Harvard University under the supervision of N.L. Conklin-Brittain. Samples were analyzed for macronutrient content (crude protein (CP), free simple sugars (FSS), lipid (LP), and total cell wall fiber fractions (neutral-detergent fiber (NDF), acid-detergent fiber (ADF), hemicellulose (HC), cellulose (Cs), and sulfuric acid lignin (Ls)) as a percentage of field dry matter (% FDM). Field dry weights of leaf and herb samples were measured in the field prior to sample storage and later re-measured once samples achieved constant weight in the lab to determine moisture content more accurately. Fruit and termite samples preserved in ethanol were dried in the lab to a constant hot weight within a 50°C electric convection oven. The leftover residue containing soluble nutrients after the ethanol had evaporated was scraped from each sample tray and returned to the sample to retain as many of the simple sugars and fats present in the food as possible. For each chemical assay, all food samples were dried to a constant weight, divided into two sub-samples, hot weighed, ground, analyzed in duplicate, and averaged for reporting purposes. All samples were ground at the same mesh-size, with only one species of sweet and sticky fruit (*Landolphia* sp.) requiring application of dry ice while grinding.

CP content was assayed using the Kjeldahl procedure and estimated as total nitrogen multiplied by 6.25 (Pierce and Haenisch 1948). Total nitrogen was determined by digesting the sample in a mixture containing Na_2SO_4 and CuSO_4 , after which “distillate was collected in 4% boric acid and titrated with 0.1 N HCl” (Van Soest 1994; "p. 140 in:" Conklin and Wrangham

1994). Limited sample weights precluded us from measuring insoluble nitrogen fractions using neutral-detergent extraction. FSS content was determined using a colorimetric assay of phenol/sulfuric acid (DuBois et al. 1956) with sucrose as a sugar standard (Strickland and Parsons 1972). LP content was assayed by extracting lipids in petroleum ether over a 4-day period at room temperature, a method modified from the Association of Official Analytical Chemists (Williams 1984). Total cell wall fiber fractions were determined using fiber filtration analysis (Van Soest 1994; Conklin-Brittain et al. 1998). In the first step, the sample is subjected to neutral-detergent fiber (NDF) analysis, in which all insoluble fibers are measured together as the NDF fraction. Next, the NDF undergoes an acid-detergent fiber (ADF) analysis in which hemicellulose (HC) becomes soluble, but the ADF fraction still contains cellulose (Cs) and lignin (Ls). If ADF is subtracted from NDF this results in the HC fraction in the sample (Conklin-Brittain et al. 1998). In the final stage, the Cs fraction within the ADF becomes soluble when subjected to 72 % sulfuric acid (Conklin-Brittain et al. 1998). Subtracting lignin (left in the residue) from ADF yields an estimate of the Cs fraction (Williams 1984; Conklin-Brittain et al. 1998). The dry matter (DM) of each food item was determined by drying sub-samples (equilibrated to a constant temperature in the lab) at 100°C for 8 hrs (Williams 1984; Conklin and Wrangham 1994; Conklin-Brittain et al. 1998), and total ash content was determined by exposing the DM sub-samples to 520°C for 8 hrs then hot-weighing at 100°C (Conklin and Wrangham 1994; Conklin-Brittain et al. 1998).

Data analysis

Diet by feeding time and wet weight intake

The percent time spent feeding on each food item was calculated for each month by summing the number of sample points spent feeding on each item during the six follows and then dividing by the total number of feeding sample points. Monthly values were then averaged across the 11 months. The percent of the diet (based on wet weight) for each food item was calculated for each month as the product of the total feeding samples per month and the feeding rate (grams consumed per min), divided by the total number of grams of all foods consumed per month. Monthly values were then averaged for each food item across the 11 months.

Food nutrient content

In the following I present macronutrient and fiber content of gorilla foods as a percentage of dry matter (% DM). To correct for humidity fluctuations in the lab and to express nutrient content as a percentage of dry matter (% DM) rather than field dry matter (% FDM), I calculated a DM correction factor for each food by multiplying the weight of each sub-sample by its percent dry matter (Conklin and Wrangham 1994; Conklin-Brittain et al. 1998). Total non-structural carbohydrate (% DM) content was calculated after the DM correction as $100 - (\% \text{NDF} + \% \text{LP} + \% \text{CP} + \% \text{ash})$ (Conklin-Brittain et al. 1998; Rothman et al. 2007). The caloric content (Kcal/100g organic matter) of the major food types (fruits, leaves, herbs) was calculated from nutrient fractions obtained in the lab and from published human energetics data (National Research Council (U.S.). Food and Nutrition Board 1989). Atwater physiological fuel values were used to estimate caloric content of foods based on values of 4 kcal / g for CP, 9 kcal / g for

LP, and 4 kcal / g for TNC (Conklin and Wrangham 1994). Gorillas, like chimpanzees, have capacious hindguts, which means they can ferment some proportion of NDF for energy (e.g. 1.5 kcal / g NDF is the best estimate for gorillas: Conklin-Brittain personal communication). However, for the purpose of comparing broad measures of energy content among the major food types I do not present caloric content based on NDF inclusion. One limitation of this approach is that omission of energy from NDF fermentation may change the rankings of energy content of foods per gram of dry matter. This possibility should be explored in future nutrition studies.

I determined the mean concentration of crude protein (CP), free simple sugar (FSS), total non-structural carbohydrate (TNC), lipid (LP), neutral detergent fiber (NDF), hemicellulose (HC), acid detergent fiber (ADF), cellulose (Cs), lignin (Ls), ash, water (H₂O) and overall energy (Kcal) for 40 plant foods and one insect species (termites). I then tested for mean differences in each of these variables among food categories (fruit, leaf, and herb) using one-way analysis of variance (ANOVA with post-hoc Tukey HSD tests to control for the number of multiple comparisons). All fruit and herb food species with nutrient data available were classified as preferred or non-preferred food species based on whether they were consumed to a greater (preferred) or lesser (non-preferred) extent than would be expected based on availability, as outlined elsewhere (Doran-Sheehy et al. 2009a). In brief, for each fruit and herb species I calculated a preference index as the ratio of monthly consumption (based on percentage of feeding time) to monthly availability (based on average monthly phenology scores from long-term records). Fruit and herb food species with a preferences index of ≥ 1.0 were considered preferred food species and those < 1.0 were considered non-preferred food species. This yielded nine preferred fruits, nine non-preferred fruits, two preferred herbs, and five non-preferred herbs. All leaves were classified as non-preferred foods, following previous analyses (Doran-Sheehy et

al. 2009a), and thus no preferred versus non-preferred nutrient analysis was possible. I then examined the average nutrient concentrations in preferred and non-preferred fruits and herbs, and used Mann-Whitney U-tests (Siegel and Castellan 1988) to test for differences.

Cross-site comparison of the nutrient content of gorilla foods

I compared the results from this study to a comparative study of mountain gorilla diet and nutrient composition published by Jessica Rothman and colleagues (Rothman et al. 2007). Feeding data from Karisoke and Bwindi were recorded during focal feeding bouts (Watts 1984; Rothman et al. 2007). Wet weight intake data for 75 foods at Karisoke came from data on individual diets collected during a 17-month study (Watts 1984; Rothman et al. 2007). Intake data on 84 foods at Bwindi came from individual diets of 12 gorillas (including silverbacks, females, and juveniles) in the Kyagurilo group during a 12-month study (Rothman et al. 2006a; Rothman et al. 2007; Rothman et al. 2008b).

Rothman et al. (2007) reported the nutritional composition of the diet of mountain gorillas at the two sites on a wet weight basis of staple foods, which they defined as those contributing $\geq 1\%$ to the annual diet. Therefore, to provide comparable data, for all cross-site dietary comparisons, I also restrict analyses to those foods that contributed $\geq 1\%$ to the annual diet (based on wet weight) at Mondika (i.e. foods accounting for at least 0.95% of wet weight intake). Staple foods accounted for over 90% of the diet at both the Bwindi and Karisoke sites, but accounted for slightly less (85%) of the diet at Mondika. Therefore, to compare diets across sites, I recalculated the dietary percentage (by wet weight) values by scaling up the wet weight

contribution of each staple dietary item proportionally so that the total contribution of staple foods at each site summed to 100 %.

I tested for differences in the mean nutrient content of staple fruits and herbs across the gorilla sites using non-parametric Mann-Whitney U-tests and Kruskal-Wallis rank sum tests (Siegel and Castellan 1988) since the number of staple herb and fruit items in the diets were small and variable across sites. Finally, I compared the nutritional quality of staple fruits at Bwindi with the values for staple preferred and fallback fruits at Mondika using Mann-Whitney U-tests to assess variation in nutrient quality between sites. All statistical tests were two-tailed at $p < 0.05$ and run using Version 2.14.0 of R (R Development Core Team 2011).

Finally, I compared the overall nutrient composition of the gorilla diet across the three sites by summing the nutritional contribution of each important food, weighted by its contribution to the diet, following Rothman et al. (2007). This included estimating: 1) the total dry matter content of the diet, 2) the weighted dry matter contribution of each important food item to the diet, and 3) the nutrient content of each weighted item. At Mondika, nutritional data were not available for 4 of 22 important foods including 2 leaf and 2 fruit species. I estimated the nutrient content of the two missing leaf species (*Ficus* and Nganda) by substituting the mean nutrient content of leaves. Likewise, I substituted the average nutrient content of small juicy fruits ($n = 4$) for *Milicia* fruit (which are small and juicy), and I substituted the nutrient values of a congener for fruit of a species of *Landolphia* for which data were missing.

To calculate monthly nutrient contributions, the wet weight diet was expressed on a dry matter basis. To calculate dry matter intake and overall nutrient composition, I followed a three-step process (Rothman et al. 2007), which I have outlined here:

Step 1: Determine % FDM and % DM of each food item. For each staple food item, moisture content (% wet weight) was calculated as the difference between sample weight at time of collection and constant weight after drying, and percent field dry matter (% FDM) was calculated as $100\% - \% \text{moisture}$. Dry matter (% DM) was determined in the lab for each staple food item by drying samples to a constant hot weight in a 100°C oven for 8 hrs. For 14 foods at Mondika (from second collecting of plant samples) accurate assessments of moisture content were not available because of limited sample material, so the average moisture content of foods within the same food category of similar size and classification (for fruits) were supplied as estimates.

Step 2: Calculate intake by field dry weight. For each month, total wet weight intake (g) from each staple food item was calculated and multiplied by % FDM to determine monthly intake by field dry weight (g).

Step 3: Calculate dry matter intake and nutrient contribution. Dry matter intake (g) for each staple food item was calculated on a monthly basis by multiplying field dry weight (g) by dry matter (% DM). The nutrient content (e.g. CP % DM) of each staple food item was determined from chemical analysis and then divided by its percent dry matter to provide an adjusted percent nutrient content. Then, on a monthly basis, adjusted percent nutrient content (%) of each staple food was multiplied by dry matter intake (g) to indicate the amount of nutrient (g) ingested on a dry matter basis. For each month, nutrient intake (g) was summed across foods and expressed as a percentage of total dry matter intake and then averaged across months for comparison with Bwindi and Karisoke.

Results

Overall diet diversity and composition

Female western gorillas had a broad diet, consisting of 106 identified food items, including 44 fruit species, 38 dicotyledonous leaf species, 13 herb species, 1 species of bark, 5 species of flowers, and 6 insect species, including termites (*Cubitermes*). Focal animals also foraged for unidentified subterranean items in the soils of *Gilbertiodendron dewevreii* (Caesalpiniaceae) forest, a technique called here and elsewhere as soil scratching (Cipolletta et al. 2007; Breuer and Breuer Ndongou Hockemba 2011). Gorillas ingested the feces of other gorillas occasionally during months of peak fruit and seed consumption.

The diet based on wet weight was composed of 41 % fruit, 34 % herb, 20 % leaf, and 5 % termites (based on 68 foods). Of the 106 food items, 22 were staple foods. These included 10 fruit, 6 herb, 5 leaf, and 1 insect species (Table 2.1).

Nutrient composition of foods

An examination of the dry-matter nutrient content of 40 gorilla plant foods (Table 2.2) indicated that fruits contained significantly more total non-structural carbohydrates (fruit mean TNC \pm SD: 45.0 \pm 21.0; n = 18 fruits) and free simple sugars (fruit mean FSS \pm SD: 16.5 \pm 8.6; n = 18 fruits) and less crude protein (fruit mean CP \pm SD: 7.4 \pm 4.2; n = 18 fruits) and ash (fruit mean ash \pm SD: 4.1 \pm 2.2; n = 18 fruits) compared to leaves (leaf mean TNC \pm SD: 19.9 \pm 11.2; n = 15 leaves; leaf mean FSS \pm SD: 2.8 \pm 1.8; n = 15 leaves; leaf mean CP \pm SD: 19.7 \pm 6.3; n = 15 leaves ; leaf mean ash \pm SD: 8.2 \pm 3.2; n = 15 leaves) or herbs (herb mean TNC \pm SD: 11.1 \pm 7.0; n = 7 herbs; herb mean FSS \pm SD: 3.7 \pm 1.0; n = 7 herbs; herb mean CP \pm SD: 15.7 \pm 4.2; n

= 7 herbs; herb mean ash \pm SD: 17.3 ± 4.7 ; $n = 7$ herbs; Tukey post-hoc test results given in Table 2.2). In addition, fruits provided more energy (as a percentage of organic matter; fruit mean Kcal \pm SD: 231 ± 72 ; $n = 18$ fruits) and less water (as a percentage of wet weight; fruit mean H₂O \pm SD: 69.7 ± 22.2 ; $n = 18$ fruits) than either leaves (leaf mean Kcal \pm SD: 190 ± 49 ; $n = 15$ leaves; leaf mean H₂O \pm SD: 86.7 ± 8.1 ; $n = 15$ leaves) or herbs (herb mean Kcal \pm SD: 153 ± 25 ; $n = 7$ herbs; herb mean H₂O \pm SD: 93.7 ± 2.9 ; $n = 7$ herbs), although only the difference between fruits and herbs was significant (Tukey post-hoc test results given in Table 2.2). Overall, fruits (fruit mean LP \pm SD: 1.4 ± 2.1 ; $n = 18$ fruits), leaves (leaf mean LP \pm SD: 1.9 ± 1.7 ; $n = 15$ leaves), and herbs (herb mean LP \pm SD: 2.1 ± 1.0 ; $n = 7$ herbs) did not differ significantly in their lipid (LP; ANOVA: $F_{2, 37} = 0.6$; $P > 0.10$) or fiber (NDF) content (fruit mean NDF \pm SD: 42.3 ± 17.5 ; $n = 18$ fruits; leaf mean NDF \pm SD: 50.7 ± 10.0 ; $n = 15$ leaves; herb mean NDF \pm SD: 53.8 ± 5.7 ; $n = 7$ herbs; NDF ANOVA: $F_{2, 37} = 2.5$; $P > 0.10$). Herbs and leaves did not differ significantly in their macronutrient, fiber, moisture, or energy content (Tukey post-hoc test results given in Table 2.2). However, herbs had higher ash content (herb mean ash \pm SD: 17.3 ± 4.7 ; $n = 7$ herbs) compared to leaves (leaf mean ash \pm SD: 8.2 ± 3.2 ; $n = 15$ leaves; Tukey post-hoc test: $P < 0.001$) and fruits (fruit mean ash \pm SD: 4.1 ± 2.2 ; $n = 18$ fruits; Tukey post-hoc test: $P < 0.001$).

When the 40 foods were divided into preferred and non-preferred food species, this yields 9 preferred and 9 non-preferred fruits, 2 preferred and 5 non-preferred herbs, and 15 non-preferred leaves. Preferred fruits were significantly higher in mean free simple sugar concentrations (Pref fruit mean FSS \pm SD: 21.0 ± 8.2 ; $n = 9$ fruits), and trended towards higher total non-structural carbohydrates (Pref fruit mean TNC \pm SD: 53.4 ± 21.2 ; $n = 9$ fruits) and energy (Pref fruit mean Kcal \pm SD: 257 ± 70 ; $n = 9$ fruits) compared to non-preferred fruits

(Non-pref mean FSS \pm SD: 12.1 \pm 6.8; n = 9 fruits; FSS Pref vs Non-pref fruit Mann-Whitney U-test: U = 63; P = 0.05; Non-pref mean TNC \pm SD: 36.5 \pm 18.0; n = 9 fruits; TNC Pref vs Non-pref fruit Mann-Whitney U-test: U = 62; P = 0.06; Non-pref mean Kcal \pm SD: 204 \pm 67; n = 9 fruits; Kcal Pref vs Non-pref fruit Mann-Whitney U-test: U = 60; P = 0.09; Table 2.3). Preferred fruits were also significantly lower in acid detergent fiber (Pref fruit mean ADF \pm SD: 20.1 \pm 10.2; n = 9 fruits), cellulose (Pref fruit mean Cs \pm SD: 13.5 \pm 6.4; n = 9 fruits), and lignin (Pref fruit mean Ls \pm SD: 6.6 \pm 5.0; n = 9 fruits) compared to non-preferred fruits (Fall mean ADF \pm SD: 40.7 \pm 12.9; n = 9 fruits; ADF Pref vs Non-pref fruit Mann-Whitney U-test: U = 8; P < 0.01; Non-pref mean Cs \pm SD: 21.8 \pm 8.6; n = 9 fruits; Cs Pref vs Non-pref fruit Mann-Whitney U-test: U = 17; P = 0.04; Non-pref mean Ls \pm SD: 18.9 \pm 7.5; n = 9 fruits; Ls Pref vs Non-pref fruit Mann-Whitney U-test: U = 9; P < 0.01). Preferred herbs did not differ from non-preferred herbs in their dry-matter nutrient composition, including no significant differences in crude protein (CP), simple sugar (FSS), total non-structural carbohydrate (TNC)), fiber (NDF, ADF, HC, Cs Ls), energy (Kcal) and ash content (group means and Mann-Whitney U-test results given in Table 2.3).

Comparison of western and mountain gorilla diet and nutrient intake

The western gorilla diet at Mondika was more diverse than mountain gorilla diets at either site, with 22 staple foods at Mondika versus 15 at Bwindi and 9 at Karisoke (Rothman et al. 2007). Staple foods accounted for less (85 %) of the overall diet (by wet weight) at Mondika, compared to either Bwindi (96 %) or Karisoke (91 %; Table 2.4). There are notable differences in diet composition among the study sites, based on wet weight of staple foods scaled up to 100

% (Figure 2.1). Mondika diet based on wet weight intake of staple foods included 43 % fruit, 39 % herb, 12 % leaf, and 6 % termites. Compared to the Bwindi diet, the diet of western gorillas at Mondika included nearly three times more fruit, twice as much leaf, and half as much herb. The difference between gorilla diets at Mondika and Karisoke was much greater, with the Mondika diet containing roughly 200 and 100 times more fruit and leaf, respectively, and 2.5 times less herb. No insects were staple foods at either mountain gorilla site. Dead wood was not fed upon at Mondika (not shown in Figure 2.1), but it contributed 4 % to the staple diet at Bwindi (and rotting wood accounted for Watts 1984).

Average nutrient content of staple gorilla fruits and herbs differed significantly across sites (Table 2.5). Staple fruits contained more total non-structural carbohydrates (mean TNC \pm SD: 53.1 \pm 22.5; n = 10 fruits) at Mondika than at Bwindi (mean TNC \pm SD: 15.4 \pm 8.3; n = 3 fruits; Mann-Whitney U-test M vs B: U = 29; $P = 0.01$; Table 2.5), the only mountain gorilla site where fruits were a staple component of the diet. In fact, staple fruits at Bwindi had considerably lower TNC content than the staple fruits used as fallback resources at Mondika (Figure 2.2). Protein content of staple fruits was higher at Bwindi (mean CP \pm SD: 10.1 \pm 1.2; n = 3 fruits) than at Mondika (mean CP \pm SD: 5.3 \pm 3.8; n = 10 fruits), although the difference was not statistically significant (Mann-Whitney U-test: U = 5; $P = 0.11$). Neutral detergent fiber content of staple fruits at Mondika (mean NDF \pm SD: 36.6 \pm 18.7; n = 10 fruits) did not differ significantly from that of staple fruits at Bwindi (mean NDF \pm SD: 41.8 \pm 13.3; n = 3 fruits; Mann-Whitney U-test: U = 13; $P = 0.81$). Staple herbs were lower in total non-structural carbohydrates at Mondika (mean TNC \pm SD: 11.0 \pm 7.6; n = 6 herbs) compared to Bwindi (mean TNC \pm SD: 23.5 \pm 7.9; n = 10 herbs; Kruskal-Wallis test multiple comparison for M vs B: $P = 0.01$) but not compared to Karisoke (mean TNC \pm SD: 20.5 \pm 9.2; n = 9 herbs; Kruskal-Wallis test

multiple comparison for M vs K: $P = 0.23$). However, staple herbs contained more hemicellulose at Mondika (mean HC \pm SD: 19.1 ± 5.3 ; $n = 6$ herbs) than at Bwindi (mean HC \pm SD: 10.5 ± 3.0 ; $n = 10$ herbs; Kruskal-Wallis test multiple comparison for M vs B: $P = 0.01$). Staple herbs at Karisoke (mean HC \pm SD: 13.3 ± 3.8 ; $n = 9$ herbs) did not differ significantly in hemicellulose content from staple herbs at Mondika (mean HC \pm SD: 19.1 ± 5.3 ; $n = 6$ herbs; Kruskal-Wallis test multiple comparison for M vs K: $P = 0.17$). The neutral detergent fiber content of staple herbs at Mondika (mean NDF \pm SD: 54.7 ± 5.7 ; $n = 6$ herbs) was similar to that of staple herbs at Karisoke (mean NDF \pm SD: 51.3 ± 12.3 ; $n = 9$ herbs) and higher at both of these sites than at Bwindi (mean NDF \pm SD: 37.4 ± 12.8 ; Kruskal-Wallis test multiple comparison for M vs B: $P = 0.03$; for B vs K: $P = 0.06$).

Overall, the staple diet of gorillas at Mondika included nearly twice as much (34 %) total non-structural carbohydrate as staple diets at the two mountain gorilla sites (19 % and 18 % at Bwindi and Karisoke, respectively). Crude protein content of the staple gorilla diet at Mondika (CP: 12 %) was lower and neutral detergent fiber (NDF: 54 %) higher than at Bwindi (CP: 18 %; NDF: 43 %) and Karisoke (CP: 17 %; NDF: 41 %; Table 2.6).

Discussion

Western gorillas: measures of dietary composition

Fruit accounted for a substantial proportion (41 - 43 %) of the western gorilla diet at Mondika based on wet weight intake. Overall composition of the female diet based on wet weight intake was similar to previous reports based on percent feeding time (Mongo 2006;

Doran-Sheehy et al. 2006; Doran-Sheehy et al. 2009a), although the wet weight diet contained slightly more fruit and less dicotyledonous leaf than that reported for female dietary composition in the same year as this study based on feeding time (Doran-Sheehy et al. 2009a). This disparity between fruit and leaf percentages in the western gorilla diet based on feeding time versus wet weight intake widened when comparing the composition of the staple diet (based on wet weight intake) to the overall diet (based on feeding time), in which a lower percentage of leaf contributed to the staple diet (by wet weight) because fewer leaves were consumed intensively enough to be considered staple foods. Accordingly, a greater number of fruit species were consumed intensively thus explaining the larger proportional contribution of fruit to the staple diet. The total dietary breadth observed in the present study, however, defined as the total number of fruit, leaf, and herb species consumed was consistent with previous reports based on feeding time (Doran-Sheehy et al. 2009; Doran-Sheehy et al. 2006; Mongo 2006) and indirect sampling of male diet (Doran et al. 2002). Termites composed a greater percentage of the wet weight diet at Mondika (5-6 %) than that estimated for gorillas and chimpanzees elsewhere (less than 1 %, Hladik 1977; Cipolletta et al. 2007; Deblauwe and Janssens 2008; Deblauwe 2009), with the notable exception of savanna chimpanzees in which termites contributed almost one quarter (24 %) of annual feeding time in males (Bogart and Pruetz 2010)

Dietary and nutritional differences between lowland and highland gorillas

Western gorillas at Mondika consumed nearly three times the amount of fruit and half as much herb by wet weight as mountain gorillas at Bwindi and Karisoke. Although other researchers (Rothman et al. 2007) found that gorillas consumed more fruit at Bwindi than at Karisoke, they did not find differences in the nutrient composition of the diet. In contrast, I found

that the nutrient composition of the diet at Mondika included nearly twice as much total non-structural carbohydrate and more fiber and less crude protein than the diets of gorillas at Bwindi and Karisoke. This difference resulted from the consumption of more fruit at Mondika, and from inter-site variation in the quality of fruits eaten. Although Bwindi gorillas consumed more fruit than those at Karisoke, these fruits had less total non-structural carbohydrates than the fruits used as either preferred or fallback foods at Mondika. Herbs at Mondika were higher in hemicellulose and neutral detergent fiber and lower in total non-structural carbohydrates compared to herbs at Bwindi, although herbs at Mondika did not differ significantly from herbs at Karisoke in their fiber or total non-structural carbohydrate content. Mondika gorillas consumed more dicotyledonous leaf than gorillas at Bwindi or Karisoke, however leaves and herbs at Mondika did not differ significantly in protein, fiber, or non-structural carbohydrate content.

These results support the hypothesis that higher plant species diversity, lower herb densities, and higher fiber content in the foliage and fruit of western central lowland African rainforests compared to the highland habitats of mountain gorillas (Waterman et al. 1983; Gautier-Hion 1983; Tutin and Fernandez 1993; Doran and McNeilage 2001; Goldsmith 2003; Remis 2003; Rothman et al. 2006b) has led to differences in the nutritional chemistry of western lowland and mountain gorilla diets. The comparison of diets in this study indicates a much greater degree of variability in gorilla nutrient composition across sites than was found by Rothman et al. (2007), suggesting that broad-scale environmental changes in the nutritional chemistry of important food species have led to variation in nutrient consumption. Alternatively, species-specific differences in digestive physiology may have led to differences in dietary choice, particularly if nutritional differences reflect or are adapted to local conditions they may persist in places or times of year when fruit availability is low. More nutritional data (weighted

by dry matter intake) from other lowland gorilla sites are needed to survey the full range of variation in gorilla nutrient consumption and the factors that influence it, and to test whether: A) gorilla diets at sites with lower plant diversity and less succulent fruit such as the disturbed logged forests at Campo (Calvert 1985) and Rio Muni (Jones and Sabater Pi 1971) have lower nutritional contributions from non-structural carbohydrate than those of gorillas in mature undisturbed lowland forests, and whether: B) the nutritional composition of the western gorilla diet varies inter-annually with reduced non-structural carbohydrate and increased fiber intake during years of lower-than-average fruit availability yet still contains more soluble sugar and less protein overall compared to mountain gorillas.

Gorillas, as many other primates, prefer ripe sugary fruit whenever available, and like humans, have fairly low protein requirements due to their slow growth rates (Ofstedal 1991). As a consequence, diets of wild gorillas should be relatively high in non-structural carbohydrates and low in protein, as seen in chimpanzees and bonobos (Conklin-Brittain et al. 1998; Hohmann et al. 2006). Mountain gorillas present an exception to this nutrient profile (Table 2.6), however, with their high-protein diets that at times exceed nutritional requirements (Rothman et al. 2008a; Rothman et al. 2011). The high emphasis on protein in the diet of mountain gorillas has been explained by the prevalence of protein-rich foliage in their habitats (Waterman et al. 1983; Plumptre 1995; Rothman et al. 2006b). Furthermore, the mountain gorilla diet is unusually low in non-structural carbohydrates compared to diets of western gorillas in this study and to chimpanzees, guenons, and mangabeys at Kibale, a middle-elevation site in Uganda (Table 2.6). The low non-structural carbohydrate diet seen in mountain gorillas is an outlier among apes and at least some African monkeys with non-specialized guts and can be attributed to the scarcity and low quality of fruit in the high-altitude habitats of Bwindi and Virunga.

For at least one group of western gorillas at Mondika, the nutrient composition of the diet resembled the diets of chimpanzees more than the diets of mountain gorillas, except that Mondika gorillas had higher intake of fiber (NDF) than chimpanzees and mountain gorillas because of the high fiber content of leaves and herbs at Mondika. In this respect, the diet of Mondika resembled that of western gorillas at Bai Hokou (Popovich et al. 1997). Herb pith, in particular, is thought to be reliable source of fermentable fiber (hemicellulose and cellulose) for African apes (Wrangham et al. 1991; Rothman et al. 2007). This appears to be the case at Mondika as well, since several important herb species, including the shoots and mature seeds of *Haumania* (Maranthaceae), shoots of *Megaphrynium* (Maranthaceae), and stems of *Aframomum* (Zingiberaceae) and *Palisota* (Commelinaceae) contained high concentrations of neutral detergent fiber or hemicellulose (Supplemental Table 2.1). If we proceed with the basic assumption that gorillas can access approximately 1.5 kilocalories per gram of NDF through microbial fermentation then the total energy gained from dry matter would increase by roughly 42 % from the baseline energy intake calculated without the inclusion of NDF. When factoring in food nutrient percentages of total dry matter intake from the present study, I would then estimate that roughly 30 % of total energy intake would come from fermentable fiber (i.e. based on NDF accounting for 54 % of dry matter intake at 1.5 kcal / g NDF), 50 % from simple sugars (i.e. based on TNC accounting for 34 % of dry matter intake at 4 kcal / g TNC), 18 % from proteins (i.e. based on CP accounting for 12 % of dry matter intake at 4 kcal / g CP), and 2 % from lipids (i.e. based on LP accounting for < 1 % of dry matter intake at 9 cal / g LP) .

Local variation in ecological conditions, such as light exposure, soil characteristics, and microbial activity, may play very important roles in affecting the nutritional chemistry of leaves (Ganzhorn and Wright 1994; Chapman et al. 2003). Similar effects on the nutritional chemistry

of herbs may operate at local and regional levels, as suggested by the much higher crude protein content of herb stems eaten by western gorillas at Bai Hokou in Central African Republic and Mondika in Republic of Congo compared with Campo in Cameroon and Lope in Gabon (Remis 2003; Rothman et al. 2006b; Mongo 2006). Additional studies of local and regional variation in herb nutritional quality and availability may enhance our understanding of gorilla herb choice (Conklin-Brittain et al. 2001; Ganas et al. 2009), and explain why gorillas eat some herbs year-round while others serve as nourishment during periods of fruit scarcity.

It is presently unclear whether gorillas show inter-specific or sub-specific variation in digestive physiology and efficiency of hindgut fermentation (Rogers et al. 1990; Watts 1996; Remis 1997; Conklin-Brittain et al. 1998; Doran and McNeilage 1998; Delgado and van Schaik 2000). The ability to digest neutral detergent fiber efficiently via microbial fermentation and derive energy from its products, including fatty acids and proteins (Rothman et al. 2006b), may be critically important during periods of fruit scarcity. Energy yields from microbial fermentation are non-trivial in captive western gorillas, with neutral detergent fiber digestibility ranging from 45 to 70 % depending on the proportion of cellulose and lignin present (Remis and Dierenfeld 2004), and short-chain fatty acids resulting from microbial fermentation in gorillas may supply as much as 30 – 60 % of their metabolic energy requirements (Popovich et al. 1997). The herb pith and leaves eaten by western gorillas at most study sites contained more fiber (NDF) than those eaten by mountain gorillas (Remis 2003; Rothman et al. 2006b) and this study was no exception. Based on the sweeter fruits and more fibrous herbs in the western gorilla diet, it would seem that western gorillas living in mature lowland rainforest have access to a higher non-structural carbohydrate and complex carbohydrate diet than what is available to mountain gorillas.

In conclusion, geographical, historical, and altitudinal differences between west-central African lowland rainforests and east African montane forests have apparently led to ecological differences in the availability, distribution, and nutritional chemistry of fruits and terrestrial herbs, which in turn have produced fundamental changes in gorilla nutrient acquisition. Gorillas at one lowland site, Mondika, fed on a broader array of staple foods, including fruits and seeds from a greater number of species than at two mountain gorilla sites, which was consistent with the higher densities, diversities, and availability of ripe fruit in lowland forests compared to montane environments.

The evolutionary implications for fundamental divergences in nutrient intake on life history strategies are potentially great. Primates limited by access to easily-assimilable energy sources can suffer periods of net negative energy balance, weight loss, and concomitant physiological stress, which may constrain infant growth and development, delay conception, affect time of weaning, extend inter-birth intervals, or increase susceptibility to disease. In Hanuman langurs, seasonal shortfalls in the availability of high quality resources produced poor nutritional and energetic status among females, promoted weight loss, and delayed conceptions (Koenig et al. 1997; Koenig 2000; Koenig and Borries 2001). Moreover, higher quality diets at Jodhpur, a provisioned Hanuman langur population in India, led to decreased birth seasonality, younger age at first birth and weaning, and shorter inter-birth intervals compared to an unprovisioned wild population of Hanuman langurs in Ramnagar, Nepal (Koenig and Borries 2001; Borries et al. 2001). Nutritional effects on female reproduction also occur in large-bodied apes with long inter-birth intervals such as wild chimpanzees. In chimpanzees, the timing of conceptions was linked to the availability of high-quality foods (Sherry 2002; Emory Thompson 2005), and females that used core foraging areas with more preferred foods had shorter-interbirth

intervals and higher infant survival compared to females that used lower quality core foraging areas (Emory Thompson et al. 2007). Accordingly, body masses of chimpanzees recorded during periods of frequent provisioning were higher than those recorded during periods of non-provisioning in one population (Pusey et al. 2005), and between-population variation in inter-birth intervals was associated with differences in habitat quality (Emory Thompson 2005; Emory Thompson et al. 2007).

Although gorillas do not show birth seasonality there is some evidence that western lowland gorillas differ from mountain gorillas in their developmental life history including delayed infant weaning age and longer inter-birth intervals by about one year in wild western gorillas compared to mountain gorillas (Stoinski et al. 2013). This may seem paradoxical if wild western gorilla diets contain more easily-assimilable energy than mountain gorilla diets, however the slower developmental life history in wild western gorillas may have been selected for by ecological conditions of energy risk (Janson and van Schaik 1993) such as widely fluctuating fruit availability within and between years (Stoinski et al. 2013). To clarify the links between nutrient intake and life history parameters in long-lived species with long infant dependency periods future comparative studies of ape populations should examine how changing nutrient profiles (particularly the ratio of protein to non-structural carbohydrate) affect aspects of growth and reproduction, including infant growth patterns, age at first reproduction, weaning age, and length of inter-birth intervals, and whether gorillas exhibit a range of nutritional variation similar to that observed in other ape species.

Tables and Figures

Table 2.1. Diet of adult female western gorillas ranked by percent intake by wet weight averaged across 11 months. Food types included fruits (FR), herbs (HE), insects (IN), dicotyledonous leaves (LE), flowers (FW), and other (OT). Food items analyzed for nutrient content are indicated by *. Foods with feeding rates (items / min) measured during focal follows are indicated by †. Foods with feeding rates measured opportunistically at food patches are indicated by §. Absence of wet weight data is indicated by na.

Species	Family	Local name	Food type	Preferred/ Non-pref	% Feed time	% Wet weight
Staple food items						
<i>Haumania danckelmaniana</i> *†	Maranthaceae	Genye	FR	Preferred	12.0	12.1
<i>Palisota ambigua</i> *†	Commelinaceae	Doto	HE	Non-pref	2.6	9.9
<i>Haumania danckelmaniana</i> *†	Maranthaceae	Basele	HE	Preferred	6.2	9.6
<i>Klainedoxa gabonensis</i> *†	Irvingiaceae	Bokoko	FR	Preferred	3.9	8.5
<i>Palisota brachythyrsa</i> *†	Commelinaceae	Mangabo	HE	Non-pref	3.6	6.5
<i>Cubitermes sp.</i> *†	Termitidae	Kusu	IN		5.6	4.7
<i>Aframomum limbatum</i> *†	Zingiberaceae	Njombo	HE	Non-pref	8.9	4.2
<i>Gambeya lacourtiana</i> *†	Sapotaceae	Bambu	FR	Non-pref	0.5	3.9
Unknown*†	Unknown	Ekombe	LE	Non-pref	1.8	3.2
<i>Celtis mildbraedii</i> *†	Ulmaceae	Ngombe	LE	Non-pref	4.9	3.1
<i>Landolphia sp.1-2</i>	Apocynaceae	Pembe-Ndembo	FR		0.8	3.0
<i>Duboscia macrocarpa</i> *†	Tiliaceae	Nguluma	FR	Non-pref	2.3	2.8
<i>Aframomum subsericeum</i> *†	Zingiberaceae	Njokoko	HE	Non-pref	3.7	2.1
<i>Pterocarpus soyauxii</i> *†	Papilionaceae	Embema	FR	Non-pref	0.7	1.9
<i>Ficus sp. 1</i>	Moraceae	Ngumu	LE		1.4	1.6

Species	Family	Local name	Food type	Preferred/ Non-pref	% Feed time	% Wet weight
Staple food items (cont.)						
<i>Gilbertiodendron dewevreii</i> *†	Caesalpinaceae	Bemba	FR	Preferred	0.7	1.6
<i>Megaphrynium macrostachyum</i> *†	Maranthaceae	Ngungu	HE	Non-pref	1.3	1.3
<i>Milicia excelsa</i>	Moraceae	Mobangi	FR		1.6	1.2
<i>Whitfieldia elongata</i> *†	Acanthaceae	Indolu	LE	Non-pref	2.6	1.1
Unknown	Unknown	Nganda	LE		1.0	1.0
<i>Anonidium mannii</i> *†	Annonaceae	Mobei	FR	Preferred	0.7	1.0
<i>Tetrapleura tetraptera</i> *†	Mimosaceae	Ekombolo	FR	Non-pref	1.1	1.0
Other food items in diet						
<i>Vitex doniana</i> *†	Verbenaceae	Mongweagwea	FR	Preferred	1.1	0.9
<i>Thomandersia hensii</i> *†	Acanthaceae	Ingoka	LE	Non-pref	0.9	0.9
<i>Polyalthia suaveolens</i> *§	Annonaceae	Motunga	FR	Non-pref	1.7	0.9
<i>Ficus sp. 2</i> *§	Moraceae	Dobu	LE	Non-pref	0.5	0.9
<i>Gilbertiodendron dewevreii</i>	Caesalpinaceae	Bemba	LE		0.8	0.9
<i>Gnetum africanum</i> *†	Gnetaceae	Koko	LE	Non-pref	1.2	0.7
<i>Angylocalyx pynaertii</i> *†	Papilionaceae	Manjombe	FR	Preferred	0.6	0.6
<i>Hydrocharis chevalieri</i> *†	Hydrocharitaceae	Kongwasika	HE	Preferred	2.3	0.6
<i>Duboscia viridiflora</i> *†	Tiliaceae	Nguluma green	FR		0.9	0.5
Unknown*†	Unknown	Kpekeke	LE	Non-pref	1.2	0.5
<i>Landolphia sp.3</i>	Apocynaceae	Ita ti pembe	FR		0.1	0.4
Unknown	Unknown	Mbongo	LE		< 0.1	0.4
Unknown	Unknown	Mosesenge	LE		0.5	0.4

Species	Family	Local name	Food type	Preferred/ Non-pref	% Feed time	% Wet weight
Other food items in diet (cont.)						
<i>Dialium sp.</i> †	Caesalpiniaceae	Mbaso	FR		1.5	0.4
Unknown*†	Unknown	Ita ti edutu	LE	Non-pref	0.3	0.4
Unknown	Unknown	Epopolo	LE		0.3	0.3
<i>Grewia oligoneura</i> *†	Tiliaceae	Buku	FR	Non-pref	0.4	0.3
<i>Angylocalyx pyraertii</i> *†	Papilionaceae	Manjombe	LE	Non-pref	1.4	0.3
<i>Apocynaceae sp.1</i> *†	Apocynaceae	Ivua	LE	Non-pref	0.1	0.3
Unknown*	Unknown	Ekule	LE	Non-pref	0.2	0.3
Unknown	Unknown	Mondamandam	LE		0.2	0.2
<i>Drypetes diopa</i> *§	Euphorbiaceae	Tembo	FR	Preferred	0.9	0.2
Unknown*†	Unknown	Tondo	LE	Non-pref	0.1	0.2
Unknown	Unknown	Mwala	LE		0.2	0.2
<i>Pycnobotrya nitida</i>	Apocynaceae	Mongenje	LE		0.2	0.1
Unknown	Unknown	Ngange	LE		0.2	0.1
<i>Angylocalyx pyraertii</i>	Papilionaceae	Manjombe	FW		0.1	0.1
Unknown	Unknown	Mbatama	LE		0.1	0.1
Unknown*†	Unknown	Edutu	LE	Non-pref	0.2	0.1
Unknown	Unknown	Ita ti mazembe	LE		0.1	0.1
Unknown	Unknown	Mafuja	LE		0.1	0.1
<i>Landolphia sp.4</i> *†	Apocynaceae	Bosindja	FR	Preferred	< 0.1	0.1
<i>Tiliacora sp.</i>	Menispermaceae	Etokobola	LE		0.1	0.1
<i>Thomandersia hensii</i>	Acanthaceae	Ingoka	FW		0.1	0.1

Species	Family	Local name	Food type	Preferred/ Non-pref	% Feed time	% Wet weight
Other food items in diet (cont.)						
<i>Gnetum sp.</i>	Gnetaceae	Ita ti koko	LE		0.1	0.1
Unknown*§	Unknown	Mbongo	FR	Non-pref	0.2	0.1
<i>Desplatsia sp.</i>	Tiliaceae	Liamba	LE		0.1	0.1
<i>Dialium sp.</i>	Caesalpiniaceae	Mbaso	LE		< 0.1	< 0.1
<i>Milicia excelsa</i>	Moraceae	Mobangi	LE		< 0.1	< 0.1
Unknown	Unknown	Ita ti tondo	LE		0.1	< 0.1
Unknown	Unknown	Ita ti ngange	LE		< 0.1	< 0.1
Unknown	Unknown	Binju	LE		< 0.1	< 0.1
<i>Palisota brachythyrsa</i>	Commelinaceae	Mangabo	LE		< 0.1	< 0.1
Unknown	Unknown	Mongenge	LE		< 0.1	< 0.1
Unknown*†	Unknown	Mazembe	LE	Non-pref	< 0.1	< 0.1
Unknown	Unknown	Mbongobongo	LE		< 0.1	< 0.1
<i>Tabernaemontana penduliflora</i>	Apocynaceae	Etokoloko	FR		< 0.1	< 0.1
<i>Hexalobus crispiflorus</i>	Annonaceae	Pota	FR	Preferred	0.0	0.0
<i>Barteria fistulosa</i>	Passifloraceae	Ngomangoma	Skin	Non-pref	0.0	0.0
<i>Landolphia sp. 2</i>	Apocynaceae	Ndembo	Skin	Non-pref	0.0	0.0
Unknown	Unknown	Soil scratch	OT		1.5	na
Unknown	Unknown	Bambwa ant	IN		1.0	na
Unknown	Unknown	Ndia ant	IN		0.9	na
<i>Celtis mildbraedii</i>	Ulmaceae	Ngombe	FW		0.8	na
<i>Grewia sp.?</i>	Tiliaceae	Buku ti ngu	FR		0.7	na

Species	Family	Local name	Food type	Preferred/ Non-pref	% Feed time	% Wet weight
Other food items in diet (cont.)						
<i>Sarcophrynium schweinfurthianum</i>	Maranthaceae	Kaya	HE		0.6	na
<i>Laccosperma secundiflora</i>	Arecaceae	Gao	HE		0.5	na
<i>Nauclea diderrichii</i>	Rubiaceae	Mwase	FR		0.4	na
Unknown	Unknown	Kpomba	FW		0.4	na
<i>Megaphrynium macrostachyum</i>	Marantaceae	Ngungu	FW		0.4	na
<i>Barteria fistulosa</i>	Passifloraceae	Ngomangoma	FR		0.3	na
<i>Caloncoba welwitschii</i>	Flacourtiaceae	Esoku	FR		0.3	na
<i>Diospyros mannii</i>	Ebenaceae	Mulumbo	FR		0.3	na
<i>Aframomum subsericeum</i>	Zingiberaceae	Njokoko	FR		0.2	na
<i>Diospyros bipindensis</i>	Ebenaceae	Ita ti babangu	FR		0.2	na
<i>Diospyros crassiflora</i>	Ebenaceae	Lembe	FR		0.2	na
<i>Diospyros ituriensis</i>	Ebenaceae	Babangu	FR		0.2	na
<i>Megaphrynium macrostachyum</i>	Maranthaceae	Ngungu	FR		0.2	na
<i>Nauclea gillettii?</i>	Rubiaceae	Mwase ti ngu	FR		0.2	na
<i>Pancovia</i> sp.?	Sapindaceae	Ita ti ingoyo	FR		0.2	na
<i>Celtis adolfi-friderici</i>	Ulmaceae	Kakala	FR		0.1	na
<i>Chytranthus macrobotrys</i>	Sapindaceae	Motokodi	FR		0.1	na
<i>Haumania</i> sp.?	Maranthaceae	Ita ti basele ti	HE		0.1	na
<i>Myrianthus arboreus</i>	Moraceae	Ngata	FR		0.1	na
<i>Pancovia laurentii</i>	Sapindaceae	Ingoyo	FR		0.1	na
<i>Pycnobotrya nitida</i>	Apocynaceae	Mongenje	HE		0.1	na

Species	Family	Local name	Food type	Preferred/ Non-pref	% Feed time	% Wet weight
Other food items in diet (cont.)						
<i>Irvingia excelsa</i>	Irvingiaceae	Payo	FR		< 0.1	na
<i>Keayodendron brideloides</i>	Euphorbiaceae	Embundunbund	FR		< 0.1	na
<i>Aframomum limbatum</i>	Zingiberaceae	Njombo	FR		< 0.1	na
<i>Aframomum</i> sp.?	Zingiberaceae	Njombo ti ngu	HE		< 0.1	na
<i>Desplatsia</i> sp.	Tiliaceae	Liamba	FR		< 0.1	na
<i>Dioscoreophyllum cumminsii</i>	Menispermaceae	Mola	FR		< 0.1	na
Unknown	Unknown	Mobobo	FR		< 0.1	na
Unknown	Unknown	Unidentified sp.	HE		< 0.1	na
Unknown	Unknown	Ejeke termite	IN		< 0.1	na
Unknown	Unknown	Ngomangoma	IN		< 0.1	na
Unknown	Unknown	Mondamandam	FR		< 0.1	na
Unknown	Unknown	Assorted unknown spp. ¹	IN		(0.3)	(na)
Unknown	Unknown	Assorted unknown spp. ²	LE		(1.2)	(1.3)
N = 90 species (min)	N = 26 families (min)	N = 106 food items				

¹ Includes assortment of unidentified ant species, which together accounted for 0.3% of feeding time.

² Includes assortment of unidentified leaf species, which together accounted for 1.2% of feeding time and 1.3% of intake.

Table 2.2. Macronutrient, fiber, energy, and moisture content of western gorilla fruits, leaves, and herbs at Mondika.

Assay	Mean % DM (SD)			ANOVA		Tukey HSD		
	Fruit	Leaf	Herb	F	<i>P</i>	FR vs LE	FR vs HE	LE vs HE
CP	7.4 (4.2)	19.7 (6.3)	15.7 (4.2)	24.5	***	***	**	ns
FSS	16.5 (8.6)	2.8 (1.8)	3.7 (1.0)	23.0	***	***	***	ns
TNC	45.0 (21.0)	19.9 (11.2)	11.1 (7.0)	15.6	***	***	***	ns
LP	1.4 (2.1)	1.9 (1.7)	2.1 (1.0)	0.6	ns	ns	ns	ns
NDF	42.3 (17.5)	50.7 (10.0)	53.8 (5.7)	2.5	(*)	ns	ns	ns
HC	11.9 (9.5)	14.1 (6.0)	18.1 (5.4)	1.7	ns	ns	ns	ns
ADF	30.4 (15.5)	36.6 (10.0)	35.6 (8.6)	1.1	ns	ns	ns	ns
Cs	17.6 (8.5)	20.3 (5.6)	24.5 (6.9)	2.3	ns	ns	(*)	ns
Ls	12.8 (8.8)	16.3 (8.4)	11.1 (4.3)	1.2	ns	ns	ns	ns
Ash	4.1 (2.2)	8.2 (3.2)	17.3 (4.7)	45.4	***	**	***	***
Kcal	231 (72)	190 (49)	153 (25)	5.0	*	ns	*	ns
H ₂ O	69.7 (22.2)	86.7 (8.1)	93.7 (2.9)	4.8	*	(*)	*	ns
N	18	15	7					

Post-hoc Tukey HSD tests were conducted to test for differences between fruits (FR), leaves (LE) and herbs (HE). $P < 0.001 = ***$; $0.001 > P < 0.01 = **$; $0.01 > P < 0.05 = *$; $0.05 > P < 0.10 = (*)$; $P > 0.05 = ns$. Key: CP = crude protein; FSS = free simple sugars; TNC = total non-structural carbohydrates; LP = lipid; NDF = neutral detergent fiber; HC = hemicellulose; ADF = acid detergent fiber; Cs = cellulose; Ls = lignin; Kcal = energy estimate (Kcals/100 g organic matter, excluding NDF); Moisture content (H₂O) was calculated as % wet weight on a smaller data set of 13 fruit species, 8 leaf species, and 5 herb species.

Table 2.3. Mean nutrient content (% dry matter) of preferred and non-preferred fruit and herb species in the diet of western gorillas at Mondika.

Assay	Mean (% DM)		Mann-Whitney	<i>P</i>
	Preferred (SD)	Non-pref (SD)		
Fruits				
CP	6.6 (3.9)	8.2 (4.7)	31	0.44
FSS	21.0 (8.2)	12.1 (6.8)	63	0.05
TNC	53.4 (21.2)	36.5 (18.0)	62	0.06
LP	0.7 (0.7)	2.0 (2.7)	26	0.20
NDF	34.9 (17.1)	49.6 (15.4)	20	0.08
HC	14.8 (12.2)	9.0 (4.8)	51	0.38
ADF	20.1 (10.2)	40.7 (12.9)	8	< 0.01
Cs	13.5 (6.4)	21.8 (8.6)	17	0.04
Ls	6.6 (5.0)	18.9 (7.5)	9	< 0.01
Ash	4.5 (2.9)	3.6 (1.2)	43	0.89
Kcal	257 (70)	204 (67)	60	0.09
N	9	9		
Herbs				
CP	14.2 (1.4)	16.3 (5.0)	4	0.86
FSS	4.1 (0.6)	3.6 (1.1)	6	0.86
TNC	15.0 (4.7)	9.6 (7.5)	7	0.57
LP	2.2 (0.8)	2.1 (1.2)	6	0.99
NDF	50.3 (2.7)	55.2 (6.2)	2	0.38
HC	19.0 (9.2)	17.8 (4.7)	5	0.99
ADF	31.3 (6.5)	37.4 (9.4)	3	0.57
Cs	20.0 (7.1)	26.3 (6.7)	2	0.38
Ls	11.3 (0.5)	11.1 (5.2)	6	0.86
Ash	18.4 (9.6)	16.8 (3.1)	5	0.99
Kcal	165 (19)	148 (27)	7	0.56
N	2	5		

Bold p-values indicate significant difference between preferred and non-preferred fruit species at $P < 0.05$ or trend at $P < 0.10$. See Table 2.2 key for nutrient abbreviations. Sample sizes (N) are provided for preferred and non-preferred fruit species and for preferred and non-preferred herb species.

Table 2.4. Inventory of staple gorilla food types at Mondika, Bwindi, and Karisoke.

	Western Mondika	Mountain Bwindi	Mountain Karisoke
N staple foods	22	15	9
Fruit	10	3	0
Herb	6	10	9
Leaf	5	1	0
Insect	1	0	0
Dead wood	0	1	0
% of diet (by wet weight) accounted for by staple foods	85 %	96 %	91 %

Data are from this study (Western gorillas: Mondika) and Rothman et al. (2007; Mountain gorillas: Bwindi and Karisoke). Fruit includes pulp and seeds; herb includes stem, shoot, pith, peel, and herb leaf; leaf includes dicotyledonous leaf.

Table 2.5. Mean (SD) nutrient content (% dry matter) of fruit and herb species in the staple diet of western (Mondika) and mountain (Bwindi; Karisoke) gorillas.

	Mondika	Bwindi	Karisoke	U / X ²	P
Staple fruits					
CP	5.3 (3.8)	10.1 (1.2)	na	5	0.11
TNC	53.1 (22.5)	15.4 (8.3)	na	29	0.01
NDF	36.6 (18.7)	41.8 (13.3)	na	13	0.81
HC	12.1 (12.4)	9.9 (2.6)	na	11	0.57
Cs	14.0 (8.5)	15.6 (8.4)	na	11	0.57
N	10	3	0		
Staple herbs					
CP	16.1 (4.5)	20.3 (9.2)	15.3 (9.0)	1.8	0.40
TNC	11.0 (7.6)	23.5 (7.9)	20.5 (9.2)	7.4	0.02
NDF	54.7 (5.7)	37.4 (12.8)	51.3 (12.3)	7.8	0.02
HC	19.1 (5.3)	10.5 (3.0)	13.3 (3.8)	9.2	0.01
Cs	24.4 (7.5)	18.0 (11.6)	25.8 (11.7)	4.0	0.13
N	6	10	9		

Assays include crude protein (CP), total non-structural carbohydrate (TNC), neutral detergent fiber (NDF), hemicellulose (HC), and cellulose (Cs). Data from Bwindi and Karisoke are from Rothman et al. (2007). Mann-Whitney (U) tests were performed for two-site (Mondika vs Bwindi) comparisons. Kruskal-Wallis tests (X²) were performed for three-site (Mondika vs Bwindi vs Karisoke) comparisons. Number (N) of staple fruit and herb species at each site are provided. Significant differences among sites are bolded at probability (P) < 0.05.

Table 2.6. Nutrient contributions (percentage of dry matter intake) to gorilla diets at Mondika (in bold), Bwindi, and Karisoke with comparisons to chimpanzees, bonobos, and three species of African monkey with non-specialized guts.

Site	Species	CP	TNC	NDF	HC	Cs
Mondika	Western lowland gorilla (<i>Gorilla gorilla</i>)^a	11.9	33.5	53.9	17.5	19.4
Bwindi	Mountain gorilla (<i>Gorilla beringei</i>) ^b	18.2	18.8	42.9	10.8	17.5
Karisoke	Mountain gorilla (<i>Gorilla beringei</i>) ^b	17.2	18.2	41.2	12.5	19.8
Kibale	Chimpanzee (<i>Pan troglodytes schweinfurthii</i>) ^c	9.5	38.8	33.6	13.7	11.8
Salonga	Bonobo (<i>Pan paniscus</i>) ^d	8.3	---	26.8	10.1	11.5
Kibale	Blue monkey (<i>Cercopithecus mitis stuhlmanni</i>) ^c	17.6	35.3	32.3	11.8	12.3
Kibale	Red-tailed monkey (<i>Cercopithecus ascanius schmidtii</i>) ^c	17.6	36.5	31.3	11.4	11.6
Kibale	Mangabey (<i>Lophocebus albigena johnstoni</i>) ^c	16.3	34.0	32.0	12.0	11.9

Data are from ^a This study, ^b Rothman et al. (2007), ^c Conklin-Brittain et al. (1998) and ^d Hohmann et al. (2006). Key: crude protein (CP); total non-structural carbohydrate (TNC); neutral detergent fiber (NDF); hemicellulose (HC); cellulose (Cs).

Supplemental Table 2.1. Nutrient content (% dry matter) of staple gorilla foods at Mondika, in descending order of wet weight contribution.

Species	FT	P/ NP	% Intake	SD Intake	CP	NDF	HC	Cs	TNC	LP	FSS	Ls	Ash
<i>Haumania danckelmaniana</i>	FR	P	12.1	18.6	10.9	70.0	40.6	21.1	13.2	1.2	8.2	8.2	4.8
<i>Palisota ambigua</i>	HE	NP	9.9	5.9	13.0	45.0	18.6	21.8	18.7	2.1	4.2	4.6	21.2
<i>Haumania danckelmaniana</i>	HE	P	9.6	4.6	15.2	52.2	25.5	15.0	18.3	2.7	4.5	11.6	11.6
<i>Klainedoxa gabonensis</i>	FR	P	8.5	10.1	3.3	41.4	11.0	18.0	52.1	0.4	25.0	12.5	2.8
<i>Palisota brachythyrsa</i>	HE	NP	6.5	4.8	16.3	58.9	15.8	35.1	9.7	2.1	3.2	8.0	13.0
<i>Cubitermes</i> sp.	IN	?	4.7	3.6	18.5	58.1	8.6	0.0	0.2	0.7	0.2	0.0	59.6
<i>Aframomum limbatum</i>	HE	NP	4.2	2.7	10.1	53.5	25.5	17.9	15.3	4.0	4.7	10.0	17.1
<i>Gambeya lacourtiana</i> (Ekombe)	FR	NP	3.9	9.2	3.5	32.8	2.8	7.6	52.7	8.7	13.4	22.4	2.2
<i>Celtis mildbraedii</i> LE+BK	LE	NP	3.2	6.2	25.1	29.6	7.0	11.9	32.5	5.4	4.1	10.7	7.5
<i>Celtis mildbraedii</i> LE+BK	LE	?	3.1	3.6	18.1	55.6	23.8	21.5	15.3	1.9	2.8	10.4	9.1
<i>Landolphia</i> sp. 1-2 ^a	FR	P	3.0	4.1	2.1	8.0	4.4	3.1	88.9	0.0	33.1	0.5	1.0
<i>Duboscia macrocarpa</i>	FR	NP	2.8	4.4	4.0	56.4	5.3	31.3	36.8	0.0	12.4	19.9	2.8
<i>Aframomum subsericum</i>	HE	NP	2.1	1.8	19.1	58.8	13.0	28.6	2.5	1.6	3.9	17.2	18.0
<i>Pterocarpus soyauxii</i>	FR	NP	1.9	6.3	12.0	48.2	9.3	18.7	33.1	1.2	11.4	20.3	5.4
<i>Ficus</i> sp. 1 ^b	LE	NP	1.6	4.2	19.6	50.0	13.2	20.2	19.7	1.9	2.8	16.6	8.1
<i>Gilbertiodendron dewevrei</i>	FR	P	1.6	3.5	7.0	40.1	28.1	6.5	50.1	0.9	14.2	5.4	2.0
<i>Megaphrynium macrostachyum</i>	HE	NP	1.3	0.8	22.8	59.7	16.1	28.2	1.8	0.7	1.8	15.5	14.9
<i>Milicia excelsa</i> ^c	FR	P	1.2	4.0	7.1	30.4	8.0	14.6	53.6	0.4	22.8	7.8	8.5
<i>Whitfieldia elongata</i>	LE	NP	1.1	3.4	24.5	46.0	18.6	15.8	14.7	2.0	3.0	11.6	12.8

Species	FT	P/ NP	% Intake	SD Intake	CP	NDF	HC	Cs	TNC	LP	FSS	Ls	Ash
(Nganda) ^b	LE	NP	1.0	0.6	19.6	50.0	13.2	20.2	19.7	1.9	2.8	16.6	8.1
<i>Anonidium mannii</i>	FR	P	1.0	3.2	1.0	19.6	7.8	8.6	75.7	0.6	27.5	3.2	3.2
<i>Tetrapleura tetraptera</i>	FR	NP	1.0	2.4	1.7	19.2	3.9	10.2	75.2	0.1	26.8	5.1	3.7
Total			85.3										

Nutrient content (% dry matter) of staple food items was determined from chemical analysis for 18 (bolded text) of 22 foods. For two staple fruit species and two staple leaf species, I estimated nutrient content and percent wet weight intake based on ^a sister species from the same Genus or ^c fruits of similar size and construction, or based on ^b average measurements in the analyzed leaf sample. Intake estimates were calculated as the product of actual feeding time and average feeding rate (mean N of items/min) and fresh mass (mean g/item) of similar foods. Key: FT = food type: FR = fruit, seed; HE = herb stem, shoot, root; IN = insect; LE = tree leaves, young tree bark/twigs, woody shrub/liana leaves; P / F = preferred (P); non-preferred (NP) food species; CP = crude protein; NDF = neutral detergent fiber; HC = hemicellulose; Cs = cellulose; TNC = total non-structural carbohydrates; LP = lipid; FSS = free simple sugars; Ls = lignin.

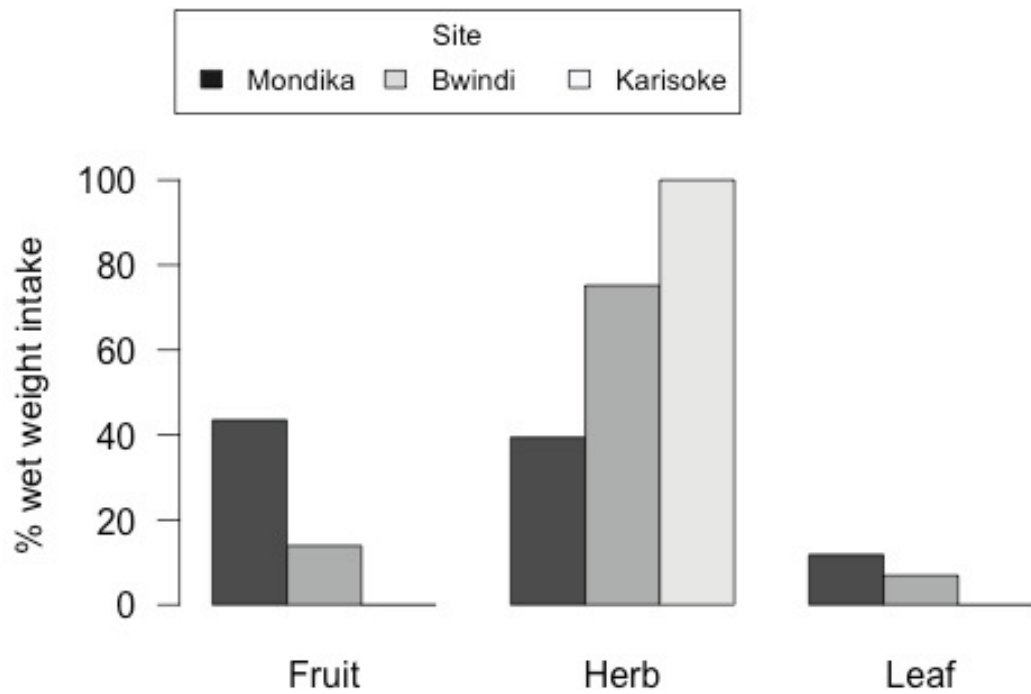


Figure 2.1. Mean percentage (wet weight based on staple foods scaled up to 100 %) of fruit, herb, and leaf in gorilla diets at Mondika, Bwindi, and Karisoke.

Data for Bwindi and Karisoke were calculated from Rothman et al. (2007).

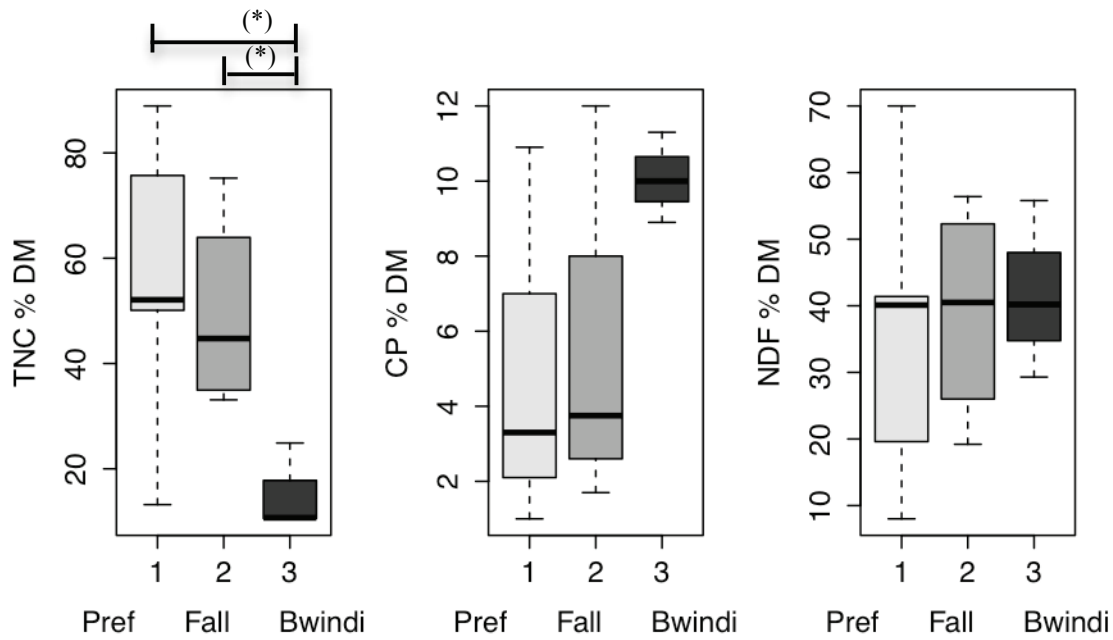


Figure 2.2. Total non-structural carbohydrate (TNC), crude protein (CP), and neutral detergent fiber (NDF) content (% dry matter) of preferred (Pref: n = 5) and non-preferred (Fall: n = 4) fruits in the staple diet at Mondika compared to staple fruits (n = 3) at Bwindi.

Box plots present the median (black bar), interquartile range (box), and the minimum and maximum values (whiskers) for each group. (*) indicates a trend for significant pair-wise difference at $p < 0.10$ using Mann-Whitney U-tests.

CHAPTER THREE:
**Female agonistic relationships, steepness of dominance hierarchies, and the role of the male
in reinforcing within-group social relationships in wild western gorillas (*Gorilla gorilla*)**

Abstract

Socioecological models attempt to explain variation in female social relationships and patterns of dispersal within and between primate species living in different environments based on variation in resource characteristics, including the density and distribution of resources and the size of food patches relative to group spread. Some species, however, do not fit neatly into the model's categorical predictions. In gorillas, our prevailing understanding of within-group social relationships has been shaped almost entirely by long-term research on Karisoke mountain gorillas (*G. beringei*). At Karisoke, mountain gorillas subsist almost entirely on abundant and evenly distributed herbs and feeding competition has limited effects on female reproductive rates. Most female dominance relationships are considered undecided, which is thought to be associated with low or negligible levels of contest feeding competition. In contrast, western gorillas (*G. gorilla*) eat a more varied diet consisting of more fruit and are thought to face stronger within-group contest competition than mountain gorillas because of their increased consumption of high quality and potentially monopolizable fruits, although patch characteristics are needed to assess the monopolizability of fruits in western gorilla habitats. Here, I examine whether increased frugivory (if fruit is an indicator of contest competition) in western gorillas is associated with increased rates of aggression over fruit, a greater proportion of decided aggression and decided dominance relationships, and a steep and linear dominance hierarchy compared to mountain gorillas. Research on female agonistic relationships was conducted in a

single group of habituated wild western gorillas, comprised of six adult females, one silverback male, and their offspring, over 14 months (2004-2006) at the Mondika Research Center bordering the Central African Republic and Republic of Congo. I conducted 224 half-day focal follows of 4 (of 6) adult females. To calculate rates of aggression in the context of feeding (fruit; herb; leaf; insect) and non-feeding activities (resting; traveling; access to silverback), I recorded all occurrences of focal agonism directed and received during follows. These data were supplemented by opportunistic recording of non-focal aggression, female coalitions, and male interventions in female conflicts. Results indicated that the bulk (89 %) of female aggression (n = 551 events) occurred in the context of feeding, and that a considerable proportion (60 %) of feeding aggression (n = 489 events) occurred over fruit and flower. Decided dominance relationships were indicated for many but not all (8 of 15) dyads based on aggression, as was a steep dominance hierarchy, despite some (11-14 % of) aggression against the hierarchy. Most female dominance relationships remained stable for at least 2.5 years, which may be indirectly attributed to the male's rare but consistent support in favor of higher-ranking competitors. Findings suggest that increased fruit consumption in at least one gorilla population was associated with increased aggression over high quality and potentially monopolizable resources, more clearly defined within-group female social relationships, and differences in the direction of male support, challenging current socioecological categorization of gorilla society.

Introduction

Primates are among the most social orders of mammals (Dunbar 1998; Perez-Barberia et al. 2007). The majority of primates live in bisexual groups (van Schaik and Kappeler 1997;

Kappeler and van Schaik 2002), and they are noted for their complex social relationships with group members (Cheney et al. 1987). One major potential cost of living in a group is feeding competition (Alexander 1974; Macdonald 1983; van Schaik 1983; Walters and Seyfarth 1987; van Schaik 1989; Janson and Goldsmith 1995). Because mammalian female reproductive success often depends on foraging efficiency (Trivers 1972; Bradbury and Vehrencamp 1977; Ritchie 1990; Conradt et al. 1999; Jonsson et al. 2002), differences in the form and strength of feeding competition have been hypothesized to influence the nature of female relationships (Wrangham 1979; Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Koenig 2002; Isbell and Young 2002; Boinski et al. 2002). When high-quality resources are distributed in patches that are large enough to accommodate some, but not all group members, individuals who are more aggressive (Janson 1985; Vogel 2005), socially dominant (Robinson 1981; van Noordwijk and van Schaik 1987; Barton and Whiten 1993; Koenig et al. 1998; Koenig 2000), or have more allies (Whitten 1988a; Saito 1996) may gain more of the resources than others (van Schaik 1989; van Schaik 1996; Koenig 2002). Thus, when the majority of high-quality foods can be monopolized, within-group contest (WGC) competition might predominate. This situation is expected to cause a cascade of effects on female relationships including unidirectional dominance relationships and linear dominance hierarchies (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997).

To explain the relationship between food distribution, feeding competition, and variation in female social relationships, van Schaik (1989), based on Wrangham's (1980) initial approach, developed a socioecological model that was later extended (van Schaik 1996; Sterck et al. 1997). The model has five major components that concern the strength of WGC competition and how it shapes female social relationships in group-living nonhuman primates. First, when many dietary

items can be monopolized and WGC competition is strong, the model predicts that aggression or displacements (over food) will be common (van Schaik 1989; van Schaik 1996), although low-ranking females might often avoid high-ranking females at monopolizable resources (Whitten 1983; Janson and van Schaik 1988), with the consequence that aggression rates would be relatively low (Koenig and Borries 2006; Koenig and Borries 2009). Second, within dyads of females, one will reliably elicit submission from the other, leading to the establishment of consistent, unidirectional (van Schaik 1989), or decided (Sterck et al. 1997) dominance relationships. However, if individuals have knowledge about asymmetrical relationships (Maynard Smith and Parker 1976) that are based on the potential to use force or recruitment of allies (Lewis 2002) then frequent use of force may not be required to maintain differences in power. Third, it is predicted that many or most of these relationships will be transitive, i.e., if $A > B$ and $B > C$, then $A > C$, rendering hierarchies linear (van Schaik 1989; Sterck et al. 1997). Fourth, when patches are large enough to allow several (but not all) individuals to feed concurrently, kin-based coalitions should allow better access to food, and thus females will be expected to remain in their natal groups with kin (van Schaik 1989; Sterck et al. 1997). Fifth, coalitions among maternal kin reinforce relative ranks (van Schaik 1989; Sterck et al. 1997) and promote stable matrilineal dominance hierarchies (Chapais 1992; Chapais 2004).

In contrast, when the majority of foods is indefensible WGC competition is expected to be weak, and displacements or aggression over food should be rare since their use will not translate into greater food intake (van Schaik 1989; van Schaik 1996). Competitive ability could vary considerably but not be exercised often under these circumstances or it may rarely be worthwhile for superior competitors to escalate contests leading to inconsistent dominance relationships (van Schaik 1989). In cases where females form linear hierarchies they would more

likely result from contests over access to preferred social partners such as a male (Watts 1994) or group membership (Jones 1980) than from contests over food (van Schaik 1996; Sterck et al. 1997; Koenig 2002). In addition, because female alliances should not improve access to foods that are indefensible, females may benefit little from remaining in their natal group and may instead emigrate if risk of predation is low (van Schaik 1989; Sterck et al. 1997). Ranks (if present) are predicted to become relatively unstable without reinforcement from alliances, and dominance hierarchies are expected to be shallow (de Vries et al. 2006), non-linear, and individualistic (van Schaik 1989; Koenig 2002).

Parts of the van Schaik model as they relate to food distribution and its effects on agonism and female social relationships are well supported, while others are lacking evidence, and still others are not well supported (Isbell 1991; Koenig 2002; Isbell and Young 2002; Koenig and Borries 2006; Thierry 2007; Koenig and Borries 2009). The first premise that increased reliance on monopolizable food items leads to more frequent food-related agonism has received some empirical support based on comparative studies of closely related species living in different environments, such as olive and mountain baboons (Barton et al. 1996), Surinamese, Peruvian, and Costa Rican squirrel monkeys (Mitchell et al. 1991; Boinski 1999; Boinski et al. 2002), and provisioned and unprovisioned Japanese macaques (Hill 1999). However, the predicted pattern was not clearly supported for sympatric primates with differing diets, such as long-tailed macaques and Thomas' langurs (Sterck and Steenbeek 1997) and vervet monkeys and Patas monkeys (Isbell and Pruettz 1998) given that rates of agonism were surprisingly similar between both species of a pair despite differences in the size and distribution of food patches. Further criticism of the first premise (Koenig and Borries 2006; Koenig and Borries 2009) has cited the mismatch in Hanuman langurs between high quality monopolizable resources in the diet (with

evidence for within-group contest competition based on rank-related energy gain) and highly variable rates of food-based agonism (Sterck 1999) that depend on group size and group spread as well as patch characteristics (quality, size, density, distribution).

More recently, it was demonstrated that rates of agonism among female primates were positively associated with the number of female competitors within a group and not by the amount of fruit in the diet according to phylogenetic comparisons across primates (Wheeler et al. 2013). These findings a) refute the hypothesis that fruit-feeding- in comparison with leaf- or insect-feeding- is associated with higher rates of female agonism among primates (e.g. see: Snaith and Chapman 2007), and b) calls into question the utility of comparing rates of agonism between groups of different sizes.

The second premise that females have consistent, unidirectional, or decided dominance relationships in response to repeated agonistic encounters that produce winner-loser effects over time (Chase et al. 1994), has mainly received support from primate species with frequent agonistic interactions, such as yellow baboons (cf. Hausfater 1975; Hausfater 1975; Hausfater et al. 1982), olive baboons (Barton and Whiten 1993), Japanese macaques (cf. Furuichi 1983; Furuichi 1983; Hill and Okayasu 1995), ring-tailed lemurs (Erhart and Overdorff 2008), and capuchin monkeys (Janson 1985; Vogel and Janson 2007). However, some researchers, including Isbell and colleagues (Isbell 1991; Isbell and Young 2002) have challenged the assumption that high rates of agonistic interactions indicate decided dominance relationships (reviewed in: Koenig and Borries 2006). For example, unidirectional female dominance relationships have been described for all or most female dyads within two groups of Phayre's leaf monkeys at one site despite low rates of agonism (Koenig et al. 2004). Other researchers,

including Watts (pers comm.), argue that the proposed relationship between rates of agonism and decided dominance relationships was not a postulate of the original van Schaik model in contrast to Isbell and colleagues' interpretation.

The third premise of the model, that groups with decided dominance relationships form linear hierarchies, has long been assumed but few studies have tested for linearity and examined the degree to which dominance relationships are asymmetrical, although some exemplary studies have examined the consistency of relationships and linearity of hierarchies in tandem (Borries et al. 1991; Watts 1994; Koenig et al. 2004; Lu et al. 2008). Even so the third premise needs further testing because high directional consistency (DCI) is not synonymous with high linearity (h) as many have assumed (Isbell and Young 2002; Koenig and Borries 2006).

To-date, predictions related to sex-biased dispersal are somewhat defunct in the context of socioecological models because of the many inconsistencies coming from empirical data on wild primate populations (Koenig and Borries 2009). However, the best standing evidence for the fourth premise concerning the relationship between resource characteristics, kin-based coalitions, and female philopatry comes from comparative studies of squirrel monkeys (Mitchell et al. 1991; Boinski 1999; Boinski et al. 2002). The squirrel monkey data suggest that the size and density of fruit patches determined the prevalence of kin-based coalitions within groups and depending on the scarcity or pervasiveness of coalitions either female-biased dispersal or female philopatry ensued (Boinski 1999; Boinski et al. 2002).

The fifth premise that kin-based coalitions promote rank establishment and maintenance remains one of the better-established tenets of the model. In savanna baboons and some macaque societies, a female's rank often depends greatly on the support and availability of close maternal

relatives (reviewed in: Datta 1992; Silk 2002; Chapais 2004). Accordingly, the prevalence of female coalitions and the number and quality of allies influenced female rank relations in rhesus and Japanese macaques (Chapais 1983; Mori et al. 1989; Chapais et al. 1991; Chapais 1992), savanna baboons (Cheney 1977; Walters 1980; Pereira 1989), gelada baboons (Dunbar 1980), vervet monkeys (Cheney 1983; Hunte and Horrocks 1987). However, there are notable exceptions to this pattern of frequent or invariable use of nepotistic support as seen in some species of macaques (Sterck et al. 1997; Thierry 2007), blue monkeys (Cords 2000), and Hanuman langurs (Borries et al. 1991; Borries 1993). In the case of Hanuman langurs kin-based coalitions were rare and hierarchies unstable despite the availability of female kin (Borries et al. 1991; Borries 1993), indicating that female dominance relationships can become unstable in the absence of frequent nepotistic support (Cords 2000; Pazol and Cords 2005).

Here, I seek to test whether the predicted associations between food, agonism, and the nature of female agonistic relationships within current socioecological models (van Schaik 1989; Sterck et al. 1997) are present in gorillas based on environmental and dietary differences between populations. In the absence of data on monopolizability, I examine the social consequences of increased fruit consumption in wild western gorillas (*Gorilla gorilla*) as compared to published reports for mountain gorillas (*Gorilla beringei*) from two populations, Karisoke, in the Virunga Volcanoes of Rwanda, Uganda, and the Democratic Republic of Congo, and Bwindi in Uganda. Gorillas offer a suitable comparison because they inhabit a wide range of environments that vary in the composition of plant communities and the density and distribution of preferred foods, resulting in dietary differences between sites (Watts 1996; Doran and McNeilage 1998; Goldsmith 2003; Yamagiwa et al. 2005; Rothman et al. 2007). Yet, our current understanding of the social consequences of feeding competition in wild gorillas is

restricted to long-term studies of mountain gorillas at a single site, Karisoke (Harcourt 1979a; Harcourt 1979b; Watts 1985; Watts 1990b; Watts 1994; Watts 1997; Watts 2001; Watts 2003; Robbins et al. 2005; Harcourt and Stewart 2007) and is supplemented by a recent study of mountain gorillas from a second site, Bwindi (Robbins 2008).

For mountain gorillas at Karisoke, the staple diet is composed entirely of abundant evenly distributed herbaceous vegetation (Watts 1984; Rothman et al. 2007) resulting in little within-group feeding competition overall (Watts 1985; Watts 1990b; Watts 2001; Watts 2003; Harcourt and Stewart 2007), although contests have been observed over access to seasonal bamboo shoots (Watts 1984; Watts 2001). Consistent with the framework of the current socioecological model, female feeding aggression at Karisoke occurred no more often than would be expected based on time spent feeding (Watts 1994). Most aggression within dyads was bidirectional in initiation, the bulk of aggression was undecided, and many or most female agonistic relationships were undecided on the basis of aggression (Watts 1994), although in certain dyads one individual was clearly dominant to the other (Harcourt 1979a; Stewart and Harcourt 1987; Watts 2001; Harcourt and Stewart 2007). As a consequence, females at Karisoke could not be ordered into a significant linear hierarchy based on aggression (Watts 1994), although linear hierarchies could frequently (but not always) be detected on the basis of displacements (Watts 1994; Robbins et al. 2005), with some individuals remaining dominant over others for more than 25 years (Robbins et al. 2005). However, accurate counts of displacements within dyads can be highly subjective because ‘displaced’ individuals may move for reasons unrelated to a motivation to avoid the approaching individual (Watts personal communication).

For mountain gorillas at Bwindi, fruit accounted for a greater proportion (15 % by wet weight) of the diet (Rothman et al. 2007) and higher rates of feeding aggression over fruit as compared to herbs were observed (Robbins 2008). However, female dyadic relationships were often bidirectional based on aggression and most aggression was undecided (Robbins 2008) like the pattern described for Karisoke. Unlike at Karisoke, female mountain gorillas at Bwindi could be arranged into a significant linear hierarchy based on aggression, but the hierarchy based on displacement data failed to reach significance and differed in rank order from that based on aggression (Robbins 2008). Either this finding casts doubt on the existence of rank differences among Bwindi mountain gorillas or the pattern reflects expectations based on asymmetries in power. That is, displacements may occur when the resource is not worth fighting over, and it is equally likely that the dominant individual will relinquish the resource to the subordinate as the subordinate will displace the dominant. However, if the resource has value it should be worthwhile to the dominant to direct aggression and consistent asymmetries in power should be revealed. Furthermore, female rank in mountain gorillas is ultimately thought to have little or no effect on individual foraging efficiency (Watts 1985; Watts 1994; Watts 2001; Watts 2003; Robbins 2008).

In contrast with mountain gorillas, western gorillas are considerably more frugivorous and their diet is more variable throughout the year (Doran-Sheehy et al. 2009a; Masi et al. 2009). Yet very little is known about their social relationships in the wild (Doran and McNeilage 2001; Stokes 2004). If fruit is an indicator of contest competition, which has its detractors (Koenig 2000; Koenig and Borries 2009; Wheeler et al. 2013), I examine whether increased frugivory in wild western gorillas compared to mountain gorillas is associated with a higher proportion of aggression during feeding, increased rates of aggression over fruit, a greater proportion of

decided aggression and decided female dominance relationships, and a steep and linear female dominance hierarchy. Fruits eaten by western gorillas are of higher quality than those eaten by mountain gorillas (see Chapter 2), and some fruits are concentrated in small trees (i.e. 20-50 cm DBH) that cannot always accommodate all group members (personal observation), such as *Anonidium mannii*, *Vitex welwitschii*, and *Pancovia laurentii* (Doran et al. 2002). Other fruits are concentrated within trees of medium (50-80 cm DBH) or large (> 80 cm DBH) size that occur at low densities (i.e. < 3 stems/hectare) in the environment (Doran et al. 2002), including four staple fruit species, *Klainedoxa gabonensis*, *Duboscia macrocarpa*, *Gambeya lacourtiana*, and *Tetrapleura tetraptera* (see Chapter 2). Thus, based on the high quality and uneven spatial concentration of western gorilla fruits and the small size of some fruiting trees and the rarity of others, there may be an ecological basis to expect that at least some fruit species in the western gorilla diet are contestable. If contest competition occurs within groups of western gorillas then aggressive competition during feeding may be associated with a suite of social consequences that can be tested here and compared to mountain gorillas.

Specifically, I examine whether most female aggressive conflicts occur in the context of feeding and determine what proportion of aggressive interactions are decided (both overall and in feeding context), and what proportion of feeding aggression occurs over fruit. Second, I test whether individuals vary in their overall competitive ability on the basis of aggression using David's scores (de Vries et al. 2006). Third, I determine what proportion of female dyads are decided based on aggression and then explore whether decided relationships remain stable throughout the present study. Fourth, to examine the nature and characteristics of dominance hierarchies, I first test whether females can be arranged into a significant linear hierarchy based on aggression and then assess the directional consistency (DCI) of dominance relationships using

MatMan (de Vries 1998). Fifth, I compare the cardinal ranks of female gorillas based on MatMan with those of David's scores, discuss any differences, and evaluate the steepness of the hierarchy following the procedure outlined by de Vries and colleagues (2006). Sixth, I discuss differences in the information generated from different methods of assessment of dominance relationships, hierarchies, and ranks.

Predictions

I predict that higher rates of aggression will occur among female western gorillas when feeding on fruit compared to mountain gorillas (Table 3.1). Next, I predict that increased rates of aggression over fruit will be associated with a greater proportion of decided outcomes (Table 3.1) in female western gorillas compared to mountain gorillas. A greater proportion of decided outcomes may also be accompanied by less bi-directionality in initiation of aggression, although the use of bi-directionality as a proxy for directional consistency may obscure actual asymmetries in relationships if the dyad is not unidirectional but one female consistently directs aggression toward the other more often compared to the other. If female western gorillas have a greater proportion of decided outcomes than mountain gorillas, I predict that a greater prevalence of decided aggression will be associated with a greater proportion of asymmetric dyads (Table 3.1) and a linear and steep dominance hierarchy in female western gorillas compared to mountain gorillas. Data concerning the characteristics of food patches, group spread, and frequency of kin-based coalitions is unavailable for western gorillas. Thus, I simply examine whether female coalitions occur more frequently in western gorillas compared to mountain gorillas at Karisoke (Table 3.1), and if so, whether female dominance relationships in western

gorillas show stability over time. To test each prediction I compare results in western gorillas to previous descriptions of female agonistic relationships in wild mountain gorillas by Watts (1991; 1994; 1997; Watts et al. 2000; 2001; 2003), Robbins (Robbins et al. 2001; Robbins et al. 2005; 2008), and Harcourt (1979a; 1979b; Stewart and Harcourt 1987; Harcourt and Stewart 2007).

At Karisoke, female coalitionary support is rare among unrelated females, but more common between relatives (Harcourt 1979a; Stewart and Harcourt 1987; Watts 1997; Watts 2001; Harcourt and Stewart 2007) and females who maintained high rank throughout their lives tended to live with adult female kin for much of their lives (Robbins et al. 2001; Watts 2001; Robbins et al. 2005). Long-term associations depended on stable groups that remain intact for long periods as for instance in multi-male groups of mountain gorillas (Stewart and Harcourt 1987; Robbins et al. 2001; Harcourt and Stewart 2007). In contrast, western gorillas groups contain only one silverback male and the group disbands upon his death (Robbins et al. 2001; Doran and McNeilage 2001; Robbins et al. 2004). As a result, western gorilla groups tend to disintegrate more rapidly and female secondary dispersal is common (Stokes et al. 2003). Thus, demographic constraints in western gorilla groups may prevent long-term female membership in the same group and in turn reduce the likelihood of female coalitions. Thus, I predict that roughly the same proportion of dyads or fewer will show stability in dominance relationships in western gorillas as at Karisoke (Table 3.1). Finally, if clear and stable dominance relationships are indicated, I assess whether the stability of dyadic relationships is reinforced by female coalitionary support.

Lastly, I test whether the male acts to minimize rank differences among females by breaking apart female conflicts or to facilitate egalitarian relationships by performing control

interventions in favor of weaker competitors, as occurs in mountain gorillas (Harcourt 1979b; Watts 1994; Watts 1997; Watts et al. 2000; Watts 2001; Watts 2003). Alternatively, if the male favors females of higher social status over others then I explore whether some females dominance relationships are derived based on male support using the concept of derived dominance within an interpretive framework of power (Lewis 2002).

Methods

Study site

Data were collected on a single group of wild western gorillas (*Gorilla gorilla*) during a 14-month period (December 2004 - October 2005 and June - August 2006) at the Mondika Research Center (02° 21' 859" N, 016° 16' 465" E), a 50 km² sector of tropical lowland forest situated along the boundaries of Central African Republic (Dzanga-Ndoki) and Republic of Congo (Nouabale-Ndoki). The study site consists of three major habitat types: mixed species tropical lowland forest, monodominant *Gilbertiodendron dewevrei* (Caesalpinaceae) forest along streams, and swamp forest bordering the Ndoki River (Doran et al. 2002; Mehlman and Doran 2002). The site has never been logged and there is little to no human disturbance in the area (Doran et al. 2002). Long-term records indicate that rainfall and fruit availability are seasonal at the site (Doran-Sheehy et al. 2009a). Mean annual rainfall is 1600 mm (n = 8 years of rainfall data), with less than 50 mm of rainfall per month within the two-to-three month annual dry season between December and February and more than 200 mm of rainfall per month in August and September (Doran-Sheehy et al. 2009a). Fruit availability peaks during a two-to-three month period between June and September and dips to an annual low between December

and March (Doran-Sheehy et al. 2009a). Other details of the study site, including densities of fruiting trees and herbs, have been described elsewhere (Doran et al. 2002; Mehlman and Doran 2002; Doran-Sheehy et al. 2006).

Study subjects and sampling protocol

The study group was initially composed of one adult silverback male, six adult females and their offspring. Four of six females were well habituated and the subject of focal follows (Altmann 1974) during 1129 focal hours of observation. In June 2005 one habituated focal female (EB) disappeared from the group. A second non-focal female (VI) disappeared in November 2005.

I conducted full-day focal follows ($n = 66$ follows; 4 female subjects) initially, from December 2004 to May 2005. Once I could reliably locate a second focal subject at mid-day I conducted half-day follows ($n = 158$ follows; 3 female subjects) from June 2005 onward. For comparative purposes, I later converted all full-day follows to half-day follows for a total of 224 follows. The average duration of focal follows was 5.04 ± 1.8 (SD) hours ($n = 224$ follows), and the number of follows and total focal time was roughly equivalent for the three females who were present throughout the entire study period (Table 3.2). Mean focal sampling time did not differ among the four females during full-day follows (ANOVA: $F_{3,61} = 0.34$, $p = 0.798$) or among the three females during half-day follows (ANOVA: $F_{2,149} = 0.52$, $p = 0.595$).

During focal female follows, I recorded: 1) one-minute instantaneous sampling of activity (feeding [food species; part]; resting [sleeping; sitting; standing; vigilance]; traveling [walking; climbing; running]; social behavior [playing; affiliation; agonism]) during four 10-minute sampling periods per hour (00-09, 15-24, 30-39, 45-54 min), and 2) continuous recording of all

agonism initiated or received by the focal female. Displacements without associated aggression occurred rarely in the present study (i.e. less than 20 displacements were recorded) and in other studies of wild western gorillas (Stokes 2004). Thus, displacements could not be compared with those from other gorilla studies presumably because of differences in group cohesion between sites. All assessments of female rank, dominance relationships, and dominance hierarchies were made strictly on the basis of aggressive acts and signals.

My definitions of aggression, response to aggression, and the context in which it occurred were based on those used in studies of mountain gorillas (Watts 1994; Robbins 2008).

Aggression included: 1) aggressive signals, i.e. agonistic vocal threats known as pig grunts (Fossey 1972; Harcourt 1979a; Harcourt 1979b), and 2) aggressive acts of either moderate (i.e. lunging, screaming, stealing food, locomotor or postural display) or high (i.e. hitting, biting, forcing down, and fighting) intensity. For each aggressive event, I recorded the 1) identity of actor and target, 2) reaction of target, including: submission (i.e. cowering, avoiding, fleeing, pausing, or stopping activity), retaliation (i.e. returning aggression), or ignoring (i.e. no visible response), 3) context of aggression (feeding [food species; part], resting, traveling, access/proximity to silverback, other, unknown), 4) if the silverback was present (i.e. visible or audible to observer at ≤ 20 m), and 5) whether (and by whom) coalitionary support was given or received. Each aggressive event was later categorized as either decided or undecided, following Watts (1994). Outcomes were considered decided when the target responded submissively and the actor showed no sign of submission. Outcomes were rated as undecided if the target retaliated or ignored the aggression.

I used focal female aggression data ($n = 295$ events) to measure the rate and context of aggression. I also recorded all aggression between females other than focal individuals ($n = 210$

events) *ad libitum* (Altmann 1974) during the same time period and used these data along with focal data to construct dominance hierarchies. I included aggression data from long-term project data collected by myself, Diane-Doran-Sheehy, or Roberta Salmi, prior to the study period (n = 46 events; aggression data collected during the period of September – November 2003 on the same 6 adult females) to assess stability of rank through time.

Data Analysis

Rates of female aggression

For all focal follows I calculated the overall rate of aggression as the number of aggressive acts directed toward or received from other females divided by duration (in hours) of focal follow. Additionally for each focal follow, I calculated an overall rate of aggression in the context of feeding (i.e. number of aggressive acts during feeding / observed feeding hours) and in the context of not feeding (number of aggressive acts outside feeding / non-feeding hours observed) as well as in the context of females eating major different food types (fruit; leaf; herb). I tested whether rates of aggression differed between feeding and non-feeding contexts, or between food-type feeding contexts using pairwise t-tests in SPSS 15.0.

Methods used to assess dominance characteristics and female rank

To assess linearity of the dominance hierarchies, I used MatMan 1.1, providing the corrected Landau's Index, h' (de Vries 1995), and tested for significance using a randomization test in MatMan (de Vries 1995). In addition, MatMan provides the Directional Consistency Index (DCI), which gives the frequency with which the behavior occurred in its most frequent direction relative to the total number of times the behavior occurred (van Hoof and Wensing

1987) summed over all dyads in a group. I also counted the number of one-way relationships (i.e. the number of dyads in which aggression is shown in one direction only, irrespective of the frequency of the behavior. In two-way relationships, dyadic interactions occurred at least once in both directions.

I assessed female rank using two methods of analysis. First, I used the reordered dominance matrix provided by MatMan. The reordering in MatMan minimizes the number and strength of inconsistencies among individuals (de Vries 1998). If the hierarchy is significantly linear, the ordering sequence provides a unique hierarchy based on the I&SI method. In this reordered matrix the top individual was assigned a cardinal rank of 1, the lowest ranking individual a cardinal rank of 6. Although MatMan analyses are informative about the transitivity of dyadic relationships and social structure of the group they do not provide information about the strength (steepness) of the hierarchy or whether females vary continuously in overall competitive ability. As a second method for assessing rank, I therefore calculated normalized David's scores (de Vries et al. 2006) of the form P_{ij} for each individual based on dyadic dominance indices. Normalized David's scores (herein referred to as Norm DS) take the relative strength of opponents into account (de Vries et al. 2006) and have been shown to reflect individual competitive ability in macaques (Bissonnette et al. 2009). In addition to a continuous measure of rank, the steepness of the hierarchy, which can vary from 0 (essentially egalitarian) to 1 (strictly despotic dominance hierarchy), was measured as the slope of the least-square linear regression of Norm DS scores plotted in cardinal rank order. This measure is referred to as strength of a hierarchy. I used the steepness package, Version 0.1 for R (Leiva and de Vries 2009) to i) compute dyadic dominance indices that adjust for unequal sample sizes across dyads, ii) generate Norm DS which correct for errors introduced by chance, iii) calculate the steepness

of the hierarchy, and iv) test whether the observed hierarchy was significantly steep compared to an expected hierarchy based on 9,999 randomizations of the data.

I also determined whether females could be considered dominant to others having won significantly more than 50 % of aggressive interactions within a dyad using goodness-of-fit (G-) tests (Sokal and Rohlf 1995). Because many dyadic relationships were bidirectional (i.e., subordinate females sometimes initiated aggression against dominants), I also ran G-tests in R (R Development Core Team 2009) on simulated data to determine the minimum sample size that would be required to detect a significantly decided relationship with differing levels of rank asymmetry. For example if asymmetry is complete, with the dominant member of the dyad winning 100 % of encounters, a sample size of three events would be sufficient to detect a significantly decided relationship. However, as the degree of asymmetry decreases, with the dominant member winning 70 % or 60 % of encounters, the number of dyadic events needed to detect a significantly decided relationship increases to 25 and 96, respectively (Table 3.3).

Different data sets used to assess dominance characteristics and female rank

In previous studies of African apes, whether linear dominance hierarchies were observed depended on the type of behavior analyzed. For example, Vervaecke and colleagues (2000) found a stronger dominance hierarchy in female bonobos based on certain behaviors, such as fleeing upon aggression, than on others, such as yielding or teeth-baring in response to aggression received. In mountain gorillas, female linear dominance hierarchies were typically detected from displacement data (Watts 1994; Robbins et al. 2005) but not from aggression (Watts 1994). Furthermore, in some taxa, not all agonistic events are decided (Rowell and Olson 1983; Watts 1994; Isbell and Pruettz 1998; Vervaecke et al. 2000; Su and Birky 2007; Robbins

2008). Because interactions resulting in clear outcomes are classically used to define dominance relationships (Schjelderup-Ebbe 1922; Hausfater et al. 1982; de Waal 1989; Drews 1993), results of analyses based on decided outcomes may differ from results of analyses based on all aggression including undecided outcomes, although to date this has not been tested. Therefore to determine whether results are influenced by the type of aggression examined, I assess female rank and dominance relationships using four aggression data sets. The data sets include: 1) aggression (n = 551 events, including decided and undecided signals and acts), 2) aggressive signals (n = 484 events), 3) decided aggression (n = 263 events), and 4) decided aggressive signals (n = 222 events). Moderate and high intensity acts occurred too infrequently (n = 66 events) to examine all dyadic relationships.

Analysis of female rank stability

To assess the stability of female rank over time I tested whether dominance relationships, steepness of hierarchies, and rank order remained constant during the 2.5 years that data were available. I examined the proportion of aggressive signals initiated by the dominant individual within each dyad during four time periods (of 3-to-4 months each) separated by at least four months (Period 1 = Sept. 2003- Nov. 2003; Period 2 = Nov. 2004 – Jan. 2005; Period 3 = Jun. 2005- Sept. 2005; Period 4 = Jun. 2006 –Aug. 2006). I analyzed this data set for two reasons. First, I could not rule out the possibility that the outcomes of high intensity female aggression were influenced by the presence of the male (see results), whereas those of aggressive signals were not. Thus the use of aggressive signals (rather than all aggression) allowed me to control for the potential influence of the male and to assess female competitive ability more directly, assuming females did not use contextual information to decide whether signals were unlikely to

escalate, affording them with a choice to ignore signalers with superior fighting ability. Second, I used all aggressive signals to maximize dyadic data available within each period. Despite this, sample size for each time period was limited particularly in the earliest time periods, and data were not available for all dyads in every time period. Data were more plentiful for focal subjects so I began by examining whether dominance relationships in all focal pairs persisted throughout the study before I examined the pattern with non-focal dyads. To do this I measured the percentage of aggressive signals initiated by each member of a dyad within each of the four time periods. I considered dominance relationships to be stable when the dominant individual (i.e. the individual that initiated the majority of aggressive signals in the first period) initiated more than 50 % of aggressive signals in all subsequent periods for which data were available. I considered the dyadic relationship unstable if the (initially) dominant individual initiated less than 50 % of aggression in any of the subsequent time periods. The amount of data contributing to each time period was not accounted for in the determination of stable dominance relationships.

Within each period, I calculated Norm DS to assess whether female cardinal ranks remained stable throughout the study and to verify that the steepness of dominance hierarchies remained relatively constant over time. I chose this method because it allowed me to assess characteristics of dominance hierarchies during periods when only four females were present.

Role of the male

To examine whether male presence interacted with female rank to influence the outcome of moderate intensity aggression among females, I ran a generalized linear mixed effect model (GLMM) with a logit link function (assuming a binomial distribution) built for the glmer function within the lme4 package in R version 2.14.0 (Bates et al. 2011). I tested for the fixed

effects of male presence (2 levels: present within 20 m; absent within 20 m) and female rank class (2 levels: top three ranking females; bottom three ranking females; calculated based on cardinal ranks using decided aggression) on the aggressor's ability to win (1 = win; 0 = lose) moderate intensity aggression while accounting for the random effect of female aggressor ID. For the GLMM, the glmer function uses the Laplace approximation to calculate probability for each fixed effect level. Initial examination of decided aggressive signals showed that male presence did not influence a female's ability to win mild aggression (i.e. decided aggressive signals), thus I restrict analysis to decided acts of moderate intensity, for which the presence or absence of the silverback male was known (n = 33 of 36 moderate intensity acts).

Results

Type, frequency, and context of female aggression

Female-female aggression (n = 551 events) consisted primarily of aggressive signals, (88 %; n = 484 signals), although some moderate (11 %; n = 60 acts) and a few high (1 %; n = 6 acts) intensity acts of aggression were recorded. Nearly half (48 %) of all aggression was decided (n = 551 events). As the intensity of aggression increased, from mild (signals) to moderate and high intensity aggression, the proportion of decided aggression also increased, with 46 % of signals (n = 484 signals), 60 % of moderate (n = 60 acts), and 83 % of high (n = 6 acts) intensity acts decided.

Most aggression (89 %; n = 551 events) occurred during feeding, with only 4 %, 2 %, and 3 % occurring in the context of traveling, resting, or competition for proximity to the silverback, respectively. The bulk (59 %) of feeding aggression (n = 489 events) occurred over

access to fruits and flowers. Nearly half (48 %) of all food-related aggression ($n = 489$ events) was decided. The proportion of food-related aggression that was decided differed by food type, including relatively high percentages of decided aggression for fruits and flowers (47 %; $n = 290$ events), leaves and young bark (50 %; $n = 92$ events), ants and termites (60 %; $n = 40$ events), and miscellaneous foods such as gorilla feces (85 %; $n = 20$ events) and a relatively low percentage of decided aggression for herbs (30 %; $n = 47$ events).

The average rate of female-female aggression during focal samples was 0.28 ± 0.36 (SD) events per hour ($n = 224$ follows). Aggression rates (events / hr during 224 follows) were nearly eight times higher on average during feeding (mean \pm SD: 0.55 ± 0.89 events / hr) compared to non-feeding (mean \pm SD: 0.07 ± 0.19 events / hour; $t_{1,223} = 8.1$, $p < 0.001$), and the rate of aggression in the context of feeding was five times higher when gorillas were feeding on fruit (mean \pm SD: 1.43 ± 4.92 events / hr) than when they were feeding on herbs (mean \pm SD: 0.27 ± 1.32 events / hr; $t_{1,223} = 3.4$, $p < 0.001$) or leaves (mean \pm SD: 0.27 ± 1.12 events / hr; $t_{1,223} = 3.4$, $p < 0.001$).

Directionality of relationships and linearity of hierarchy

The dominance hierarchies obtained from the two larger data sets (all aggression; all aggressive signals) were significantly linear with a linearity index of 1.0, whereas those derived from the two smaller data sets (decided aggression; decided aggressive signals) had lower linearity indices and tests for linearity were not significant (Table 3.4). The directional consistency index ranged from 0.72 to 0.78, and was highest based on aggressive signals, regardless of whether these led to decided outcomes. A greater percentage of dyads in the larger data sets (i.e. 80 % for all aggression and 87 % for aggressive signals) exhibited some bi-

directionality (i.e. two-way relationships) with at least one event initiated by each dyad member than in the smaller data sets (53% for decided aggression and 60% for decided aggressive signals). Eleven to fourteen percent of aggressive interactions were directed against the hierarchy (Table 3.4).

Female rank, competitive ability, and steepness of hierarchies

Despite variation in linearity, the cardinal ranks of females obtained from the I&SI method using the four data sets was similar. The same individuals ranked first (MA) and fourth (UG) in all data sets. Females occupying the second and third rank held the same position in three of four data sets, but switched places with each other in the fourth data set. The same was true for females in rank position five and six.

Supplemental Table 3.1 illustrates the calculation of Norm DS for one data set (decided aggressive signals) picked at random. Female rank order based on Norm DS from the four data sets are shown graphically in Figure 3.1. The cardinal ranking of the six females was nearly the same in all four data sets. In each case the observed steepness of the hierarchy differed significantly from the steepness to be expected under the null hypothesis (Figure 3.1) in which the direction or outcome of dyadic events were randomly re-sampled. Thus, clear differences in female competitive ability can be inferred from a steep dominance hierarchy. In two of four data sets one female (MA) was clearly dominant to all others and another female (BE) was lowest ranking (Figure 3.1; Supplemental Figure 3.1). However, differences in individual competitive ability were less pronounced for other females. For example, females ranked second and third (ME and VI) had similar Norm DS (Figure 3.1) in two of four data sets, and cardinal ranks shifted within this pair based on the data set used, suggesting these two females were too close in

power to have a decided agonistic relationship with each other. Three (to four) layers of competitive ability were indicated in each data set. Based on all aggression and aggressive signals, the three layers consisted of one top-ranking individual (MA), four middle-rankers (ME; VI; UG; EB), and one bottom-ranker (BE; Figure 3.1). However, differences in the middle and bottom layers occurred based on decided aggression and decided aggressive signals, such that an alternative hierarchy, comprised of one top ranker (MA); two middle-rankers (VI; ME) and three bottom rankers (UG; EB; BE) was indicated based on Norm DS (Figure 3.1).

Degree of directionality in dyads

Next I considered all dyads and asked whether in each of the four data sets one female consistently initiated significantly more aggression compared to the other using G-tests (Table 3.5). Decided dominance relationships were indicated for 8 of 15 dyads for each data set used (with another dyad showing a trend for asymmetry), except for the largest data set (i.e. all aggression) in which 9 of 15 dyads were considered decided based on G-tests (Table 3.5). Probabilities were not adjusted for multiple tests because samples sizes were prohibitively small for many dyads and the chance of detecting significant asymmetries was instead assessed via G-test simulations at differing samples sizes.

I next considered whether an inability to detect significant directionality in the remaining six (to seven) dyads resulted from symmetry in who initiated aggression (with each member of the dyad initiating close to 50 % of aggressive events) or whether one individual initiated considerably more aggression than the other, but sample size was too small to detect a decided relationship. For every dyad, I determined the percentage of events initiated for each data set, the sample size, and whether significant directionality existed (Table 3.6). For five of the six dyads

in which both females were focal subjects (Dyads F1-F5), there was significant directionality in aggression, with the dominant member initiating 81-100 % of aggressive interactions, regardless of the data set used (Table 3.6; and the sixth dyad had very few interactions). Females who were closer in overall competitive ability, such as MA and ME, had slightly greater bidirectionality, with the dominant member initiating 83 % and winning 81 % of aggressive encounters. By contrast the top ranking female (MA) initiated 85 % and 96 % of aggression and won 94 % and 97 % of aggressive interactions with the fifth (EB) and sixth (BE) ranking females, respectively. The second highest-ranking focal female (ME) initiated 73 % and 89 % of aggression and won 92 % and 79 % of aggressive encounters with EB and BE, respectively. The only unresolved dyad involving two focal subjects was that of the fifth (EB) and sixth (BE) ranking females. Although EB initiated or won more aggression towards BE in all four data sets, the pair engaged in aggression with each other only seven times, and a significant directionality was found only in the largest data set (i.e. all aggression). On average the dyadic sample size for the focal dyads ranged from 31 events (SD = 30) for the smallest data set (i.e. decided aggressive signals) to 75 events (SD = 65) in the largest data set (i.e. all aggression). Thus these data sets were large enough to detect directionality when the dominant individual won 70 % of events (Table 3.3).

In contrast, the directionality of relationships involving females that did not serve as focal subjects was less clear, in part because of small sample sizes. The average dyadic sample size for UG in the largest data set (i.e. all aggression) was 8 (SD = 6, range = 0-14, n = 5 dyads) and for VI was 13 (SD = 11, range = 3-30, n = 5 dyads). Thus, for most dyads containing at least one non-focal female (Dyads NF1-NF9) the sample size in most data sets was sufficient to detect directionality only when the relationship was entirely unidirectional or when the dominant individual initiated 90 % of events. In spite of this, clear directionality, with one individual

significantly more often initiating or winning over the other in a minimum of two data sets, were detected in five dyads involving a non-focal subject (MA-VI; MA-UG; VI-UG; ME-UG; UG-BE; Table 3.6). One dyad was completely unresolved (VI-ME), indicating that neither individual was dominant over the other. Finally, for two dyads (UG-EB and VI-EB), directionality of the relationship was unresolved due to limited interactions (0 and 3 events, respectively) between them.

In summary, I detected significant asymmetry in directionality within 5 of 6 focal dyads and in 5 of 9 non-focal dyads, for a total of 10 out of 15 dyads. For the remaining 5 dyads, I detected no asymmetry in directionality of aggressive events within two dyads (VI-ME; VI-BE) and there was no (UG-EB) or very limited (VI-EB; EB-BE) data in the other three.

Stability in female dominance relationships

Dominance relationships between pairs of focal females ($n = 6$ dyads) remained stable throughout the study (Figure 3.2 A). Data from two or more consecutive time periods (Period 1: Sep- Nov 2003; Period 2: Nov 2004 – Jan 2005; Period 3: Jun-Sep 2005; Period 4: Jun-Aug 2006) were available for five of six focal dyads. In all, the female who initiated the majority of aggressive signals in the first period continued to initiate the majority throughout subsequent periods. This directionality was maintained within 71 % (12 of 17) of dyad-periods with data for these five dyads, despite small sample sizes and in spite of the disappearance of one focal subject (EB) at the start of the third period. Thus, five of six focal dyads maintained stable dominance relationships throughout the study period.

Dominance relationships for dyads that included at least one non-focal female ($n = 9$ dyads) were less stable (Figure 3.2 B). Stable dominance relationships were indicated for three or

four of the nine dyads involving at least one non-focal female (MA-VI, MA-UG, UG-BE and possibly VI-BE; Figure 3.2 B). For two others (ME-VI and ME-UG), directionality of aggressive signals appeared to reverse during the study, although sample sizes for these dyads were small and they showed substantial bi-directionality. Data from two consecutive periods were not available for three other dyads (VI-UG, VI-EB, UG-EB).

The female hierarchy based on Norm DS for the same data set during the four time periods is shown in Figure 3.3. Cardinal ranks of the four focal females (1= MA, 2= ME, 3= EB, 4= BE) remained unchanged. However, the Norm DS (and cardinal ranks) of the two non-focal females (UG and VI) varied and suggests that their exception to the pattern observed among focal females relates to UG's and VI's unhabituated status. During the first period VI ranked higher than all other females except MA. Yet, VI's high rank during period 1 was based on the fact that she initiated aggressive signals against MA (once out of three events) and BE (once out of one event), and not because she initiated aggressive signals against any of the three others (UG, ME, EB) that were purported to rank beneath VI. The steepness of the hierarchy during period 1 was low (0.30) but significant despite a small sample size ($n = 29$ events) and absence of data for six dyads. For the remaining time periods steepness was higher and significant (Figure 3.3).

Frequency and direction of female coalitions

Female coalitions were extremely rare. I observed only 18 during 1129 hours of focal sampling. One female intervened in support of another in only 2 % of dyadic female conflicts. In ten of 12 coalitions (83 %) in which all participants were identified, both coalition partners outranked their target.

Frequency, direction, and impact of male interventions

The silverback intervened in female-female conflicts in only 5 % of (19 of 346) conflicts in which he was present. In 84 % (16 of 19) of these, he clearly supported one female over another, rather than simply stopping the aggression. Furthermore, in 81 % of these 16 cases he supported the higher ranking of the two females involved, insuring a decided outcome in favor of the higher ranking female.

Female behavior might be influenced not only by interventions of the male, but his presence close to the conflict. When females engaged in conflicts of moderate intensity (i.e. events that escalated beyond mild threats but did not involve contact aggression) the presence of the male did not have a significant influence on whether the female aggressor won or lost the conflict (GLMM, male presence yes: $\beta = 0.322$; SE = 1.45; z-value = 0.22; $P = 0.82$; rank class aggressor high: $\beta = 2.52$; SE = 1.35; z-value = 1.87; $P = 0.06$; model intercept: $\beta = 0.48$; SE = 1.27; z-value = 0.38; $P = 0.71$).

Although high-intensity aggression was rare, four of six cases occurred in the absence of the male (binomial test 2-tailed: $p = 0.69$; assuming absence and presence of male was equally likely to occur- 3:3) and a lower ranking female initiated and won five of the six conflicts of high-intensity against a higher ranking female (binomial test 2-tailed: $p = 0.22$; assuming high- and low-ranking females were equally likely to win: 3:3). These results were not significant at small sample sizes.

Discussion

Assessments of rank, dominance relationships, and hierarchy characteristics

Adult female western gorillas from a medium-large social group at Mondika differed in their overall competitive abilities on the basis of aggression, which was nearly always directed in the context of feeding. To determine whether my assessment of female rank, dominance relationships, and hierarchy characteristics varied by the type of aggression data (Watts 1994; Vervaecke et al. 2000; Robbins 2008) and method used (Gammell et al. 2003; Bayly et al. 2006) to define rank, I used four data sets and three types of measurements that identify different aspects of female agonistic relationships. I discuss these different aspects initially based on the results from one data set, all aggression.

From the I&SI method, the female dominance hierarchy had a linearity index of 1.0 and was significantly linear. This result indicates that dominance relationships are transitive, and the assumption would be that no two females hold the same rank. However, this assumption no longer holds when examining the same data set based on Norm DS; Some females held roughly the same rank based on overall competitive ability while others differed in rank considerably. When females were ranked based on Norm DS their cardinal ranks were the same as those based on the I&SI method, with the exception that the second and third ranked females switched positions.

Thus, if one were to use these results to make predictions concerning rank and energy intake the predictions would differ based on whether cardinal ranks from MatMan or continuous ranks from Norm DS were used. Specifically, based on the linear hierarchy produced in MatMan (proceeding from the simple assumption that ranks were transitive) I would predict that all females would differ in energy intake, particularly if access to contestable food was based on an

individual's resource holding potential alone and not based on coalitionary support. However, using the same rationale based on results from Norm DS I would predict that some but not all females would vary in energy intake. For instance, I might not expect the second (ME) and third (VI) ranking female to differ significantly in energy intake but I would expect a rank-related difference in energy intake between the alpha female (MA) and any other female.

When testing for decided dominance relationships, an asymmetry in the directionality of aggression was indicated for 8 (or 9) of 15 dyads. For the remaining six dyads, I would not expect decided dominance relationships in two (based on David's scores: VI-ME and UG-EB) and for the other four the total numbers of events per dyad were only 5, 3, 11, and 7 respectively, below the minimum sample size requirement specified in Table 3.3. This suggests that strict tests of dyadic asymmetry may only be practical when all individuals routinely interact with each other. Alternatively, one important caveat to working with dyadic data is that it is still worth knowing whether many or most dyads show some bidirectionality even when sample sizes are limited or data is missing for a few dyads.

Dominance has been measured on the basis of different behaviors (displacements, aggression, submissive signals) and in some cases these different behaviors (e.g. displacements vs. aggression) yield different results (Watts 1994; Vervaecke et al. 2000; Robbins 2008). Therefore I considered the effect of using different data sets (initiation and outcomes of aggressive behaviors) to determine female dominance ranks from a single method, using MatMan as an example. Aggressive signals known as pig grunts (Fossey 1972) or cough grunts (Harcourt et al. 1993) accounted for the bulk of female aggression in western gorillas (this study; Stokes 2004) and were most commonly observed during feeding bouts. This frequent but mild form of aggression yielded similar results to that based on all aggression, which included

conflicts of moderate and high intensity, although the high-intensity acts added little to the outcome of the statistical tests and mostly counted as wins against the hierarchy. Furthermore, in species where there is some bi-directionality in aggression within dyads, authors have distinguished between events that were decided and those that were undecided. When examining the results based on the four data sets significant linear hierarchies were indicated for the two larger data sets (aggression; aggressive signals), but not for the two smaller data sets with decided outcomes. On one hand this finding suggests that based on the outcomes of decided interactions, which are classically used to define dominance relationships (Schjelderup-Ebbe 1922; Drews 1993) that females did not form a significant linear dominance hierarchy in western gorillas. This issue was explored further by assessing whether significant hierarchies were driven by the presence of fewer unknown or two-way dyads in the larger data sets. This hypothesis could be rejected because the number of two-way dyads was greater in the two larger data sets and the percent of unknown dyads was the same in all data sets except decided aggressive signals (Table 3.4). Furthermore, the percent of acts against the hierarchy in the two larger data sets was the same or greater as in the two smaller data sets (Table 3.4), thus it is more probable that the likelihood of finding significantly linear dominance hierarchies was sample size dependent as other studies have reported (Burns 2002; Robbins et al. 2005) but also driven in part by the presence of inconsistencies. Linearity measures should be thus interpreted with caution when there are only 6 individuals in the group (Appleby 1983; i.e. the minimum for detecting significant linearity: Koenig and Borries 2006), when dyadic sample sizes are small (i.e. ≤ 10), and at least one inconsistency is present.

Additionally, cardinal ranks of females differed slightly between the four data sets, but these differences were not clearly linked to whether decided or all events were used. Rather,

when considered in light of Norm DS the only changes in cardinal ranks occurred between females who differed little in overall competitive ability. One clear implication of this study is that when there is variability in female power, with some females differing from their competitors in fighting ability more than others, Norm DS provide the best resolution for characterizing small, medium, and large differences in female power (Lewis 2002) within social groups.

Female rank in western gorillas

In this examination of female agonistic relationships within one group of wild western gorillas decided dominance relationships were documented in at least 53 % of all dyads. In two thirds of the remaining dyads, one female won a disproportionate amount (≥ 67 %) of decided aggression. Dominance relationships were particularly well resolved for focal dyads for which observation time was most extensive in that dyadic tests of asymmetry showed significant directionality in aggression for five of six dyads. Results based on the other three data sets were similar. Many, though not all, females differed in overall competitive ability based on Norm DS in each of the four data sets. Three layers of rank (alpha; middle; low) were deciphered from the patterning of Norm DS in each dataset. Female aggression occurred most often (89 %) during feeding, particularly over access to fruit. Rates of aggression while females were feeding on fruit were nearly five times higher than while they were feeding on herbs or leaves and nearly half of all food-related conflicts were decided, suggesting that dominance can predict whether one dyad member achieves priority of access to food. In addition, most dominance relationships were stable particularly among the focal females. Rank stability was unlikely to depend heavily on female coalitions since they occurred rarely (in only 2 % of female dyadic conflicts), although

when female coalitions occurred, they consistently supported the hierarchy (in 83 % of coalitions). Similarly, the dominant male intervened in female conflicts infrequently (in 5 % of female conflicts in which he was present) but when doing so he consistently provided coalitionary support to the higher-ranking female competitor (in 81 % of cases). Thus, the stability of female dominance relationships might result either from derived dominance due to the male's favoring of high status females (Lewis 2002), from intrinsic individual characteristics (i.e. body size; ability to use force; age), or from a combination of both.

Previous work on agonistic relationships in wild female western gorillas conducted at a swampy clearing (Mbeli bai) led one investigator (Stokes 2004) to conclude that female western gorillas have weakly defined agonistic relationships. Stokes (2004) based her argument on the finding that nearly all female aggression at the clearing was ignored or met with retaliation. By contrast, I demonstrated that aggressive competition among habituated females at Mondika was linked to food and that aggressive conflicts during feeding occurred most frequently over access to potentially monopolizable foods (fruits). Recent work by Scott and Lockard (1999; 2006; 2007) in provisioned zoo gorillas are consistent with some of the patterns described here. In their studies gorillas were given a steady diet of foliage but were also given access to high quality food items in defensible patches. Some females were able to consistently exclude others (Scott and Lockard 2006) and monopolization of clumped high quality resources was tied to high social status despite the absence of a linear hierarchy (Scott and Lockard 1999). In the future I encourage field research on western and mountain gorillas to focus on basic aspects of female sociality and feeding competition so that comparative data from multiple habituated groups become available to assess intra- and inter-specific variation in dominance relations and patterns of competition.

Finally, since the directional consistency index (DCI) has been cited as a more suitable measure of the degree to which dyadic relationships are unidirectional or consistent as compared to linearity (Isbell and Young 2002; Koenig and Borries 2006), I compare the DCI for western gorillas in this study (0.72-0.78) with that of 20 other species who were studied in the wild with a female group size of 6 or more and for whom aggression data were evaluated (Burns 2002). This comparison revealed that western gorillas fell well below several species of female cercopithecoïd monkeys in their DCI, including Japanese macaques (DCI: 1.00, Furuichi 1983), vervet monkeys (DCI: 0.99, Cheney and Lee 1981) and olive baboons (DCI: 0.96, Barton and Whiten 1993), but also compared to western chimpanzees (DCI:0.93, Wittig and Boesch 2003), although the chimpanzee hierarchy was constructed from greeting interactions and may show less directional consistency based on agonism. The DCI of western gorillas instead more more closely resembled that of the western black-and-white colobus (DCI: 0.75, Korstjens et al. 2002), brown woolly monkeys (DCI: 0.77, Nishimura 1994) and Patas monkeys (DCI: 0.78, Isbell and Pruettz 1998).

Inter-specific variation in female agonistic relationships

Here I raise the issue of how differences in the interpretation of results between studies of mountain gorillas (*G. beringei*) and those from the present study (*G. gorilla*) may impact our understanding of variation in the nature of female agonistic relationships across different environments. In the present study, I found almost no unidirectional relationships, and yet for most dyads one female typically won aggressive conflicts more often than the other. Several previous studies of female agonism in mountain gorillas ("e.g." Harcourt and Stewart 1987; Watts 1994; Harcourt and Stewart 2007) have tended to take bi-directionality to mean

dominance relationships are undecided. However, ratios of bi-directionality within a dyad can range from a highly asymmetrical relationship of 99 : 1, to a perfect symmetrical relationship of 50 : 50. This observation has two implications for interpreting dominance relationships: 1) the presence of a bi-directional relationship does not preclude the presence of a decided dominance relationships, and for some species 2) bi-directional dyads within a social group may be quite variable in directional asymmetry. The findings presented here suggest that a higher proportion of dyads show directional asymmetry compared to mountain gorillas although this must be verified using data from Watts' (1994). I urge future studies of female rank to use Norm DS as a supplement to dyadic tests for asymmetry, since the David's score method appears less sensitive to sample size requirements and offers a quantitative measure of individual differences in competitive ability. With respect to the socioecological model, the importance of female rank will depend on whether females differ in their rates of energy gain. If rank has energetic consequences in western gorillas, which are currently classified as dispersal egalitarian based on the socioecological model (Sterck et al. 1997), this will call into question the model's predicted link between rank and within-group feeding competition in female dispersing species. I will examine whether females from this study exhibit rank-related differences in energy intake in a forthcoming paper (Chapter 4).

Some features of female social relationships are likely universal to western and mountain gorillas while others appear fundamentally different. Most female aggression in gorillas is mild (Watts 1994) with pig grunts accounting for the bulk of aggression (this study; Harcourt 1979a; Stokes 2004; Robbins 2008) and a considerable proportion of aggression is either ignored or met with counter-aggression (this study; Watts 1994; Watts 2001; Stokes 2004; Robbins 2008). The majority of dyads at each site show some bi-directionality in aggression, with at least one event

initiated or won by each dyad member (this study; Watts 1994; Robbins 2008) In most studies researchers have reported the presence of a dominant individual in some but not in all female dyads (Watts 1994; Stokes 2004; Robbins et al. 2005; Harcourt and Stewart 2007), although the relative proportions of these are known to vary across groups. Rank is not principally based on female coalitionary support (this study; Watts 1997; Watts 2001; Watts 2003) and thus female social relationships in gorillas are thought to be individualistic (Watts 2001; Robbins et al. 2005; Harcourt and Stewart 2007; Robbins 2008) and not nepotistic. Other aspects of female agonistic relationships in western gorillas at Mondika differ in fundamental ways from those previously described for mountain gorillas at Karisoke and Bwindi. In the following section I describe each of these aspects as they relate to predictions based on the socioecological model with the aim of addressing how increasing fruit consumption along a continuum- from very low at Karisoke to low at Bwindi and to moderate at Mondika- have shaped differences in female social relationships.

Gorillas and the socioecological model

Results of the present study show that increased consumption of fruit in western gorillas was associated with higher rates of aggression over fruit, a greater proportion of decided aggression, decided dominance relationships in many dyads, and a steep dominance hierarchy in comparison with mountain gorillas. As predicted, the percentage of decided aggressive events was greater both overall (48 %) and in the context of feeding (48 %) in western gorillas compared to mountain gorillas (Table 3.1). Rates of feeding aggression over fruit were also higher at Mondika than at Bwindi (Table 3.1) based on a comparison of the same number of females in both study groups. In the future it may be informative to adjust rates of aggression at

Mondika and Bwindi by the amount of time females spend in close proximity to at least one other female to account for differences in group spread and cohesion between sites, but at present these data are not available.

Decided agonistic relationships were present in many or most female dyads at Mondika (Table 3.6). By comparison, few dyads at Karisoke contained a dominant individual who won the majority of decided aggression (Watts 1994; Watts 2001; Harcourt and Stewart 2007). Similarly, Robbins (2008) concluded that female agonistic relationships in mountain gorillas at Bwindi were weak and not fundamentally different from those described for Karisoke based on the observation that Bwindi gorillas had low levels of decided aggression (6 % overall, 10 % during feeding), female ranks shifted depending on the data set used, and a non-trivial amount of aggression went against the hierarchy (25 % overall). Robbins (2008) further reasoned that the amount of within-group contest competition at Bwindi was probably not sufficient to reach the threshold at which females develop decided dominance relationships. Unfortunately, dyadic aggression data from Bwindi were not available for comparative purposes to calculate what proportion of dyads were asymmetric.

My findings only partially supported the third premise that hierarchies are expected to be significantly linear if decided dominance relationships are present. As predicted female western gorillas directed a lower percentage of aggression (14 %) against the hierarchy when compared to mountain gorillas at Bwindi (Table 3.1; Robbins 2008), but similar to Bwindi the female hierarchy was significantly linear based on all aggression initiated. More specifically, females at Mondika could be ordered into a hierarchy that was significantly steep based on all data sets examined and significantly linear only when the number of interactions was large.

Concerning the final premise, I predicted based on more rapid turnover of one-male groups in western gorillas compared to mountain gorillas that female coalitions would occur at a similar frequency or less frequently than that reported for Karisoke. As expected, female coalitions occurred very infrequently (only 2 % of contests), which was lower but still consistent with the low percentage (4 % of contests) described for mountain gorillas at Karisoke (Table 3.1; Watts 1997). Despite the low frequency of female coalitionary activity in the present study, stable dominance relationships were indicated for all interacting dyads containing focal individuals over the course of at least 2.5 years. The stability of relationships containing at least one non-focal individual was more variable, with some dyads showing high stability and others instability in directionality. At Karisoke, maternal kin were sometimes observed to live in the same group for many years and in these groups a handful of females maintained high rank over decades (Watts 2001; Robbins et al. 2005; Harcourt and Stewart 2007). Additionally, based on a long-term study of female displacements at Karisoke 80 % of dominance relationships remained stable between successive evaluations (Robbins et al. 2005).

Finally I examined the role of the male as a potential mediator of female dominance relationships since males occasionally buffer female aggression within social groups of mountain gorillas (Watts 1991; Watts 1994; Watts 1997; Watts et al. 2000; Watts 2001; Watts 2003) and in a host of other species including hamadryas baboons (Kummer 1967; Colmenares and Lazaro-Perea 1994), Thomas' langurs (Steenbeek 1996; Sterck 1997; Sterck and Steenbeek 1997), chimpanzees (Goodall 1986; Nishida 1989; Kahlenberg et al. 2008), golden monkeys (Ren et al. 1991; Watts et al. 2000), macaques (Ehardt and Bernstein 1992), horses (Berger 1986), zebras (Klingel 1967; Penzhorn 1984), European starlings (Eens and Pinxten 1996), and cichlid fish (Walter and Trillmich 1994). In contrast to the pattern of male policing described for Karisoke

mountain gorillas, in which males intervene to control female aggression by stopping the conflict (Watts 1985; Stewart and Harcourt 1987; Watts 1994; Watts 2001; Watts 2003), the male at Mondika consistently provided coalitionary support to the higher-ranking female when intervening in female conflicts. A similar pattern was described in captivity; silverbacks consistently supported high status residents over low status newcomers during interventions (Scott and Lockard 1999; Scott and Lockard 2007). Male interventions in favor of high status individuals are somewhat unusual for primate species with female-biased dispersal (reviewed in: Ehardt and Bernstein 1992; Watts et al. 2000), however they may be a source of derived dominance for females living in societies with individualistic dominance hierarchies.

Streamlining the model: recommendations from this study

It is well known that some primates show inconsistencies with predictions of the current ecological model (Thierry 2007; Koenig and Borries 2009). For one, rates of female agonism are not clearly associated with dietary categories such as fruit or with monopolizable resources as previously hypothesized; Instead female agonistic rates vary positively with female group size and (potentially by) degree of terrestriality (Wheeler et al. 2013). Also, low-ranking females may avoid high-ranking females at contestable food patches, such that dominants achieve higher food intake than subordinates despite low rates of agonism (Robinson 1981; Whitten 1983; van Schaik and van Noordwijk 1988; Koenig et al. 1998). Thus future incarnations of the current socioecological model must consider that low rates of agonism would not preclude a substantive ratcheting upward of contest competition, even though results of the this study showed that increased aggressive competition over fruit was associated with more fruit in the diet.

Second, studies of African elephants (Archie et al. 2006) and Hanuman langurs (Borries et al. 1991) have shown that even when female kin are widely available and linear dominance hierarchies occur, dominance relationships do not always have a strong nepotistic component. Instead dominance relationships may be more individualistic, such that rank depends to a large extent on individual factors such as age (Borries et al. 1991; Archie et al. 2006), size (Archie et al. 2006), and experience. The absence of kin biases in elephants may not necessarily point to a weakness in a socioecological model developed specifically for primates, however this example does highlight limits for the model's applicability to social non-primate animals. Results from the present study show that, like Pharye's leaf monkeys (Koenig et al. 2004), significant dominance hierarchies based on agonistic competition for resources can occur in female dispersing species in the absence of frequent kin based support. Data on relatedness between females in this study were not available, but even if one pair of females were close relatives (as suggested by group averages reported in: Bradley et al. 2007), there would still be little evidence for a consistent pattern of nepotistic support since female coalitions were rare. This does not preclude the importance of rare but critical coalitionary support between female kin in escalated conflicts in which wounds can be inflicted to daughters or sisters as in Karisoke mountain gorillas (Watts 1997; Watts 2001; Watts 2003). Despite these important exceptions, there is growing evidence that the nepotistic component of the model is not as strongly associated with steep and linear dominance hierarchies as once thought (Broom et al. 2009; Koenig and Borries 2009).

A third inconsistency with the model stems from work on sympatric colobines (Korstjens et al. 2002), mountain gorillas (Robbins et al. 2005), mantled howlers (Zucker and Clarke 1998), and western chimpanzees (Wittig and Boesch 2003), in which linear dominance hierarchies were

detected in female dispersal societies. However, female rank in these species more closely reflects competition for access to male services, group membership, or safety than competition for food. In addition, Koenig and Borries (Koenig and Borries 2009) recently advocated that future socioecological models exclude female dispersal from its predictions because female transfer decisions are often affected by a variety of proximate and ultimate factors not directly related to contest feeding competition.

One alternative view that may also explain the presence of steep or linear dominance hierarchies in western gorillas and other primates such as Pharye's leaf monkeys (Koenig et al. 2004) in which female dispersal is common and competition is clearly over access to food takes into account the mediating force of a dominant male. Using the concept of power Lewis (2002) distinguished between individually-based dominance, which depends on intrinsic features of the individual such as body size and ability to use force, and derived dominance, which is based on coalitionary support. For females that undergo natal and secondary dispersal both intrinsic dominance and derived dominance may be potential sources of power. In the present study, contrary to the pattern of male policing reported for mountain gorillas (Watts 1994; Watts et al. 2000; Watts 2001; Watts 2003), on the rare occasions when the male intervened directly in female conflicts he consistently provided coalitionary support to the higher-ranking female competitor which should act to reinforce and possibly promote stability of female dominance relationships. If the best allies are those with superior fighting ability, then a silverback with a body size twice as large as the average female (Smith and Jungers 1997) should be of great value to females even if coalitionary support is offered infrequently.

I suggest that more studies explicitly investigate the role of males in mediating food-related aggression among females since they may either blunt or enhance female dominance

relationships. In addition, while female natal dispersal depends mainly on the tradeoff between the costs (e.g. inbreeding; scramble competition) and benefits (e.g. familiarity with home range; kin-based support) of philopatry (Pusey 1987; Pusey 1992), secondary transfer decisions are shaped by other extrinsic factors such as targeted aggression from conspecifics (Crockett and Pope 1988; Pope 2000), infanticide risk based on female (Crockett and Janson 2000) or male group size (Stewart and Harcourt 1987; Watts 1989; van Schaik and Kappeler 1997; Broom et al. 2004; Robbins et al. 2008), the presence of extra-group males (Steenbeek 1996), and the relative quality of group males (Sicotte 1993; Sicotte 2002). To this end the male's superior power may act as an effective substitute for kin-based coalitions in species that have limited access to female relatives due to constraints on female philopatry. Other non-mutually exclusive factors such as female age, group tenure, and body size should also be examined to better partition variance in female competitive ability in primate societies with non-nepotistic, individualistic dominance hierarchies.

In summary, building on the recommendations offered by Koenig and Borries (2006; 2009), and based on the findings of the present study, I stress the importance of making three refinements to current socioecological models. First, extending from Sterck et al. (1997) models should carefully consider the potential behaviors of males and their influence on female social relationships apart from infanticide and in addition to male policing (i.e. friendships; presence of male while foraging), particularly in societies with a strong degree of sexual dimorphism. Second, future models should soften the hypothesized association between the steepness and linearity of dominance hierarchies and nepotism. This argument is supported by recent mathematical modeling showing that several factors other than philopatry influence variation in dominance hierarchies, such as variance in relatedness within groups, the value of resources and

rank at different stages of life, and the likelihood and consequences of interventions, in addition to reproductive skew, demography, and variation in resource holding potential (Broom et al. 2009). Third, female dispersal should be excluded from socioecological predictions related to contest feeding competition, following the rationale of Koenig and Borries (Koenig and Borries 2009). For one, whether females disperse or not does not consistently influence their agonistic relationships because female residence is not a prerequisite for despotic female relationships (Broom et al. 2009). Secondly, dispersal can be driven by factors other than within-group feeding competition such as group size, habitat disturbance, aggression from other females, infanticide risk, and the relative quality of males (Watts 1990b; Glander 1992; Sicotte 1993; Steenbeek 1996; Sterck 1997; Sterck 1998; Pope 1998; Crockett and Janson 2000; Pope 2000; Stokes et al. 2003).

Tables and Figures

Table 3.1. Testing the links between increased percentage of potentially monopolizable food items (percent frugivory) in the diet, context of aggression, and female agonistic relationships in three populations of gorillas. Data on mountain gorillas form the basis for predictions in western gorillas.

Predictions of van Schaik (1989) model	Mountain gorillas		Western gorillas
	Karisoke ^a	Bwindi ^b	Mondika (predictions)
1 Increased % of monopolizable foods in diet	2 % ^{3c}	11 %	36 % ^d
Increased rate of feeding aggression over fruit	na	0.47 events / hr	> 0.47 events / hr
Higher % of decided outcomes:			
2 Overall / Feeding	18 % / 24 %	6 % / 10 % ⁶	> 18 % / > 24 %
3 Higher % of asymmetric dyads	10 ⁴ - 25 ⁵ %	7 % ⁷	> 25 %
3 Linear dominance hierarchy (aggression)	No	Yes	Yes
Reduced % of aggression against hierarchy	na	25 %	< 25 %
4 More frequent female coalitions	4 % of contests ^e	na	≤ 4 % of contests
Female rank stability	Yes: 80 % of dyads ^f	na	≤ 80 % of dyads
Hypothesized strength of contest competition	Very weak	Weak	Weak-to-moderate

^a = Watts 1994; ^b = Robbins 2008; ^c = Watts 1984; ^d = Doran-Sheehy et al. 2009; ^e = Watts 1997; ^f = Robbins et al. 2005.

³ Average proportion of fruit and bamboo shoots in diet by wet weight intake.

⁴ Percent of dyads in which the majority of aggression was decided; calculated from Watts 1994, p 351.

⁵ Percent of unidirectional dyads based on aggression initiated (Karisoke); calculated from Watts 1994, p 351.

⁶ Calculated from Robbins 2008, Table IVB.

⁷ Percent of unidirectional dyads based on aggression initiated (Bwindi); calculated from Robbins 2008, Table III.

Table 3.2. Monthly distribution of full- and half-day focal follows for four adult female western gorillas (MA; ME; BE; EB).

Month	MA			ME			BE			EB		
	N follows		N focal hrs	N follows		N focal hrs	N follows		N focal hrs	N follows		N focal hrs
	Full	Half		Full	Half	Full	Half	Full	Half	Full	Half	
2004												
Dec	1	0	6.86	0	0	---	1	0	8.76	2	0	15.17
2005												
Jan	2	0	15.69	3	0	17.96	3	0	20.48	3	0	19.50
Feb	3	0	24.33	3	0	19.82	3	0	24.20	4	0	34.16
Mar	2	0	17.48	3	0	23.29	3	0	23.64	3	0	20.29
Apr	6	0	40.31	5	0	40.29	4	0	32.00	5	0	37.50
May	0	0	---	2	0	7.32	2	0	8.24	2	0	8.66
Jun	0	2	9.25	0	2	9.21	0	2	9.20	1	0	4.98
Jul	0	6	25.06	0	4	16.07	0	8	34.10	0	0	---
Aug	0	6	23.13	0	5	20.64	0	6	24.53	0	0	---
Sep	0	14	60.80	0	9	40.20	0	9	38.63	0	0	---
Oct	0	4	17.38	0	3	11.18	0	3	12.73	0	0	---
2006												
Jun	0	9	37.11	0	9	37.64	0	10	38.62	0	0	---
Jul	0	9	38.49	0	9	37.96	0	8	33.97	0	0	---
Aug	0	6	25.11	0	7	25.42	0	8	31.73	0	0	---
Total	14	56	341	16	48	307	16	54	341	20	0	140

Table 3.3. Minimum number of aggressive events (Min N) required within a dyad to detect decided dominance relationships at $p < 0.05$, according to the degree of skew (Win ratio) in the percent of events won by each dyad member (F1; F2).

Win ratio		
F1 wins (%)	F2 wins (%)	Min N
100	0	3
90	10	5
80	20	10
70	30	25
60	40	96

Table 3.4. Summary of MatMan female dominance hierarchies using four data sets.

Dataset	n	h'	p	DCI	% unknown dyads	% two-way dyads	% events against hierarchy	Cardinal rank order
Aggression	551	1.00	0.02*	0.72	7	87	14	MA, VI, ME, UG, EB, BE
Decided aggression	263	0.66	0.21	0.74	7	60	13	MA, VI, ME, UG, EB, BE
Aggressive signals	484	1.00	0.02*	0.78	7	80	11	MA, ME, VI, UG, EB, BE
Decided aggressive signals	222	0.69	0.19	0.78	13	53	12	MA, VI, ME, UG, BE, EB

Entries are the number of aggressive events (n), linearity index (h') and p-value (p), Directional Consistency Index (DCI), the percentage of unknown and two-way dyads based on 15 dyads, and the percentage of aggressive events directed against the hierarchy (% events against hierarchy). Individuals are listed in descending order of rank based on re-ordered MatMan matrices (Cardinal ranks). Two of four hierarchies were significantly linear at $p < 0.05$.

Table 3.5. Summary of decided dominance relationships based on four data sets (A-D) using G-tests.

A) Aggression (n = 551 events)

	MA	VI	ME	UG	EB	BE	Σ
MA	---	24 ^{***}	125 ^{***}	13 ^{***}	34 ^{***}	154 ^{***}	350
VI	6	---	8 ^{ns}	3 ^{ns}	2 ^{ns}	8 ^{ns}	27
ME	26	6	---	8 ^{ns}	19 [*]	59 ^{***}	118
UG	1	2	3	---	nd	10 ^{***}	16
EB	6	1	7	nd	---	6 [*]	20
BE	6	3	10	0	1	---	20
Σ	45	36	153	24	56	237	551

B) Decided aggression (n = 263 events)

	MA	VI	ME	UG	EB	BE	Σ
MA	---	9 ^{ns}	52 ^{***}	5 ^{**}	17 ^{***}	85 ^{***}	168
VI	4	---	8 ^{ns}	4 [*]	1 ^{ns}	2 ^{ns}	19
ME	12	3	---	4 [*]	11 ^{**}	26 ^{***}	56
UG	0	0	0	---	nd	2 ^(*)	2
EB	1	0	1	nd	---	2 ^{ns}	4
BE	3	3	7	0	1	---	14
Σ	20	15	68	13	30	117	263

C) Aggressive signals (n = 484 events)

	MA	VI	ME	UG	EB	BE	Σ
MA	---	23 ^{**}	119 ^{***}	12 ^{***}	31 ^{***}	140 ^{***}	325
VI	6	---	5 ^{ns}	3 ^{ns}	2 ^{ns}	7 ^(*)	23
ME	21	6	---	7 ^{ns}	16 ^{***}	54 ^{***}	104
UG	1	2	3	---	nd	10 ^{***}	16
EB	2	1	2	nd	---	1 ^{ns}	6
BE	2	2	6	0	0	---	10
Σ	32	34	135	22	49	212	484

D) Decided aggressive signals (n = 222 events)

	MA	VI	ME	UG	EB	BE	Σ
MA	---	8 ^{ns}	46 ^{***}	4 [*]	15 ^{***}	76 ^{***}	149
VI	4	---	5 ^{ns}	4 [*]	1 ^{ns}	1 ^{ns}	15
ME	11	3	---	3 [*]	8 [*]	23 ^{***}	48
UG		0	0	---	nd	2 ^(*)	2
EB	1	0	1	nd	---	nd	2
BE	1	2	3	0	nd	---	6
Σ	17	13	55	11	24	102	222

Each female row indicates the number of aggressive events initiated (A, C) or won (B, D) against every other female and each column indicates the number of aggressive events received (A, C) and lost (B, D) against every other female. Decided dominance relationships, i.e., when one female won or initiated significantly more than 50 % of events, are indicated by ^{***}, ^{**}, ^{*}, ^(*) when probability was less than 0.001, 0.01, 0.05, and 0.1 respectively. The absence of any data for a dyad is indicated by nd, and relationships that are not decided are indicated by ^{ns}.

Table 3.6. Percentage of aggression initiated or won by the dominant female in dyads.

F/NF	Dyad	Agg	Dec agg	Agg sig	Dec agg sig	Avg %	Dec avg %	N. sig
F1	MA-ME	83	81	85	81	83	81	4
	n	151	64	140	57			
F2	MA-EB	85	94	94	94	92	94	4
	n	40	18	33	16			
F3	MA-BE	96	97	96	99	97	99	4
	n	160	88	142	77			
F4	ME-EB	73	92	89	89	86	89	4
	n	26	12	18	9			
F5	ME-BE	89	79	90	85	86	85	4
	n	69	33	60	26			
F6	EB-BE	86	66	100	---	84	---	1
	n	7	3	1	0			
NF1	MA-UG	93	100	92	100	96	100	4
	n	14	5	13	4			
NF2	ME-UG	73	100	70	100	86	100	2
	n	11	4	10	3			
NF3	UG-EB	---	---	---	---	---	---	
	n	0	0	0	0			
NF4	UG-BE	100	100	100	100	100	100	4
	n	10	2	10	2			
NF5	MA-VI	80	69	79	67	74	67	2
	n	30	13	29	12			
NF6	VI-ME	57	73	45	62	59	62	0
	n	14	11	11	8			
NF7	VI-UG	60	100	60	100	80	100	2
	n	5	4	5	4			
NF8	VI-EB	66	100	67	100	83	100	0
	n	3	1	1	1			
NF9	VI-BE	72	40	78	33	56	33	1
	n	11	5	9	3			

Percent of aggression (Agg) and aggressive signals (Agg sig) initiated, or percent of decided aggression (Dec agg) or decided aggressive signals (Dec agg sig) won by the dominant female (who is listed first) within all dyads containing focal (F1-F6) and non-focal females. Sample sizes (n) are indicated for each dyad and significant asymmetries bolded. For each dyad, the average percent asymmetry across all four data sets (Avg %) or among the two decided data sets (Dec avg %) and the total number of data sets with significant results (N. sig) are reported.

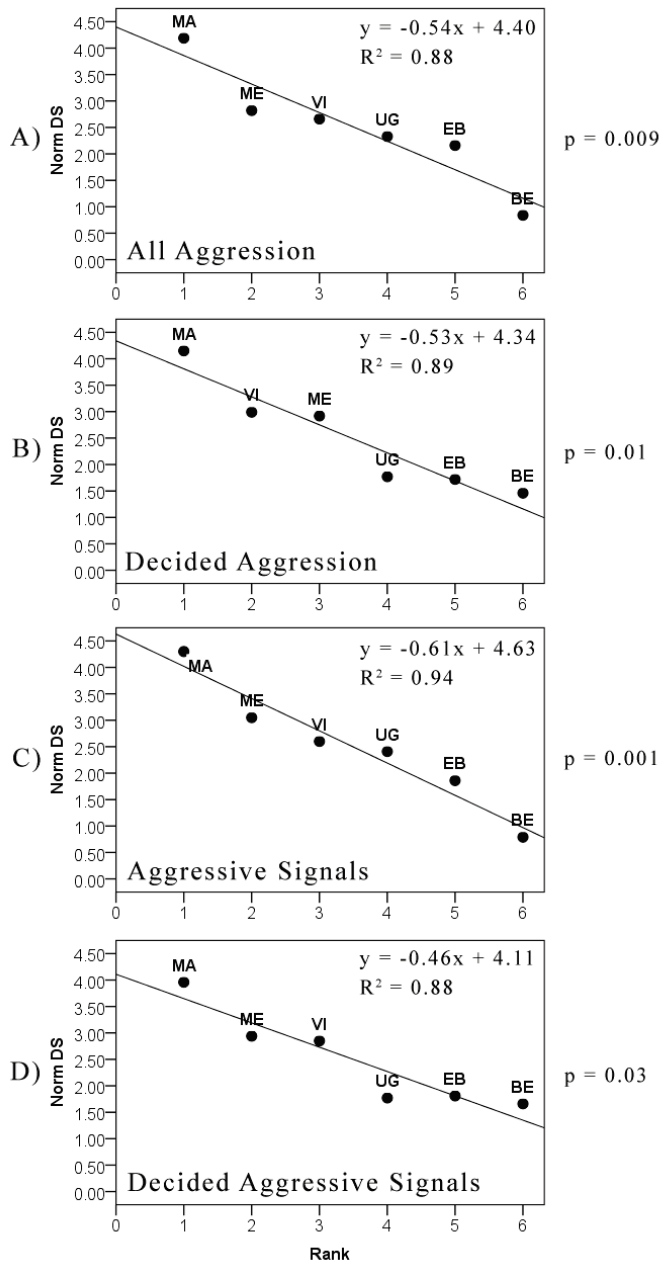


Figure 3.1. Female competitive ability and steepness of dominance hierarchies based on normalized David's scores (Norm DS) for A) aggression (n = 551 events), B) decided aggression (n = 263 events), C) aggressive signals (n = 484 events), and D) decided aggressive signals (n = 222 events).

Steepness was calculated as the absolute value of the slope (m) of the regression line indicated by the equation, $y = mx + b$. Significantly steep dominance hierarchies were indicated at $p < 0.05$.

A)

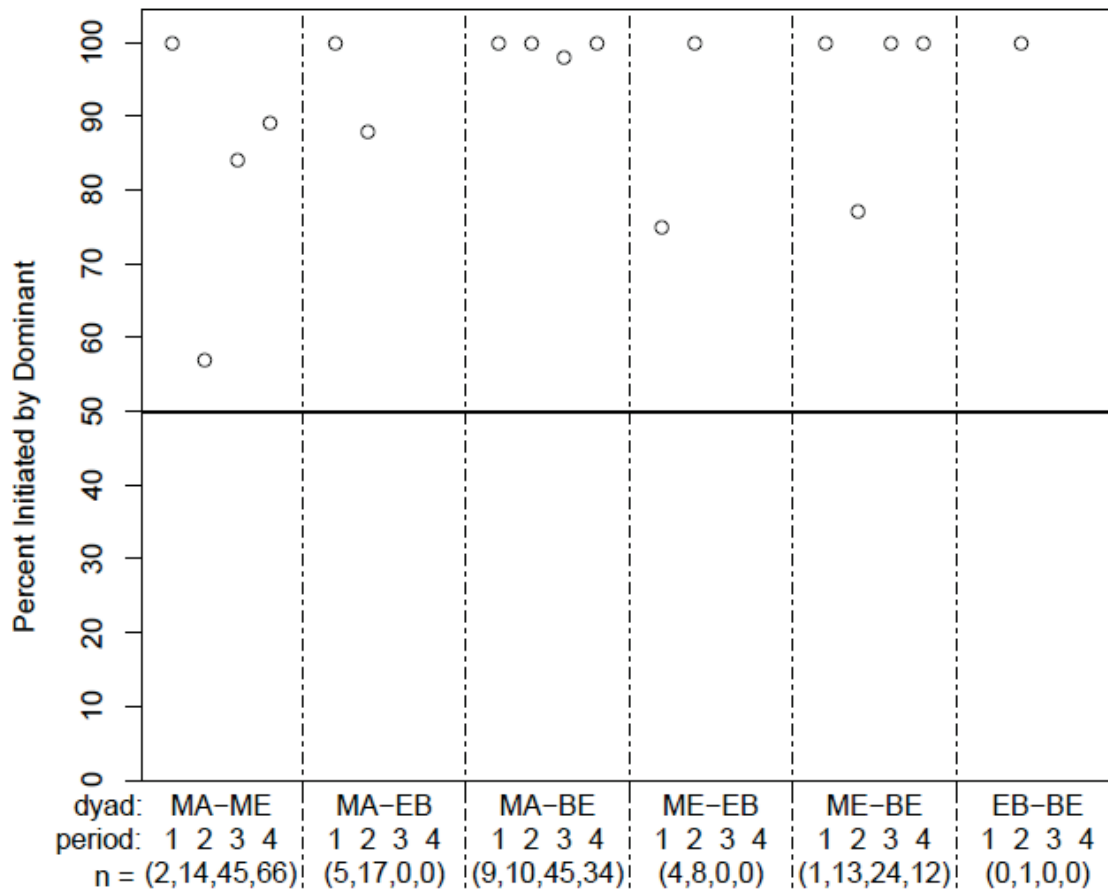
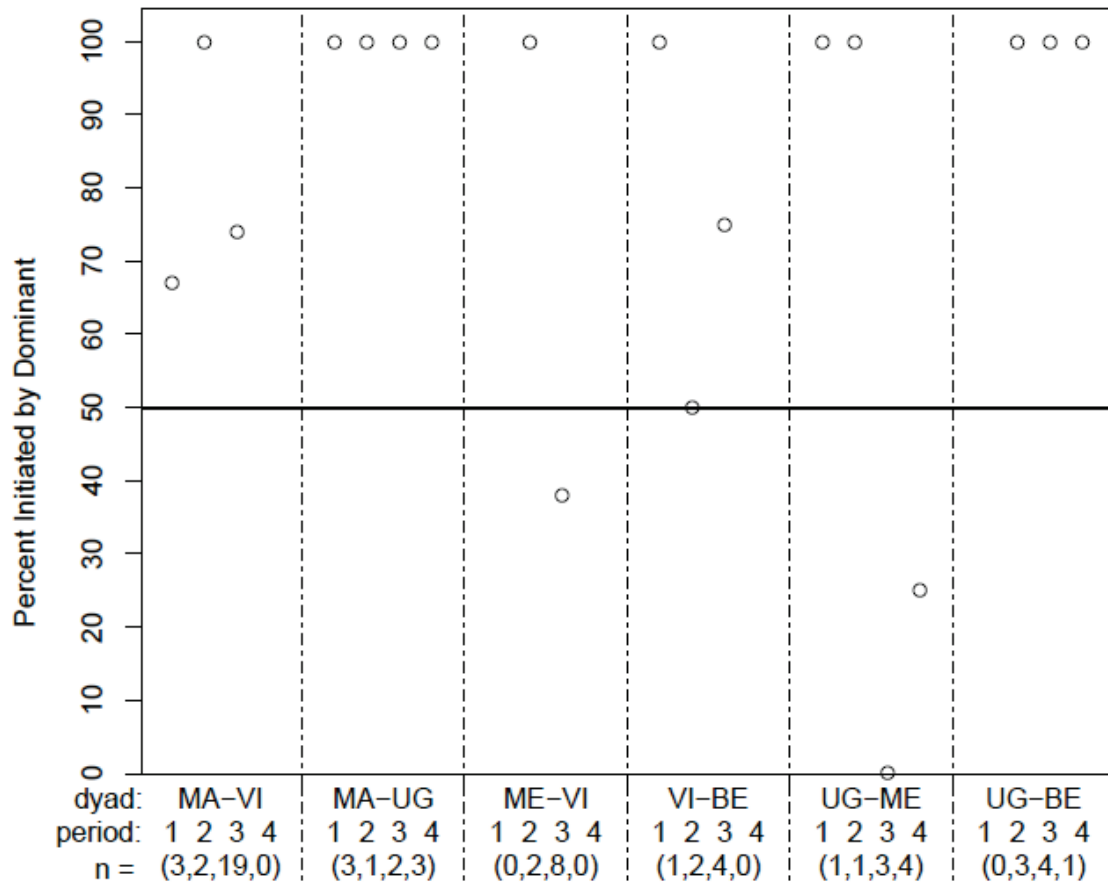


Figure 3.2. Stability of female dominance relationships in A) focal and B) non-focal dyads based on initiation of aggressive signals within four time periods.

For each dyad, the name of the dominant individual is given first on the x-axis, and the percentage of aggressive signals initiated by the dominant is indicated on the y-axis. The number (n) of aggressive signals initiated per dyad is given for each period: 1: Sep-Nov 2003; 2: Nov 2004-Jan 2005; 3: Jun-Sep 2005; 4: Jun-Aug 2006.

B)



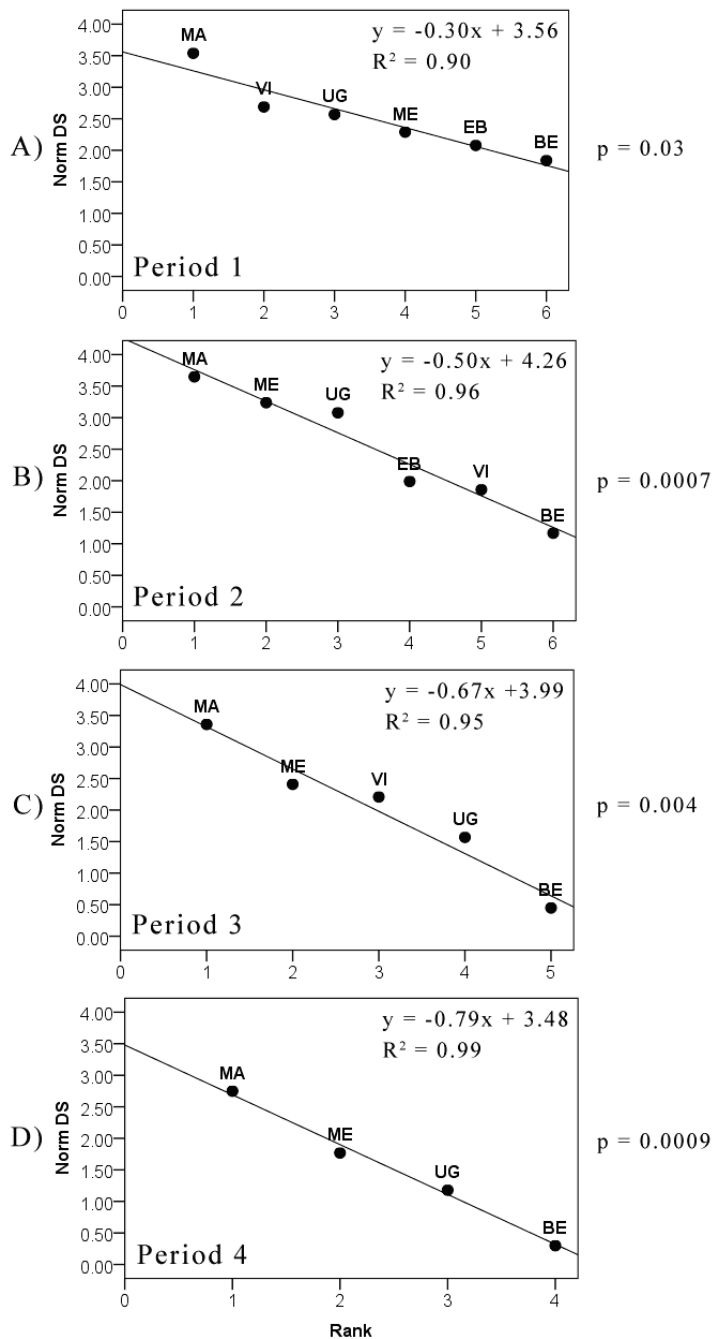
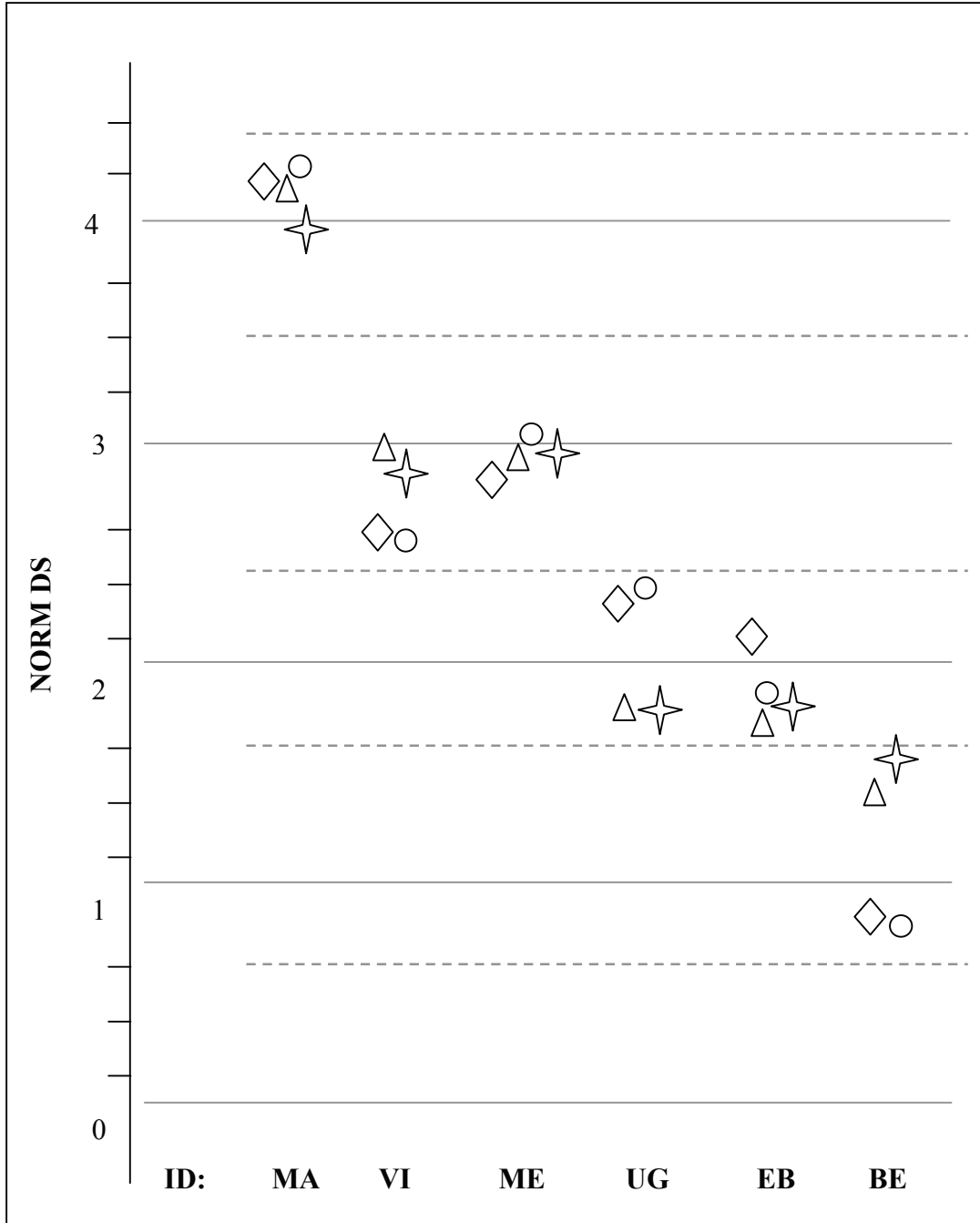


Figure 3.3 Stability of female rank and steepness of dominance hierarchies based on normalized David's scores (Norm DS) for all aggressive signals initiated within each of the four periods from Figure 3.2, including A) Period 1: n = 29 signals, B) Period 2: n = 74 signals, C) Period 3: n = 157 signals, and D) Period 4: n = 120 signals.

Supplemental Table 3.1. Calculation of David's scores using decided aggressive signals (n = 222 signals).

	Proportion of events won						Computations				
	MA	VI	ME	UG	BE	EB	w	w ₂	DS	Norm DS _{uc}	Norm DS
MA	---	0.67	0.81	1.00	0.99	0.94	4.41	6.86	9.59	4.10	3.96
VI	0.33	---	0.63	1.00	0.33	1.00	3.29	4.99	3.39	3.06	2.85
ME	0.19	0.38	---	1.00	0.88	0.89	3.34	3.94	3.36	3.06	2.94
UG	0	0	0	---	1.00	0	1.00	0.80	-5.18	1.64	1.77
BE	0.01	0.67	0.12	0	---	0	0.80	2.65	-5.37	1.60	1.66
EB	0.06	0	0.11	0	0	---	0.17	0.63	-5.79	1.54	1.81
l	0.59	1.72	1.67	3.00	3.20	2.83					
l ₂	1.09	3.17	2.26	3.98	5.62	3.76					

Rows indicate the proportion of events won within each dyad. Columns indicate the proportion of events lost within each dyad. w is the sum of the proportion of events won by each female (row). l is the sum of the proportion of events lost (column) by each female. w₂ is calculated as the sum of (the proportion of events won against opponent 1 multiplied by w value of opponent 2, the proportion of events won against opponent 2 multiplied by w value of opponent 2...the proportion of events won against opponent 5 multiplied by w value of opponent 5), and l₂ is calculated for each female as the sum of (the proportion of events lost to opponent 1 multiplied by l value of opponent 1, the proportion of events lost to opponent 2 multiplied by l value of opponent 2...the proportion of events lost to opponent 5 multiplied by l value of opponent 5). David's scores (DS) are computed for each female as $DS = (w + w_2) - (l - l_2)$, which reflects her overall success in winning interactions relative to that of all other competitors. Normalized David's Scores (Norm DS_{uc}) are a standardized version of DS that take into account female group size, and are calculated as $[DS + N((N-1)/2)/N]$. These were corrected for chance (Norm DS) based on the calculation of dyadic dominance indices using the program for R package steepness 0.1 (Leiva and de Vries 2009). Dyadic sample sizes are provided in Table 5.



Supplemental Figure 3.1. A comparison of female competitive ability in four datasets.

Differences in individual competitive ability for six females based on normalized David's scores (Norm DS) corrected for chance in four data sets, including all aggression (◇), decided aggression (△), all aggressive signals (○), and decided aggressive signals (☆). Data are from Figure 3.1.

CHAPTER FOUR:
Dominance rank and energy intake in wild western gorilla females (*Gorilla gorilla*)

Introduction

Variance in female reproductive success in mammals is determined by differential access to food (Williams 1966; Trivers 1972; Clutton-Brock et al. 1982; Wade and Schneider 1992) among other factors. Females who attain more food or have better nutrition relative to others achieve age of first reproduction earlier, have shorter lactational periods and inter-birth intervals, and faster infant growth and earlier weaning (Sadleir 1969; Gilmore and Cook 1981; Lunn et al. 1984; Asquith 1989; Hendrickx and Dukelow 1995; Gomendio et al. 1995; Takahata et al. 1998; Borries et al. 2001; Altmann and Alberts 2003a; Altmann and Alberts 2003b; Altmann and Alberts 2005). Some females acquire more food or energy than others when there is high quality monopolizable foods, often fruits and seeds (Whitten 1983; Janson 1985; van Noordwijk and van Schaik 1987; Janson 1988; Barton and Whiten 1993; Saito 1996; Koenig 2000; Vogel 2005). Monopolization of other foods such as leaves and flowers may occur as well if they are of high quality and occur in patches that are small relative to group size (Koenig et al. 1998). If feeding competition over high quality monopolizable food occurs consistently throughout the year or during critical periods for seasonally breeding populations this can lead to rank-related differences in female net energy gain and reproduction within social groups (Mori 1979; Whitten 1983; Altmann et al. 1988; Borries et al. 1991; Barton and Whiten 1993; Saito 1996; Koenig et al. 1997; Koenig 2000; Koenig 2002). This mode of feeding competition known as within-group contest (WGC) competition is thought to trigger profound effects on female social relationships

in primates including unidirectional female dominance relationships and linear dominance hierarchies (van Schaik 1989; Sterck et al. 1997; Koenig 2002).

Less clear is exactly what proportion of the overall or seasonal diet need be composed of high quality defensible foods to render rank-related differences in individual energy intake. Primate diets are variable within and among species (Altmann 1998; Davies et al. 1999; Chapman et al. 2002; Chapman et al. 2004; Potts et al. 2011), with some populations concentrating the bulk of their wet weight intake on a handful of food items (Watts 1984; Koenig et al. 1998; Rothman et al. 2007) while others broaden their diet to include hundreds of food species (Nishida and Uehara 1983; Altmann 1991), the relative contribution of which may vary throughout the year. These sources of variability in dietary composition may influence the determination of overall individual energy intake as well as periodic variations or fluctuations in female energy intake throughout the year.

In addition to variation in diet, there are many challenges associated with empirical attempts to accurately measure individual food and energy intake in wild primates (Chivers 1998; Conklin-Brittain et al. 2006; Rothman et al. 2012). There is also variation in the number of food species measured and in the type of considerations given to resource availability between studies. Researchers studying contest competition in brown and white-faced capuchin monkeys focused on the period of fruit scarcity to measure individual feeding success relative to the group mean within high quality monopolizable food patches (Janson 1985; Vogel 2005). The lean season was targeted as the focus of study in brown capuchins because quantitative fruit production data had previously indicated that total fruit production during other parts of the year exceeded what capuchins could consume (Janson 1984). One study of Japanese macaques

focused on winter months to explore whether dominant females had higher intake of a prized resource within that particular period relative to subordinates (Saito 1996). Other studies have measured individual intake of important foods contributing to at least 50 % of the total annual diet (Whitten 1983; e.g. van Noordwijk and van Schaik 1987; van Schaik and van Noordwijk 1988; Koenig et al. 1998; Koenig 2000). However, few studies have examined individual rates of food intake when females were feeding on clumped resources as well as when they were feeding on evenly distributed food species (but see e.g. Janson 1985). This is an important consideration when posing questions about overall individual feeding success because the nutrient content and spatial distribution of food items may vary considerably among species (Janson 1988; Byrne et al. 1993) and the relative contributions from different food types may fluctuate throughout the year. Intensive measures of individual feeding rates may also be required to capture rank-related differences in food or energy intake. A recent study of females in the Bwindi population of mountain gorillas showed that low-ranking females had lower energy intake compared to high-ranking females because low-ranking females fed at slower rates than high-rankers (Wright et al. 2014).

Our current understanding of the energetic consequences of differential feeding success comes mainly from monkeys who must forage cohesively to avoid exposure to predators and who feed intensively on high quality monopolizable foods such as vervet monkeys (Whitten 1983; Whitten 1988b), brown capuchins (Janson 1985), white-faced capuchins (Vogel 2005), long-tailed macaques (van Noordwijk and van Schaik 1987; van Schaik and van Noordwijk 1988), olive baboons (Barton and Whiten 1993), and Hanuman langurs (Koenig et al. 1998; Koenig 2000). It is in these primate species that rank-related effects on daily individual food and nutrient intake (Barton and Whiten 1993), individual food or energy intake on high quality

monopolizable food species (Janson 1985; Whitten 1988a; Saito 1996; Vogel 2005), individual foraging efficiency on fruit (van Noordwijk and van Schaik 1987; van Schaik and van Noordwijk 1988), or individual net energy gain as approximated by physical condition (Koenig 2000) have been documented (Koenig 2002).

Rank-based differences in feeding success are not expected in primates such as mountain gorillas from the Karisoke population (Watts 1996; Harcourt and Stewart 2007) and mountain baboons (Barton et al. 1996) that feed almost entirely on evenly distributed non-monopolizable resources. Mountain gorillas are well studied and have stable diets throughout the year consisting mainly of abundant herb leaves, pith, and peel that are perennially-available, with the exception of bamboo shoots and fruits (Watts 1984; Watts 1996; Watts 1998; Rothman et al. 2006a; Rothman et al. 2007). Consequently, food-related aggression among female mountain gorillas at the Karisoke site in the Virunga Volcanoes of Rwanda, Democratic Republic of Congo, and Uganda, occurred no more often than would be expected based on time spent feeding, and feeding contests rarely interrupted feeding bouts acutely or prompted one female to gain more of a resource than another (Watts 1985; Watts 1994). Most aggression among female mountain gorillas at Karisoke was undecided leading to undecided female dominance relationships in many or most pairs on the basis of aggression (Watts 1994). There is some controversy as to whether rank affects female reproductive success in Virunga mountain gorillas; initial reports indicated that rank effects on female reproduction were negligible (Watts 1996; Sterck et al. 1997; Watts 2003). However, recent analysis of the long-term demography data for Virunga gorillas demonstrated that high-ranking mothers had slightly shorter interbirth intervals, lower infant mortality, and higher surviving birth rates than low-ranking mothers (Robbins et al. 2007),

although no associated data on feeding competition were available to test whether rank effects on reproduction accompanied rank effects on food or energy gain.

In contrast, western gorillas live in tropical lowland rainforests that contain higher densities and diversities of fruiting trees and lianas compared to the montane environments of mountain gorillas (Goldsmith 2003), leading to increased frugivory in western gorillas (Rogers et al. 2004; Robbins 2008; Doran-Sheehy et al. 2009a; Masi et al. 2009). Western gorilla diets are composed of fruit, leaf, and herb in roughly equal proportions, which shift in their relative contributions throughout the year as a response to seasonal fluctuations in fruit availability (Williamson et al. 1990; Remis 1997; Doran et al. 2002; Remis 2003; Doran-Sheehy et al. 2009a). Western gorilla fruits contain more easily-assimilable energy than do leaves and herbs (see Chapter 2) and are preferred whenever available (Tutin et al. 1991; Remis 1997). Several fruit species consumed by western gorillas may be potentially monopolizable based on the low density of trees in the habitat for some species (e.g. *Tetrapleura tetraptera*; *Klainedoxa gabonensis*) and the small size of fruiting trees (e.g. *Vitex welwitschii*; *Pancovia laurentii*) relative to group size for other species (Doran et al. 2002). Data on the dispersion and density of items within fruiting trees, availability of alternative resources and number of individuals feeding within patches, and the rate of patch depletion would be required to assess the socioecological correlates of monopolizability for different fruit species. However, because these data are not available in the present study other potential indicators of contest competition will be explored.

Western gorillas differ from mountain gorillas in the composition of their diet (see Chapter 1), patterns of agonism, and in the nature of female agonistic relationships (see Chapter 2), which may reflect differences in contest competition. In western gorillas, most (90% of)

female aggression occurred in the context of feeding and rates of fruit-feeding aggression were higher than in mountain gorillas (see Chapter 3). Consequently, a higher proportion of female aggression in western gorillas was decided compared to mountain gorillas, leading to a higher proportion of decided female dominance relationships (see Chapter 3). However, to-date we lack a basic understanding of the energetic consequences of increased fruit consumption, increased dietary variability throughout the year, and increased rates of aggression over fruit in western compared to mountain gorillas.

Although it is well established that the amount of fruit in the diet of female western gorillas varies throughout the year (Williamson et al. 1990; Tutin et al. 1991; Remis 1997; Remis 2003) and that western gorilla fruits are richer in soluble sugar and energy compared to other food types (Rogers et al. 1990; Remis et al. 2001; Doran-Sheehy et al. 2009a) the total amount of energy consumed by female western gorillas may or may not vary throughout the year. On one hand, if fruit provides more energy than other food types female energy intake might be expected to vary throughout the year as a response to variation in fruit consumption. On the other hand, gorillas may cope with periods of fruit scarcity by increasing overall food intake. If females can compensate by feeding longer on lower quality fallback foods (Doran-Sheehy et al. 2009a; Marshall et al. 2009), then energy intake might not vary throughout the year. Western gorillas alter their diets during periods of fruit scarcity to include more leaf, herb, and non-preferred fruit (Doran-Sheehy et al. 2009a) but it is presently unclear whether they also spend more time feeding.

If female energy intake varies throughout the year in wild western gorillas, I seek to examine which factors best predict variance in overall energy intake. In previous studies of

within-group feeding competition multiple factors explained variance in female food or energy intake including food nutrient quality and abundance (Koenig et al. 1997; Koenig et al. 1998; Knott 2005; Schülke et al. 2006; Heesen et al. 2013), dominance rank (Whitten 1983; Janson 1985; van Noordwijk and van Schaik 1987; van Schaik and van Noordwijk 1988; Whitten 1988a; Barton and Whiten 1993; Saito 1996; Vogel 2005), and group size (van Schaik and van Noordwijk 1988; Janson 1988; van Noordwijk and van Schaik 1999). Rank may also interact with resource availability to influence the amount of time females spend feeding as in blue monkeys (Pazol and Cords 2005), or the amount of net energy gained as in Hanuman langurs (Koenig 2000). In blue monkeys, low-ranking females spent a significantly greater proportion of their total time feeding than did high-ranking females during periods of low and intermediate resource availability, but not during periods of high resource availability (Pazol and Cords 2005). To explore whether fluctuations in daily energy intake are associated with feeding adjustments, here I examine which factors best predict variance in daily energy intake, with a particular focus on time spent feeding per day and the proportion of fruit in the daily diet. I expect that female energy intake will be positively associated with daily feeding time and fruit consumption.

Proceeding from an understanding of the factors that influence variation in female energy intake, I next explore whether females differ in their overall rate of energy intake on the basis of dominance rank. Rank-based differences in energy intake and expenditure were recently demonstrated among female mountain gorillas in the Bwindi population (Wright et al. 2014). Differences in energy intake among high- and low-ranking ranking mountain gorilla females at Bwindi resulted from differences in their feeding efficiency (Wright et al. 2014). In comparison with Bwindi gorillas, western gorillas consume more fruit by wet weight and the fruits they eat contain more easily-accessible energy in the form of simple carbohydrates (see Chapter 2). The

proportion of the western gorilla diet (ca. 41 - 43 % fruit; Chapter 2) composed of foods that might be monopolizable (given their concentration within rare or small-to-medium sized patches) was similar to the proportion of clumped foods in the diet of olive baboons (30 %) known to exhibit rank-related differences in food intake (Barton et al. 1996). On these grounds and in light of the recent findings for Bwindi gorillas, I predict that western gorillas females will show rank-related differences in overall energy intake. Alternatively, if the amount of fruit in the overall diet is not consistent enough throughout the year or if females can spread out to avoid feeding competition during parts of the year then rank-based differences in overall individual energy intake may not be expected to occur. However, prior studies have shown large fluctuations in the composition of western gorilla diets throughout the year (Remis 1997; Remis et al. 2001; Doran-Sheehy et al. 2009a; Masi et al. 2009); if this dietary variation contributes to variance in female energy intake then individual differences in energy intake may theoretically be present during periods of high fruit consumption. Alternatively, proceeding from the assumption that whatever fruit is available during months of low fruit consumption is of much higher value to gorillas compared to other resources, rank-based differences in energy intake may instead occur during months of low fruit consumption.

If higher-ranking females gain more energy than others at some time of the year, I next examine whether aggression is the principle mechanism by which rank-related skew in individual energy intake is achieved. Other than low-ranking females avoiding high-ranking females at high quality food patches (Robinson 1981; van Noordwijk and van Schaik 1987; Whitten 1988b; Koenig et al. 1998), aggression is the principle mechanism by which higher-ranking females can achieve higher energy intake compared to others. Aggression and its effects on female fruit and energy intake are well documented in brown and white-faced capuchins

(Janson 1985; Vogel and Janson 2007). Specifically, I predict that the alpha female will acquire a greater share of high-quality food than others by aggressively interrupting other females' fruit feeding bouts and thereby gaining energy at their expense.. If supported, I assess whether increased aggression over fruit is associated with rank-related differences in individual energy intake within months of high fruit consumption when high quality foods are prevalent or within months of low fruit consumption when high quality foods are in limited supply.

Methods

Study site and study subjects

The study was conducted at the Mondika Research Center (02° 21' 859" N, 016° 16' 465" E) within the Republic of Congo and Central African Republic. The site consists of primary forest habitat including mixed semi-evergreen tropical lowland forest, monodominant stands of *Gilbertiodendron* forest, light gaps, and swamp forest (Mehlman and Doran 2002). Long term records indicate that both rainfall and fruit availability are seasonal (Doran et al. 2002; Doran-Sheehy et al. 2009a). Annual rainfall averages 1600 mm, with an annual two-to-three month dry season (with less than 50 mm of rainfall per month) occurring between December and February (Doran-Sheehy et al. 2009a). Ripe fruit availability peaks during a two-to-three month period between June and September (Doran-Sheehy et al. 2009a). The timing of the annual ripe fruit peak is highly consistent across years although the amount of fruit varies across years (Doran-Sheehy et al. 2009a). Gorillas are not seasonal breeders (Watts 1998) and long-term demography data at Mondika indicate there are no peak periods of conception (Doran-Sheehy, unpublished data).

The study was conducted between December 2004 and October 2005 on one group of habituated western gorillas (*Gorilla gorilla*) comprising one silverback male and 5-6 adult females and their offspring. Focal subjects included four adult females who permitted close following; one of these females (EB) disappeared from the group at the mid-point of the study. Female reproductive states within the same annual cycle are reported elsewhere (Chapter 2).

Data collection

Between December 2004 and May 2005 I conducted full-day focal follows, which lasted an average of 9 hours and 54 minutes (SD = 0 hr 34 min; range = 8 hr 10 min – 10 hr 39 min; n = 59 follows). A total of ten half-day follows were also collected during the first half of the study as a result of failed attempts at all-days follows. Beginning in June I switched to half-day follows, following one female in the morning (n = 45 morning or AM follows) before switching to another female in the afternoon (n = 39 afternoon or PM follows). The average duration of these follows was 5 hr 09 min (SD = 0 hr 29 min; range = 3 hr 24 min – 6 hr 01 min; n = 84 follows). Full-day follows were later converted to 118 half-days and coded as morning or afternoon samples for comparison with the 94 half-day follows for a new total of 212 half-day follows.

Due to logistical constraints, the distribution of focal follows was uneven between subjects within and between months, and the mean duration of focal follows varied between subjects, months, and by the type of follow (AM; PM; Supplemental Table 4.1). The total number of half-day follows per month ranged from 7 (June) to 37 (April) with a mean of 19 half-day follows per month (n = 11 months). There was an average of 53 half-day follows per focal

subject (n = 4 females). Overall sample sizes were similar for three of four focal subjects (MA: n = 60, ME: n = 57, BE: n = 61 half-day follows) but much lower for the fourth individual (EB: n = 34 half-day follows) because of her disappearance from the group half way into the study.

During follows, I recorded focal a) activity (feeding [food species and part], resting, traveling, or other) instantaneously at one-minute intervals during four 10-minute sampling periods per hour (00-09, 15-24, 30-39, 45-54), b) feeding rates (N of items / min) opportunistically for the most common food items (described in Chapter 2), and c) all occurrences and context of aggression given or received by the focal subject (i.e. feeding [food species; part: fruit; leaf; herb; termite; other], resting, traveling, competition for proximity to the silverback, other, unknown).

Data analysis

Standardization of focal follows

In order to directly compare data from the first and second halves of the study I converted the 59 full-day follows into 118 half-day follows and combined them with the 94 half-day follows. To reduce sampling bias I removed 26 follows that lasted less than 4.5 hours since these started late (for AM follows) or ended early (for PM follows) during times of day when feeding behavior was most common. Although there was no detectable association between follow duration and proportion of time spent feeding per follow (Supplemental Figure 4.1), follows with late start times may theoretically bias the amount of energy consumed if for example the nature of foods consumed in the early morning when the gorillas were regularly feeding (ca. 6:00-8:00) differed from those used at other times. Thus, to provide information on the timing and duration

of follows when modeling individual energy intake, I categorized each follow as type 1, 2, or 3 based on the following definitions: 1 = starting before 6:30 or ending after 17:00; 2 = starting between 6:30 – 6:59 or stopping between 16:30 – 16:59; 3 = starting between 7:00 – 7:29 or stopping between 16:00 – 16:29.

Focal follows collected during May 2005 ($n = 10$ follows) were considered problematic because I failed to follow the alpha female and were removed from consideration. This yielded a final data set of 176 half-day follows with a mean duration of 5 hr 8 min (SD: 0 hr 18 min; range: 4 hr 32 min – 6 hr 01 min). To examine the comparability of morning and afternoon follows I tested for differences in the overall proportion of time spent feeding and in the proportions of feeding time spent on different food types in morning and afternoon samples from the same day ($n = 43$ randomly selected full day follows). Results indicated that morning and afternoon follows did not differ significantly in the overall proportion of time spent feeding (Wilcoxon signed-rank test: $n = 43$ follows; $Z = -0.036$, $df = 1$, $p = 0.97$) or feeding time spent on fruit (Wilcoxon signed-rank test: $n = 43$ follows; $Z = -0.875$, $df = 1$, $p = 0.38$). However, mornings and afternoons differed significantly in the proportion of time spent feeding on leaves (Wilcoxon signed-rank test: $n = 43$ follows; $Z = -2.922$, $df = 1$, $p = 0.003$) and herbs (Wilcoxon signed-rank test $Z = -1.968$, $df = 1$, $p = 0.05$). Since I previously found no significant differences in the nutrient content of leaves and herbs (Chapter 2) this should have little effect on the results. Even so, to account for potential energetic disparities between morning and afternoon samples, follow type was coded as a fixed factor with two levels (AM; PM) for initial data exploration.

In the full data set ($n = 176$ follows) individuals were not sampled evenly across time of day or month. Therefore in some analyses I used a random subsample of the larger data set,

selecting two follows (1 AM follow; 1 PM follow) per female per month for each of the three females present throughout the 10 month-study to yield a total sample size of 60 follows.

Female rank

I determined female ranks using normalized David's scores (Norm DS) calculated from the outcomes of decided aggression as described in Chapter 3. Females in the present study varied in overall competitive ability based on Norm DS (a continuous measure of rank). One female was considered alpha (MA Norm DS = 4.2), one female was middle-ranking (ME Norm DS = 2.9) and two females had low but similar ranks (EB Norm DS = 1.7; BE Norm DS = 1.5).

Estimating energy content of foods

Caloric content (kilocalories / 100 g organic matter) of 41 gorilla foods (n = 18 fruit species; n = 15 leaf species; n = 7 herb species; 1 termite species) was determined in a prior study (Chapter 2) based on Atwater physiological fuel estimations for humans per gram of total non-structural carbohydrate (TNC), lipid (LP), and crude protein (CP). Energy derived from microbial fermentation of neutral detergent fiber (NDF) was not considered here since estimates of energy extraction are wide ranging among studies (Milton and Demment 1988; Remis and Dierenfeld 2004). Caloric content of gorilla foods estimated in this study are reported in Supplemental Table 4.3.

As described elsewhere (Chapter 2), I estimated caloric content for 10 additional fruit species and 23 leaf species eaten by gorillas during the present study. Fresh pulp weights for

fleshy fruit species with known nutrient content ($n = 14$ fruit species) were significant predictors of energetic content (linear regression: $t = 2.18$; $df = 13$, $p = 0.05$) allowing me to predict energy content for 4 of the 10 fruit species. Because fresh pulp weights were not available for the other 6 fruit species, their estimates of energy content were supplied on the basis of prior categorization of fruit species by size and construction (as described in Chapter 2). For each of the 23 leaf species, the mean energy value of leaves in the chemically analyzed sample ($n = 15$ leaf species) was substituted as an estimate of caloric content.

Dietary patterns, feeding rates, and energy intake

For each female, I used data from instantaneous activity samples to calculate the overall proportion of time spent feeding (i.e. N samples feeding / N activity samples in follow) and the proportions of feeding time spent on fruits, leaves and herbs (e.g. N feeding samples on fruit / N feeding samples in follow).

I calculated daily energy intake rate (kcal / follow / activity hr) by first multiplying five measurements for each food item i) feeding time, ii) feeding rate, iii) average wet weight (described in Chapter 2), iv) the proportion of wet weight that was dry matter (described in Chapter 2 following Koenig et al. 1997), and v) energy content (kcal / 100 g organic matter)- and then dividing this value by the total number of sampling hours per follow. Because sample sizes were limited for some foods and females had similar feeding rates when eating the same food item, I calculated an average feeding rate (i.e. mean N of food items eaten / min of observation) per food item, then multiplied this by the average wet weight of the food item (grams / food item) to estimate average intake rate (g / min). This practice of calculating a mean feeding rate

per food item is justifiable on the grounds that ingestion rates vary little within food types (Janson and van Schaik 1993; Schülke et al. 2006). I determined the proportion of wet weight that was dry matter for each food species by drying food specimens to a constant weight in the lab. Average rates of ingestion for the 41 gorilla foods with known nutrient content are reported in Supplemental Table 4.3. Total energy intake was summed across foods and divided by sampling time (N activity hrs) to determine individual rate of energy intake per follow.

To assess monthly variation in time spent feeding, in the proportions of feeding time spent on fruit, leaf, and herb, and individual energy intake rates (kcal / follow), I used feeding data from the balanced subset of two randomly selected half-day follows per focal subject per month (n = 60 follows) to calculate mean monthly values for each of these variables.

Statistical methods

Statistical analyses based on the balanced subset (60 follows)

Measurements of daily feeding time (proportions) and energy intake (interval-scaled data) were transformed so that data distributions would better conform to the assumptions of parametric testing (Sokal and Rohlf 1995). The daily proportion of time spent feeding and proportion of feeding time spent on fruit, leaf, and herb (from the subset of 60 follows) were logit-transformed $\ln(p/(1-p))$ to homogenize variances and minimize over-dispersion (Jaeger 2008). The logit transformation has gained traction over the traditional arcsine square root transformation for the purpose of analyzing (binomially distributed) proportion data with linear models (Warton and Hui 2011). To test for monthly variation in the average proportion of time spent feeding and average proportion of time spent on fruit, leaf, and herb, I performed linear mixed effect models (Kuznetzova et al. 2012) on logit-transformed data. Month was treated as a

fixed effect ($df = 9$) and female ID as a random effect to control for repeated sampling of the same individual throughout the study. The same mixed effect model design was used to test whether the relative daily proportion of time spent feeding was predicted by the proportions of feeding time spent on fruit and leaf, with month excluded as a fixed factor. To test whether the daily proportion of feeding time spent on fruit was significantly correlated with the daily proportion of feeding time spent on leaf, I tested Spearman's nonparametric correlations on untransformed fruit and leaf proportion data. Spearman's rank correlations and bivariate scatterplots were also used in initial data exploration to assess the strength, linearity, and direction of associations between feeding variables.

Logarithms of energy intake rates were taken based on the box-cox method for determining the most appropriate power transformation for interval-scaled data (Zuur et al. 2009). Model residuals were not normally distributed when based on raw energy intake data; however, residuals conformed to a normal distribution when models were run using log-transformed energy intake data. To test whether there was monthly variation in individual energy intake rates, I used a linear mixed effect model on log-transformed energy intake data with month as a fixed effect and female ID as a random effect. Next, to test alternative hypotheses with respect to which feeding variables might best predict variation in female energy intake rate, I used current methods of model selection to distinguish models looking at the effects of total feeding time, fruit feeding time, and total feeding time & fruit feeding time, using the *bbmle* package in R (Bolker 2014). The optimal or best-fitting model was selected as that which had the lowest Akaike information criteria corrected for small sample sizes, AICc (Burnham and Anderson 2004). If two models differed by less than 2.0 AICc then the model with the fewest degrees of freedom was selected (Burnham and Anderson 2002). I tested the full model against a

null model that contained the random effect of female ID (as intercept) and no fixed effects or covariates using a log-likelihood test to verify that the full model explained significantly more variance in individual energy than what would be expected by chance based on the increased degrees of freedom in the full model (Zuur et al. 2009).

For each mixed effect model, the denominator degrees of freedom was computed by the Satterthwaite approximation (Satterthwaite 1946), and corresponding statistical tests were provided in the lmerTest package for R (Kuznetzova et al. 2012) and in the anova function from the R stats package (R Development Core Team 2011). To test for individual differences in energy intake I performed a linear model (using the lm function from the R stats package, R Development Core Team 2011) on log-transformed energy intake data with female ID as a fixed effect.

Statistical analyses based on the larger data set (176 follows)

To examine whether rank was positively associated with energy intake within particular months, I utilized the larger data set of 176 follows to maximize the sample size per individual within each month. For each month, I calculated the correlation coefficient between rank (Norm DS) and energy intake rate based on the raw data using a Spearman's rank correlation. To test whether the observed distribution of correlation coefficients differed from a null normal distribution with a mean of 0, I performed a one-sample t-test (2-tailed) in R (using the t.test function from the R stats package: R Development Core Team 2011). For each month with a significant positive correlation between rank and energy intake, I tested whether rank was

positively associated with fruit consumption as measured by the logit-transformed proportion of feeding time spent on fruit within each month using Spearman's rank correlation tests.

Additional model considerations

All models examined via model selection statistics were fit using maximum likelihood (ML), and then refit for more accurate parameter estimates using restricted maximum likelihood (REML) following Zuur et al. (2009). For each mixed effect model, predictor variables that were strongly correlated ($r > 0.60$) were not included in the same models to avoid violating the principle of independence. Correlations between months were not strong and probably did little to impact the fit of models. Residuals from the best-fitting model of individual energy intake were examined for normality to ensure model validity. In initial modeling trials, follow type (2 levels: AM; PM follows) and start / stop time category (3 levels: 1; 2; 3) were found to be non-significant factors in explaining variation in feeding behavior and energy intake rate in the balanced subset of data ($n = 60$ follows). Thus, these fixed factors were dropped from inclusion in each of the mixed effect models presented here.

Aggression, rank, and energy intake (53 follows of alpha female)

To assess whether aggression was the primary mechanism by which high-ranking female gorilla(s) achieved more feeding time on fruit and higher rates of energy intake, I calculated the frequency (N of events) and rate (N of events / hr feed fruit) of aggression initiated by the top-ranking adult female (MA) toward other females in the context of feeding fruit during the course of her focal follows ($n = 53$). The top-ranking female was a suitable subject for examining

frequency of fruit aggression throughout the study, because her overall competitive ability score (MA Norm DS = 4.2) was nearly 1.5 times higher than the next highest-ranked female (ME Norm DS = 2.9) based on the outcomes of decided aggressive events, most of which occurred during feeding. To test for monthly variation in fruit feeding aggression I performed a generalized linear model (GLM) on the daily count of aggression by the alpha female towards other females (with a log link function for poisson distribution) with month (df = 9) as a fixed effect and daily feeding time (N hrs) on fruit as a covariate. Model results were inspected to determine whether months of significantly higher aggression over fruit matched those showing a positive correlation between rank and energy intake and whether months of low or zero fruit-related aggression corresponded to those showing a negative or no correlation between rank and energy intake.

Results

Overall dietary pattern and energy intake

Feeding time, which accounted for an average of 41 % (SE = 2; range: 10 – 74 %, n = 60 follows) of the daily activity budget, did not vary significantly across months (linear mixed model: month $F_{9, 50.0} = 1.49$; $p = 0.18$; Table 4.2). Time spent feeding on fruit, leaf, and herb accounted for 37 % (SE = 4; range: 0 – 94), 28 % (SE = 3; range: 0 – 80 %), and 34 % (SE = 3; range: 3 – 96 %) of daily feeding time respectively (n = 60 follows). There was significant monthly variation in time spent feeding on fruit (linear mixed effects model: fruit feeding; month $F_{9, 48.0} = 7.86$; $p < 0.001$) and leaf (linear mixed effects model: leaf feeding; month $F_{9, 48.0} = 6.95$; $p < 0.001$; Table 4.2), but not herbs (linear mixed effects model: herb feeding; month $F_{9,$

$_{48.0} = 1.03$; $p = 0.43$; female ID variance = 0.01; residual variance = 1.40). Mean within-month fruit and leaf feeding time ranged from 9 – 80 % and 4 – 58 % respectively ($n = 10$ months; Figure 4.1). Daily time spent feeding on fruit and leaves ($n = 60$ follows) were inversely correlated (Spearman's correlation: $r = -0.66$; $p < 0.001$). The amount of time that females fed each day was not predicted by either the proportions of fruit or leaf in the diet (linear mixed effects model; $n = 60$ follows: fruit feeding: $F_{1, 58.0} = 0.68$; $p = 0.41$; leaf feeding: $F_{1, 58.0} = 1.33$; $p = 0.25$; Table 4.2).

Energy intake rate (excluding contribution from neutral detergent fiber) averaged 201 kcal / hr (SE = 17; $n = 60$ follows), which translates to a minimum daily intake estimate of 2010 kcals based on missing two hours of activity per day on average. Rates of energy intake varied significantly across months (linear mixed effects model: month: $F_{9, 50.0} = 2.52$; $p = 0.02$), with the lowest amount of energy consumed in March (114 kcals / hr (SE)) and the highest in September (347 kcals / hr (SE); Figure 4.2). Energy intake was significantly higher in August ($t_{1, 50.0} = 2.4$; $p = 0.02$) and September ($t_{1, 50.0} = 3.0$; $p = 0.004$) than in other months. Energy intake increased as the overall proportion of time spent feeding increased and as the proportion of feeding time spent on fruit increased (linear mixed effects model: time spent feeding: $F_{1, 56.7} = 12.12$; $p = 0.001$; proportion of feeding time on fruit: $F_{1, 56.5} = 17.06$; $p < 0.001$). The best-fitting and most parsimonious model of daily energy intake rate included as predictors both the proportion of feeding time spent on fruit and proportion of total time spent feeding (Table 4.3).

Rank and energy intake

Females did not vary significantly in overall energy intake rate (linear model: female ID: $F_{2,57} = 0.19$; $P = 0.83$; Figure 4.3). To test whether rank (Norm DS) was positively correlated with individual rate of energy intake within each month, I used the larger data set of 176 follows and conducted Spearman's rank correlations. Rank was negatively correlated with energy intake in six of 10 months examined (Table 4.4), although not significantly so in any month. Rank was positively correlated with energy intake in four months. These included January ($n = 18$ follows; $r_s = +0.54$; $P = 0.02$), February ($n = 23$ follows; $r_s = +0.35$; $P > 0.10$), and March ($n = 17$ follows; $r_s = +0.19$; $P > 0.10$), which encompass most of the dry season plus the dry-rainy season transition, and August ($n = 13$ follows; $r_s = +0.26$; $P > 0.10$; Table 4.4). January ($n = 18$ follows; $r_s = +0.54$), February ($n = 23$ follows; $r_s = +0.35$), and June ($n = 6$ follows; $r_s = -0.60$) fell outside the 99 % confidence interval of the mean (-0.39 to +0.33) of the observed distribution of correlation coefficients. January was the only month with a significant correlation between rank and energy intake (see above) and the average rate of energy intake for the highest ranked female (Norm DS = 4.2) in January was more than twice that of the other females (mean (\pm SE) kcal / hr: Norm DS of 4.2 = 382 (\pm 78), $n = 4$ follows; Norm DS of 2.9 = 155 (\pm 28), $n = 5$ follows; Norm DS of 1.7 = 147 (\pm 26), $n = 4$ follows; Norm DS of 1.5 = 152 (\pm 49), $n = 5$ follows; Figure 4.4). However, the observed distribution of monthly correlation coefficients between rank and energy intake did not differ from a null distribution of normally distributed correlation coefficients with a mean of 0 (One-sample t-test, 2-tailed: $df = 9$; $t = -0.27$; $P = 0.80$).

The potential mechanisms of achieving higher energy intake included feeding longer and/or more rapidly on the same foods and feeding on different, higher quality foods. Of these, I had data on feeding time and diet composition, which allowed me to examine whether either or

both of these variables explained the rank-based skew in energy intake seen in January. The alpha female's greater energy intake in January was not a result of her spending more time feeding than other females, since individual variation in feeding time was negligible (linear mixed effects model: female ID: variance < 0.001; residual variance = 0.25; n = 18 follows). Rather, rank was positively correlated with fruit consumption in January (n = 18 follows; $r_s = +0.46$; $P = 0.06$), such that the alpha female's greater energy intake was directly attributed to her higher intake of fruit (mean % fruit feeding time / activity time (\pm SE): Norm DS of 4.2 = 18.0 (\pm 3.6); n = 4 follows) relative to the fruit intake of others (Norm DS of 2.9 = 11.2 (\pm 3.3); n = 5 follows; Norm DS of 1.7 = 2.5 (\pm 1.2); n = 4 follows; Norm DS of 1.5 = 9.0 (\pm 2.0); n = 5 follows).

One way by which the alpha female might have gained more fruit was through aggression. Most (90 %; n = 295 focal events) female aggression occurred during feeding, and rates of feeding aggression over fruit were more than five times higher than those over leaves and herbs (see Chapter 3). Therefore, to assess whether rank-based skew in fruit consumption during January was associated with increased aggression over fruit, I used data from the 53 focal follows of the alpha female to test whether the frequency with which she directed aggression at other females while she was eating fruit varied significantly among months. Monthly variation was significant (GLM, Month: df = 9, 43; Deviance = 38.86; Residual deviance = 72.80; $P < 0.001$; fruit feeding time: df = 1, 42; Deviance = 0.50; Residual deviance = 72.30; $P = 0.48$). However, while the frequency of fruit-related aggression was significantly higher in October than in other months (GLM, October: $\beta = 2.97$; SE = 1.03; z-value = 2.88; $P = 0.004$), this was not the case for January (GLM, January: $\beta = 1.64$; SE = 1.12; z-value = 1.47; $P = 0.14$).

Mean monthly rate of fruit-related aggression (N events / hr feed fruit) by the alpha female was highest in January (mean (\pm SE) = 16.6 (\pm 14.6) events / hr; n = 4 follows) and October (mean (\pm SE) = 11.3 (\pm 11.3 (\pm 6.5) events / hr; n = 4 follows) and lowest in December (mean (\pm SE) = 0.0 (\pm 0.0) events / hr; n = 3 follows) and March (mean (\pm SE) = 0.0 (\pm 0.0) events / hr; n = 4 follows; Figure 4.5). Two species of fruits were responsible for high rates of fruit-related aggression in January and October. In January, the alpha female directed half of her fruit-related aggression toward other females (n = 4 events) when she was feeding on an energy-rich fruit species, *Tetrapleura tetraptera* (see Supplemental Table 4.3), which accounted for 55 % (\pm SE: 21; range: 0 – 94 %; n = 4 follows) of the alpha female's daily fruit feeding time in January. *Tetrapleura tetraptera* is a medium-sized fruiting tree that occurs at low densities in the site (see Doran et al. 2002). In October, sixty-seven percent of the alpha female's fruit-related aggression directed toward other females (n = 15 events) involved feeding on succulent ripe fruit of Embundunbundu, for which energy estimates were unavailable and which accounted for only 13 % (\pm SE: 12; range: 0 – 50 %; n = 4 follows) of the alpha female's daily fruit feeding time in that month. The mean rate of fruit-related aggression directed from the alpha female toward other females while she was eating fruit was low in months of high fruit consumption (June-September: Figure 4.1; Figure 4.5).

Discussion

Female energy intake rates varied considerably throughout the year, with three times less energy acquired in the month of lowest energy intake (March: 114 kcal per hour) compared to the month of highest energy intake (September: 347 kcal per hour). Female energy intake

increased with increasing amount of fruit in the diet and increasing time spent feeding on a daily basis. However, the effect of fruit feeding on energy intake was less consistent when examined on a monthly basis. On the one hand, higher than average rates of energy intake were recorded during the two months of highest fruit consumption (August; September), suggesting that energy is most available in the environment when fruit is plentiful, a pattern consistent with increased consumption of simple sugars and total non-structural carbohydrates in Kanyawara chimpanzees during periods of high fruit availability (Conklin-Brittain et al. 1998). However on the other hand, rates of energy acquisition were surprisingly high within two consecutive months of low fruit consumption (December; January) in which fruit comprised only 19 % of the diet, suggesting that other factors such as the density of energy in staple foods play an important role in determining mean monthly rates of female energy intake. Consistent with previous studies of western gorilla dietary variability and responses to fluctuating fruit availability and consumption in different years at the site (Mongo 2006; Doran-Sheehy et al. 2006), females increased the proportion of leaf in their diet in response to decreasing fruit consumption but did not spend more time feeding, indicating that western gorillas attempt to meet their energy demands in time of fruit scarcity by adjusting the amount of foliage in their diet, not by feeding longer. Increased feeding time on foliage may constrain the total percentage of time that can be devoted to feeding versus resting, because the higher structural carbohydrate content of leaves means that they require longer gut retention times for effective nutrient extraction (Milton and Demment 1988; Dasilva 1992; Milton 1998).

One limitation of this study is that I did not try to account for energy gained from microbial fermentation of neutral detergent fiber (hemicellulose and cellulose); it can be an appreciable proportion of total energy gain in hindgut fermenting primates including

chimpanzees and gorillas (Milton and Demment 1988; Remis and Dierenfeld 2004; Rothman et al. 2006b). Leaves, herbs, and some fruits eaten by western gorillas are known to contain high levels of neutral detergent fiber (Rogers et al. 1990; Popovich et al. 1997; Remis et al. 2001; Doran-Sheehy et al. 2009a) and thus should be considered good sources of energy despite requiring long digestion times to extract nutrients from the bulk (Milton 1979; Milton 1998). By this reasoning, the fermentable fiber fractions present in foliage and other fallback foods should have provided the gorillas with more energy during months of fruit scarcity than what I estimated based on intake and gross caloric values alone. Future research should include attempts to supplement measures of food intake with estimates of individual digestion efficiency by collecting fecal samples throughout the day and weighing and chemically analyzing the fibrous matter passed into the stool to back-calculate what proportion of daily fiber intake was converted to energy.

Contrary to predictions based on the presumed link between frugivory and contest feeding competition, overall energy intake rate was independent of rank. Positive correlations between rank and energy intake occurred in only four of 10 months and the correlation was significant in only one month (January), a result that could have occurred by chance. Although aggression over fruit varied significantly among months, the frequency of fruit-related aggression was not significantly higher in the month showing a significant positive correlation between rank and energy intake than in other months. These findings indicate that lowland gorillas sometimes show rank-related effects on individual energy gain like those documented in other primates (Koenig 2002; Koenig and Borries 2006). However, gorillas are not seasonal breeders (Doran-Sheehy unpublished data; Watts 1998; Watts 1998) and their reproductive

cycles span across years instead of months (Knott 2001) so the ultimate significance of this rank effect (i.e. on individual fitness) remains uncertain.

One potential explanation for why western gorillas do not show the expected energetic outcome is that the assumption that fruits generally resemble high quality, monopolizable food inflicting contest competition might be false (Koenig et al. 1998; Wheeler et al. 2013). In parts this might relate to the large body size (Smith and Jungers 1997) and the attendant low risk of predation (Doran and McNeilage 1998; Doran and McNeilage 2001) which allow sufficiently wide group spread for poorer competitors to avoid most contests. Most research showing significant contest effects on intake of food and/or energy and on reproduction has been on smaller-bodied, cohesively foraging monkey species that rely importantly on clumped, high quality food patches (Whitten 1983; Janson 1985; Whitten 1988b; Saito 1996; Vogel 2005). Contest effects in western gorillas may only become important on the rare occasions when large high quality fruit trees force females to forage together in the same patch at times when almost no other high quality resources are available (Doran et al. 2002). Thus the typical foraging pattern for female western gorillas is characterized by relaxed group cohesion and increased group spread (Salmi 2013) compared to many other primates.

This difference in spatial foraging patterns between western gorillas and other primates for which WGC competition has been shown may be further accenuated by differences in the methods used to sample individual food intake and in the repertoire of foods included in those measurements. In the present study I followed individuals throughout the day as they fed on items with widely varying resource characteristics that together accounted for 89 % of the total annual diet by feeding time (Chapter 2). By comparison, in some previous studies researchers

compared individual feeding success on a subset of species that were important during a particular season (Whitten 1988a; Saito 1996). Other researchers compared per capita intake on many or most dietary items (Janson 1985; van Schaik and van Noordwijk 1988; Vogel 2005), which included both fruits and dispersed items such as insects during periods of limited fruit supply. For primates, periods of preferred resource scarcity are seasons of energetic stress (Foerster et al. 2012) regardless of breeding seasonality or life history strategy. If females in seasonally-breeding populations accrue energetic deficits during an annual period of resource scarcity, these deficits can affect their ability to conceive. By this principle, seasonally-breeding brown capuchin females of low rank status will face fairly straight forward reproductive consequences for their reduced food or energy intake relative to dominant females during the dry season (Janson 1985) such as delayed conception. While the reproductive consequences of contest competition might be predictable in seasonally-breeding primates such as brown capuchins, effects of rank-related variation in energy gain that occur during annual lean seasons are less predictable in non-seasonal breeders with multi-year inter-birth intervals.

Gorillas have slow life histories (Watts 1990a; Breuer et al. 2009; Stoinski et al. 2013), including long time to reproductive maturity, extended lactational periods and inter-birth intervals (Knott 2001; Breuer et al. 2009) and generation times of roughly 20 to 30 years. Within-group contest competition among female western gorillas in the present study was expressed infrequently, at least for one social group over one annual cycle. This finding was inconsistent with results for Bwindi gorillas in which rank-based differences in feeding rates were associated with rank-related differences in energy intake (Wright et al. 2014). One limitation of the present study was an inability to characterize individual differences in feeding rates due to small sample sizes and may have minimized female intake differences. However,

there are some indications that the positive correlation between female dominance rank and energy intake within each of the first three months of the year may be linked to a period of energetic stress that includes the annual dry season (Doran et al. 2002; Doran-Sheehy et al. 2009a). At the height of the lean season at Mondika, preferred fruit species are relatively scarce in the environment (Doran et al. 2002; Mongo 2006) and fruit consumption is low (Doran-Sheehy et al. 2009a), suggesting that whatever high quality foods are available should be highly prized. If the timing of contest competition is consistent across years during an energy-critical lean season, low-ranking mothers may experience cumulative energy costs that could lead to reproductive disadvantages such as delayed weaning or extended inter-birth intervals relative to high-ranking mothers.

Although lean seasons may be more important with respect to contest feeding competition in western gorillas than other times of year, it is the precise combination of underlying factors such as the dispersion, availability, and quality of resources that should predict the strength of within-group contest competition. Support for this notion comes from Hanuman langurs in which the combination of clumped high quality foods present in low abundance was associated with stronger contest competition than was the combination of foods showing a more continuous distribution in lush seasons with faster depletion times (Koenig 2000). To test whether resource dispersion and quality aligned in similar ways for western gorillas during the dry season as in Hanuman langurs during periods of increased contest competition, data on feeding competition and associated measures of resource dispersion throughout the year are needed. Long-term demographic records are needed to test whether low-ranking females in the present study group have lower reproductive rates or reduced infant survival than high-ranking females, although longitudinal data on offspring production and

survival are challenging to gather for each female because of the slow pace of western gorilla reproduction and high frequency of secondary female transfer.

Alternatively, an argument could be made that infrequent contest competition in non-seasonally breeding gorillas with multi-year inter-birth intervals has little or no impact on female reproduction based on rank, particularly if positive correlations between rank and energy intake occurred by chance. The question then becomes what selective advantage does the achievement of high rank confer in female western gorillas. The absence of a significant relationship between female rank and overall energy intake was probably not due to a paucity of monopolizable foods, given that the olive baboons in Barton et al.'s (1996) study, which showed rank-related variation in food intake (Barton and Whiten 1993), spent less time feeding on clumped foods (30 %) than did the gorillas in this study presumably (based on 41-43 % fruit in the diet; Chapter 2). High rank may however, present other advantages to female western gorillas such as reinforcing a close bond with the group male (Kummer 1967; Harcourt 1979b; Watts 1994; Steenbeek 1996; van Schaik 1996; Watts 2003), which may be critically important when female group size is limited, as may be the case for western gorillas (Doran and McNeilage 1998; Parnell 2002; Robbins et al. 2004). Support for this hypothesis is slowly emerging from Mondika from evidence showing that rank influences long distance communication with the male (Salmi 2013), secondary-transfer decisions (Doran-Sheehy, unpublished records), male mating effort (Doran-Sheehy et al. 2009b), and male support in female agonistic conflicts (Chapter 3). It is presently unclear whether females gain any direct benefit from fighting over food and why such a high proportion of female aggression occurred during feeding if rank and food intake are not closely linked throughout most of the year.

To extend our understanding of the ecological factors that influence individual energy gain and frequency of fruit-related aggression in female western gorillas, I propose three areas of future research. First, I urge western gorilla researchers to examine the resource characteristics (density and spatial dispersion; DBH; crown volume, tree height, fruit crop availability) of high quality fruit trees in connection with gorilla foraging bouts to explore the ecological determinants of individual feeding minutes, number of females in the feeding party, and frequency of fruit-related aggression within patches to compare with other studies of smaller-bodied cohesive foragers (Janson 1985; Vogel 2005; Vogel and Janson 2007). Second, a detailed study of female spatial cohesion during foraging on clumped versus dispersed resources may shed light on whether low-ranking females use alternative foraging strategies such as avoidance throughout most of the year to meet energy demands. Third, a closer look at the nutrient quality of resources available during the dry season and their variance compared to other times of year may shed light on the ecological conditions which promote a positive correlation between rank and energy intake in wild western gorillas

Tables and Figures

Table 4.1. Number and duration of follows used to examine rank and energy intake and variation in feeding behavior.

Data set	Month	BE	EB	MA	ME	Total	Mean duration of follows (decimal hrs)	SE. Mean duration of follows (decimal hrs)
Rank and energy intake: master data set of 176 follows	D	4	3	3	4	14	4.95	0.08
	J	5	4	4	5	18	5.05	0.04
	F	6	7	5	5	23	5.10	0.03
	M	5	3	4	5	17	4.98	0.05
	A	7	7	8	7	29	5.01	0.03
	J	2	0	2	2	6	5.40	0.11
	J	7	0	5	3	15	5.27	0.07
	A	5	0	4	4	13	5.18	0.07
	S	9	0	14	9	32	5.28	0.07
	O	3	0	4	2	9	5.28	0.15
	Total	53	24	53	46	176	5.13	0.02
Feeding behavior: balanced subset of 60 follows	D	2	0	2	2	6		
	J	2	0	2	2	6		
	F	2	0	2	2	6		
	M	2	0	2	2	6		
	A	2	0	2	2	6		
	J	2	0	2	2	6		
	J	2	0	2	2	6		
	A	2	0	2	2	6		
	S	2	0	2	2	6		
	O	2	0	2	2	6		
	Total	20	0	20	20	60		
Alpha female fruit-related aggression (n = 53 follows)	D	0	0	3	0	3		
	J	0	0	4	0	4		
	F	0	0	5	0	5		
	M	0	0	4	0	4		
	A	0	0	8	0	8		
	J	0	0	2	0	2		
	J	0	0	5	0	5		
	A	0	0	4	0	4		
	S	0	0	14	0	14		
	O	0	0	4	0	4		
	Total	0	0	53	0	53		

Table 4.2. Monthly variation in female feeding strategies, including time spent feeding, feeding time spent on fruit and leaf, and effects of fruit and leaf feeding on time spent feeding.

	Time spent feeding				Feeding time on fruit				Feeding time on leaf			
	<i>df</i>	<i>F</i>	<i>P</i>	<i>Var</i>	<i>Df</i>	<i>F</i>	<i>P</i>	<i>Var</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>Var</i>
I. Monthly effects												
Fixed effects												
Month	9, 50.0	1.49	0.18		9, 48.0	7.86	< 0.001		1, 48.0	6.95	< 0.001	
Random effects												
Female ID				0.00				0.02				0.19
Residual				0.46				1.22				1.46
II. Effects of a) fruit and b) leaf feeding time												
a) Covariates												
Fruit feeding	1, 58.0	0.68	0.41									
Random effects												
Female ID				0.00								
Residual				0.50								
b) Covariates												
Leaf feeding	1, 58.0	1.33	0.25									
Random effects												
Female ID				0.00								
Residual				0.49								

Model parameters for fixed effects and covariates, including F-statistic (*F*) and probability (*P*), were estimated using restricted maximum likelihood (REML). Degrees of freedom (*df*) were calculated by Satterthwaite approximation. Variance components (*Var*) for the effect of Female ID (intercept; 3 groups; 60 observations) and residual variance are indicated for each model. Significant effects are shown in bold text. Measures of variance reported as 0.00 actually signify variance of less than 0.001.

Table 4.3. Comparing models of female energy intake rate with model selection statistics and parameter estimates for best-fitting model.

	df_1	AICc	Δ AICc	w_i	df_2	β	SE	F	P	Var
Model 1										
Feeding time	4	20.0	13.1	0.00						
Model 2										
Fruit	4	15.9	9.0	0.01						
Model 3										
Feeding time + Fruit	5	6.8	0.0	0.99						
Best fitting model: Model 3										
Intercept = 2.34										
Covariates										
Feeding time					1, 56.7	0.16	0.04	12.12	0.001	
Fruit					1, 56.5	0.08	0.02	17.06	< 0.001	
Random effects										
Female ID										0.00
Residual										0.06

Model selection was conducted using maximum likelihood (ML). Parameter estimates for model selection include degrees of freedom (df_1 : based on total number of model terms and number of levels), Akaike information criterion corrected for small sample sizes (AICc), difference in AICc (Δ AICc), and Akaike information criterion weights (w_i). Parameter estimates for covariates in best-fit model, including degrees of freedom (df_2 : Satterthwaite approximation of denominator degrees of freedom), Beta estimate (β) and its standard error (SE), F-statistic (F), and probability (P), were calculated using restricted maximum likelihood (REML). Variance explained by the effect of Female ID was estimated and compared to the residual variance. Variance of 0.00 signifies Var of < 0.001.

Table 4.4. Correlation between rank and energy intake rate within months.

Month	N of follows	N of females	Correlation coefficient	<i>P</i>
December	14	4	- 0.10	> 0.10
January	18	4	+ 0.54	0.02
February	23	4	+ 0.35	> 0.10
March	17	4	+ 0.19	> 0.10
April	29	4	- 0.15	> 0.10
June	6	3	- 0.60	> 0.10
July	15	3	- 0.22	> 0.10
August	13	3	+ 0.26	> 0.10
September	32	3	- 0.18	> 0.10
October	9	3	- 0.39	> 0.10

Spearman's rank correlations were conducted. Significant correlations indicating contest competition are given in bold.

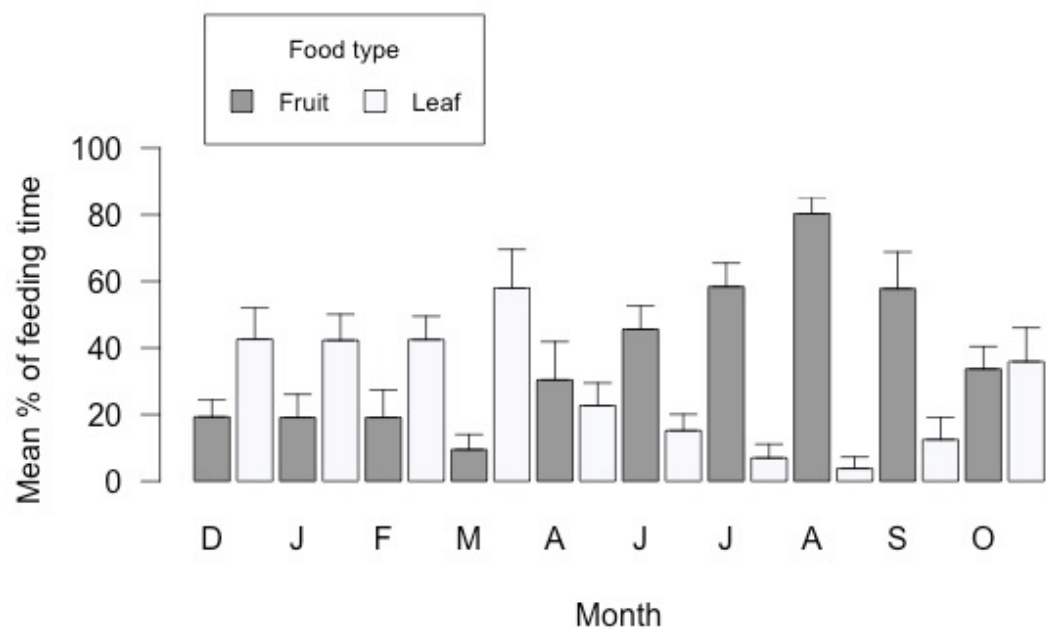


Figure 4.1. Mean monthly proportion (+ SE) of feeding time spent on fruit and leaf.

Sample size in each month is 6 follows / month.

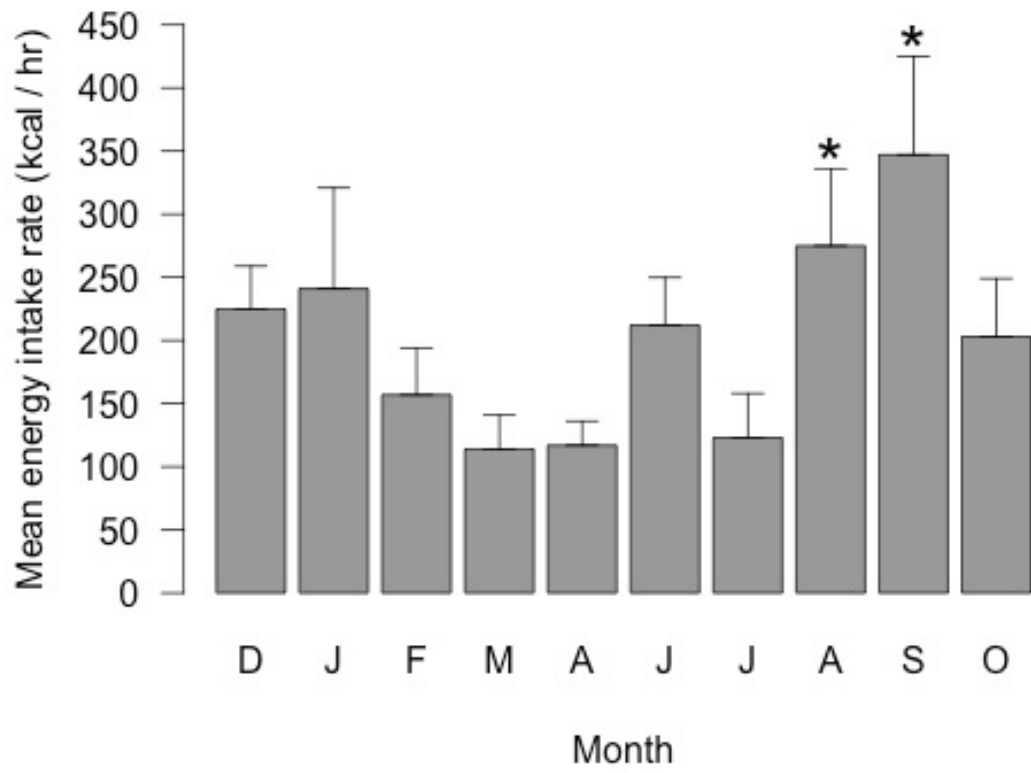


Figure 4.2. Mean monthly energy intake rate (kcal / hr + SE).

Sample size for each month is 6 follows / month.

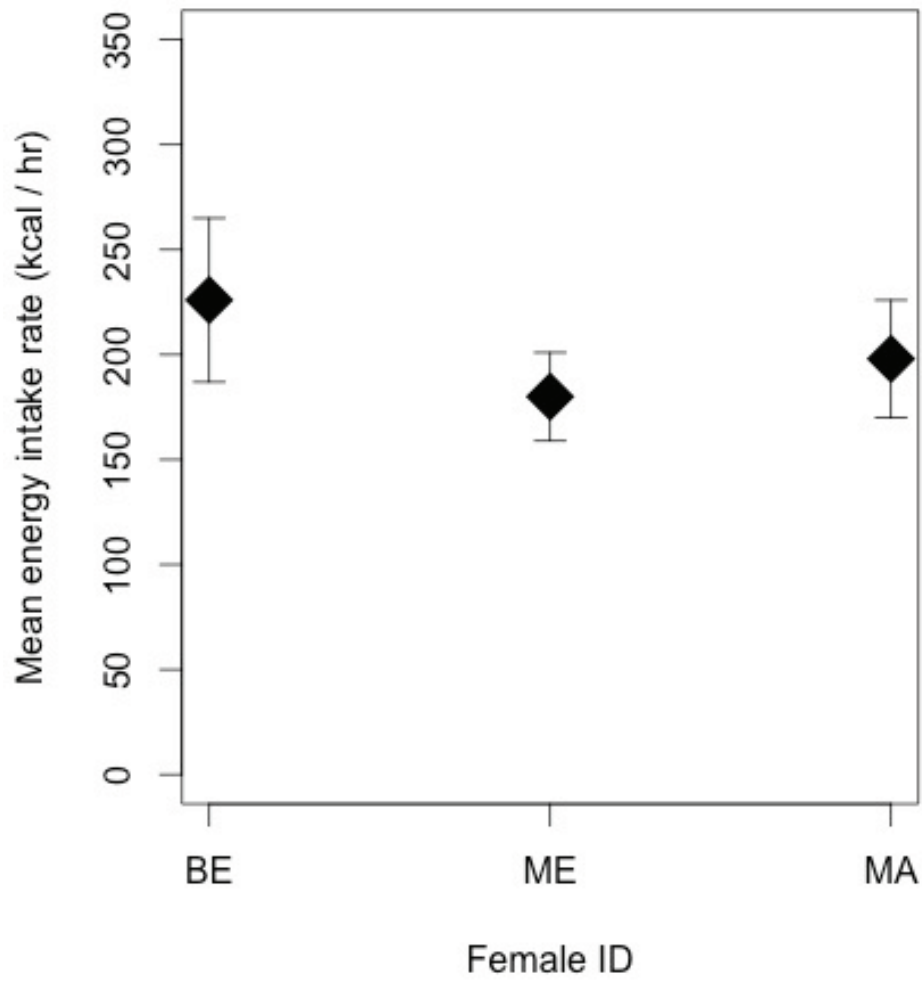


Figure 4.3. Variation in overall individual energy intake rate (kcal / hr \pm SE).

Sample size is 2 samples / female / month for a total of 20 samples per female.

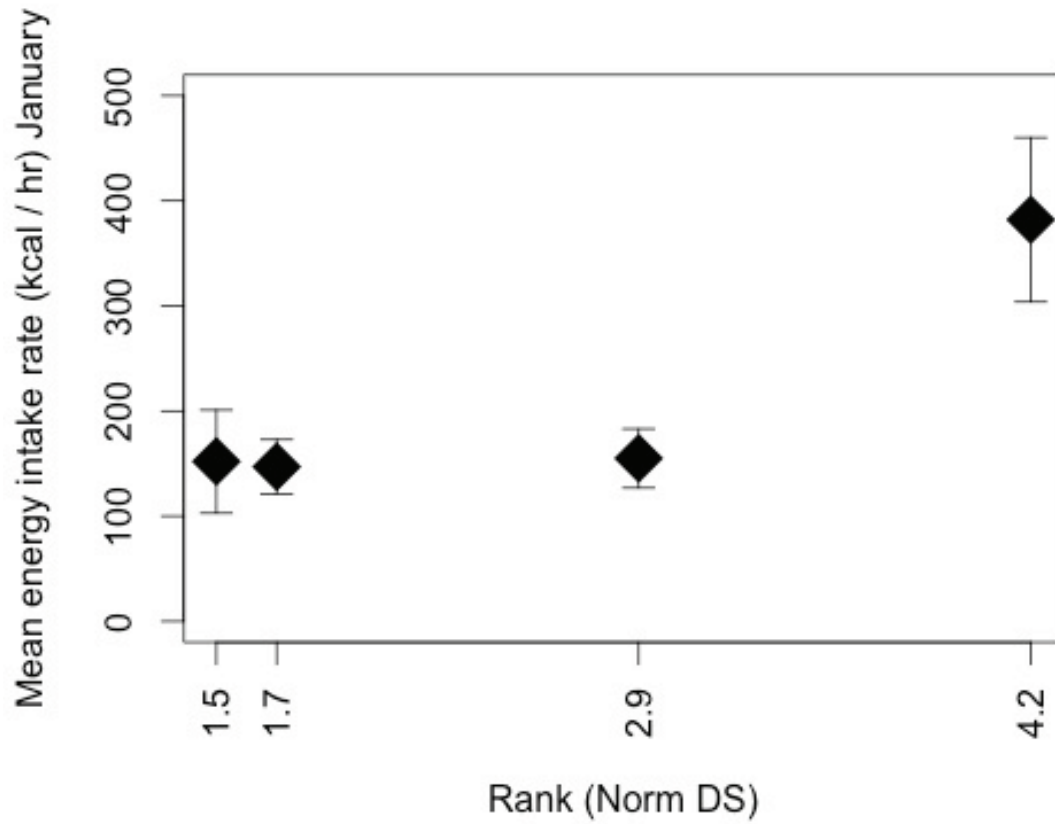


Figure 4.4. Individual energy intake rate (kcal / hr \pm SE) in January plotted against increasing female rank based on normalized David's scores.

Sample sizes of the four females are 5, 4, 5, 4, respectively.

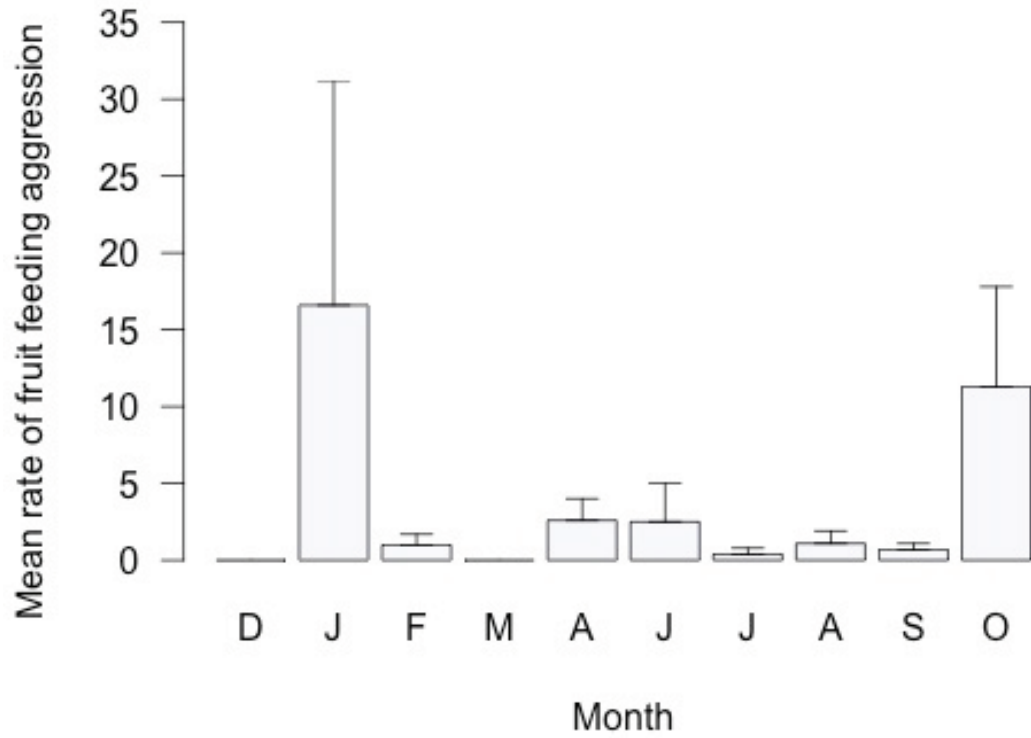


Figure 4.5. Mean monthly rate of alpha female aggression (N of events / hr + SE) toward other females while feeding on fruit.

Sample sizes per month are 3, 4, 5, 4, 8, 2, 5, 4, 14, and 4, respectively.

Supplemental Table 4.1. Distribution of 212 half-day follows by month (M; December-October) and focal female (MA, ME, BE, EB), including sample sizes (N), mean duration (Hrs), and mean start (Start), and stop (Stop) times of morning (M) and afternoon (A) follows (F).

		MA				ME				BE				EB				
M	F	N	Hrs	Start	Stop	N	Hrs	Start	Stop	N	Hrs	Start	Stop	N	Hrs	Start	Stop	N
D	M	2	4:28	7:25	11:54	2	4:36	7:17	11:54	2	5:31	6:22	11:54	2	4:41	7:12	11:54	8
	A	2	4:54	12:00	16:54	2	4:51	12:01	16:53	2	4:54	12:00	16:54	2	4:46	12:00	16:46	8
J	M	2	4:44	7:10	11:54	3	5:06	6:47	11:53	3	4:59	6:43	11:42	2	5:06	6:47	11:54	10
	A	2	5:05	12:00	17:05	2	5:08	12:01	17:09	2	5:04	12:07	17:12	3	4:45	12:23	17:09	9
F	M	3	4:41	7:12	11:54	3	5:12	6:40	11:53	3	5:05	6:49	11:54	4	4:48	7:06	11:54	13
	A	3	5:06	12:00	17:06	2	5:09	12:00	17:09	3	4:59	12:00	16:59	4	5:08	12:00	17:08	12
M	M	2	5:01	6:52	11:54	3	5:09	6:44	11:54	3	4:24	7:30	11:54	3	4:32	7:12	11:44	11
	A	2	5:00	12:00	17:00	3	4:40	12:02	16:43	3	5:04	12:00	17:04	2	4:52	12:00	16:52	10
A	M	5	4:39	7:15	11:54	5	4:35	7:18	11:54	4	4:47	7:07	11:54	4	4:21	7:32	11:54	18
	A	5	4:46	12:03	16:49	5	4:53	12:01	16:54	4	5:01	12:00	17:01	5	5:09	12:00	17:09	19
M	M	0	na	na	na	2	5:09	6:41	11:50	2	4:54	6:59	11:54	2	5:27	6:27	11:54	6
	A	0	na	na	na	1	5:24	12:00	17:24	2	3:47	12:00	15:47	1	5:09	12:00	17:09	4
J	M	1	5:54	6:00	11:54	2	4:30	7:23	11:54	1	5:24	6:30	11:54	0	na	na	na	4
	A	1	5:12	12:03	17:15	1	5:24	12:00	17:24	1	5:24	12:00	17:24	0	na	na	na	3
J	M	3	4:43	7:10	11:54	2	5:08	6:45	11:54	5	5:14	6:40	11:54	0	na	na	na	10
	A	3	5:13	12:00	17:13	2	4:44	12:24	17:09	3	5:15	12:01	17:16	0	na	na	na	8
A	M	3	4:36	7:18	11:54	4	5:03	6:48	11:51	3	4:59	6:52	11:51	0	na	na	na	10
	A	3	5:03	12:10	17:14	1	5:15	12:04	17:19	3	4:58	12:01	16:59	0	na	na	na	7
S	M	7	5:26	6:18	11:44	4	5:40	6:13	11:54	5	5:27	6:26	11:54	0	na	na	na	16
	A	7	4:56	12:02	16:59	5	5:06	12:03	17:09	4	5:12	12:00	17:12	0	na	na	na	16
O	M	2	5:34	6:19	11:54	2	5:10	6:19	11:29	1	5:49	6:05	11:54	0	na	na	na	5
	A	2	5:03	12:05	17:09	1	3:24	13:30	16:54	2	5:01	12:07	17:09	0	na	na	na	5
V	M	30	4:58	6:53	11:53	32	5:01	6:48	11:50	32	5:08	6:43	11:52	17	4:49	7:02	11:52	111
	A	30	5:01	12:02	17:04	25	4:54	12:11	17:06	29	4:58	12:01	16:59	17	4:58	12:03	17:02	101

Key: Average duration of follows uses standard time (Hrs:min); Overall (V) gives sums (N) and grand means (Hrs; Start; Stop).

Supplemental Table 4.2. Short-duration follows (< 4.5 hrs) excluded from feeding and energy intake analysis.

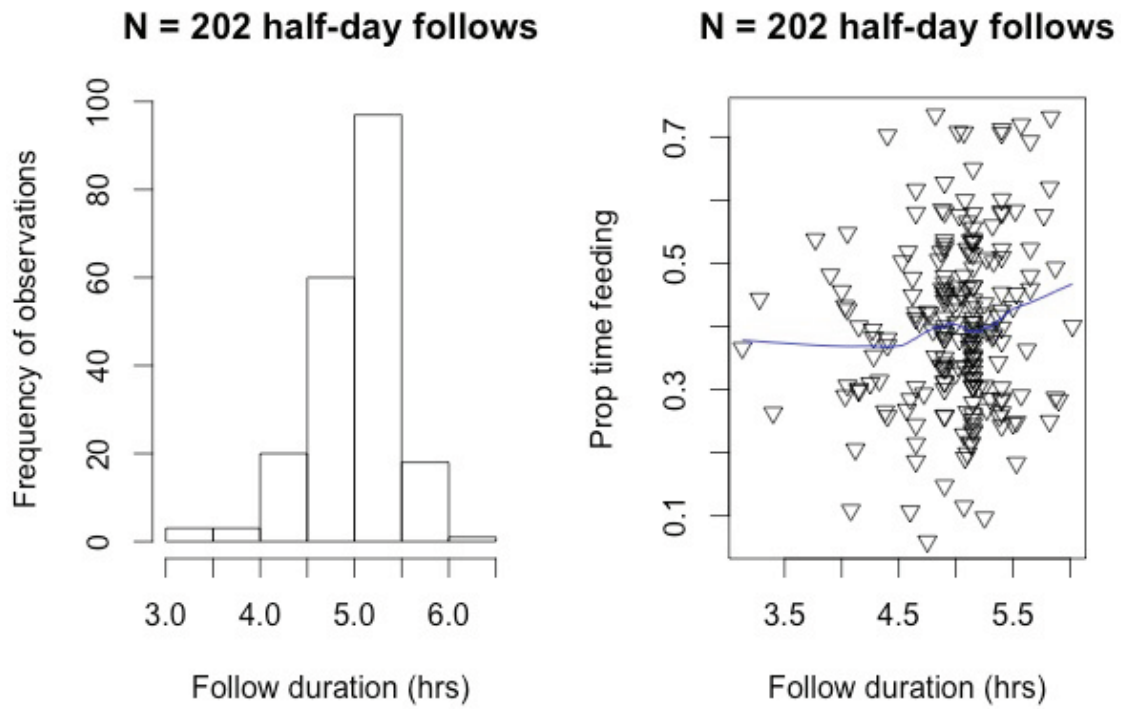
F	Month	Focal	Date	N hrs	Start	Stop	Prop Feed %	Monthly prop feed % (N)
M	December	EB	12/15/04	4.08	7:49	11:54	10.91	45 (16)
M	December	MA	12/24/04	4.05	7:51	11:54	54.79	
A	January	EB	01/04/05	4.03	13:07	17:09	43.23	42 (19)
M	February	MA	02/16/05	4.05	7:51	11:54	30.63	39 (25)
M	February	EB	02/28/05	4.05	7:51	11:54	42.68	
A	March	ME	03/03/05	4.40	12:00	16:24	70.25	41 (21)
M	March	BE	03/04/05	3.77	8:08	11:54	53.78	
M	March	EB	03/05/05	4.25	7:39	11:54	30.99	
M	March	EB	03/31/05	4.27	7:08	11:24	39.49	
M	April	EB	04/02/05	3.28	8:37	11:54	44.36	39 (37)
A	April	ME	04/04/05	4.28	12:00	16:17	35.33	
M	April	ME	04/10/05	4.28	7:37	11:54	38.24	
M	April	EB	04/13/05	4.12	7:47	11:54	20.53	
A	April	MA	04/14/05	4.03	12:15	16:17	29.01	
M	April	MA	04/20/05	3.13	8:46	11:54	36.59	
M	April	BE	04/26/05	4.33	7:34	11:54	31.45	
M	April	ME	04/30/05	4.15	7:45	11:54	40.00	
M	June	ME	06/19/05	3.90	8:00	11:54	48.18	36 (07)
M	July	ME	07/09/05	4.40	12:30	16:54	38.06	36 (18)
M	July	BE	07/30/05	4.16	7:45	11:54	30.12	
M	July	MA	07/31/05	4.38	7:31	11:54	26.54	
M	August	ME	08/08/05	4.15	7:45	11:54	29.76	34 (17)
M	August	MA	08/14/05	4.00	7:54	11:54	45.58	
M	August	MA	08/15/05	4.40	7:30	11:54	36.99	
A	August	BE	08/21/05	4.40	12:00	16:24	25.79	
A	October	ME	10/03/05	3.40	13:30	16:54	26.32	37 (10)

Key: Follows (F) conducted in the morning (M) and afternoon (A) are summarized by duration (N hrs) start and stop times and the percentage of time spent feeding (Prop feed). Monthly percentage of time spent feeding (Monthly prop feed) is provided for comparison.

Supplemental Table 4.3. Energy content (kcal/ 100 g organic matter) and intake rates (mean wet g / min) of fruits (FR = pulp; SE = seed), herbs (ST = stem; SH = shoot), termites (TE), and leaves (LE= leaf; BK = young bark) consumed by female western gorillas and sorted in descending order of caloric value by food type.

Food species	Local name	Part	Energy content (kcal)	Intake rate (g / min)
Fruits				
<i>Landolphia sp 2</i>	Bosindja	FR	368	200.8
<i>Anonidium mannii</i>	Mobei	FR	322	29.7
<i>Tetrapleura tetraptera</i>	Ekombolo	FR SE	321	17.3
<i>Gambeya lacourtiana</i>	Bambu	FR	310	163.3
<i>Vitex doniana/ welwitschii</i>	Mongweagwea	FR	279	16.1
<i>Drypetes spp.</i>	Tembo	FR	260	4.6
<i>Anglocalyx pynaertii</i>	Manjombe	FR	258	24.5
<i>Hexalobus crispiflorus</i>	Pota	FR	242	13.6
<i>Gilbertiodendron dewevrei</i>	Bemba	SE	241	47.5
<i>Klainedoxa gabonensis</i>	Bokoko	FR	232	51.0
<i>Pterocarpus soyauxii</i>	Embema	FR	203	54.89
<i>Grewia oligoneura</i>	Buku	FR	196	12.69
<i>Polyalthia suaveolens</i>	Motunga	FR	192	12.7
<i>Barteria dewevrei/fistulosa</i>	Ngomangoma	FR	170	45.7
<i>Duboscia macrocarpa</i>	Nguluma	FR	168	23.8
Unknown	Mbongo	FR	158	8.4
<i>Haumania danckelmaniana</i>	Genye	SE	112	20.6
Herbs				
<i>Palisota ambigua</i>	Doto	ST	185	78.6
<i>Haumania danckelmaniana</i>	Basele	SH	179	32.4
<i>Aframomum limbatum</i>	Njombo	ST	166	9.7
<i>Hydrocharis chevalieri</i>	Kongwasika	RT	152	4.6
<i>Palisota brachythyrsa</i>	Mangabo	ST	141	38.1
<i>Aframomum subsericum</i>	Njokoko	ST	123	10.9
<i>Megaphrynium</i>	Ngungu	SH	123	21.1
Termites				
<i>Cubitermes sp.</i>	Kusu	TE	131	18.8
Leaves				
Unknown	Ekombe	LE	301	38.8
<i>Thomandersia hensii</i>	Ingoka	LE	233	20.0
<i>Gnetum africanum</i>	Koko	LE	231	10.8
Unknown	Mazembe	LE	207	19.0
Unknown	Edutu	LE	205	9.5
Unknown	Ekule	LE	202	20.9

Food species	Local name	Part	Energy content (kcal)	Intake rate (g / min)
Leaves (cont.)				
<i>Whitfieldia elongata</i>	Indolu	LE	201	8.6
Unknown	Tondo	LE	194	52.2
<i>Aponcynaceae sp.</i>	Ivua	LE	193	37.5
<i>Ficus spp.</i>	Dobu	LE	188	31.0
<i>Celtis mildbraedii</i>	Ngombe	LE	172	8.5
Unknown	Ita ti edutu	LE	148	12.0
Unknown	Kpekeke	LE	130	7.6
<i>Anglocalyx pynaertii</i>	Manjombe	LE	90	3.7
<i>Celtis mildbraedii</i>	Ngombe	BK	156	26.8



Supplemental Figure 4.1. Histogram of follow duration and scatter-plot of relationship between follow duration and proportion of time spent feeding. Loess smoothing line (right panel) is for demonstration purposes.

CHAPTER FIVE: Summary and conclusions

In this dissertation, I examined the nutritional, social, and energetic consequences of increased frugivory in western lowland gorillas compared to their close relatives the mountain gorilla. Tropical lowland forests inhabited by western gorillas differ broadly in their ecology from the montane and afro-alpine environments occupied by mountain gorillas, including higher densities and diversities of fruiting trees, taller canopies, different plant communities, and reduced evenness and abundance of terrestrial herbs (White et al. 1995; Kuroda et al. 1996; Goldsmith 2003; Yamagiwa et al. 2003; Ganas et al. 2009). Western gorilla fruits are high quality resources (Rogers et al. 1990; Wrangham et al. 1991; Rothman et al. 2006b; Doran-Sheehy et al. 2009a), that are preferred whenever available (Williamson et al. 1990; Tutin et al. 1991; Remis 1997; Goldsmith 2003; Remis 2003), and potentially monopolizable, although this remains to be tested. Most food-related aggression among western gorilla females (60%) occurs over access to fruits. Thus, the amount of fruit in the diet may serve as a crude but simple indicator of contest competition in the absence of data on patch depletion and spatial dispersion of different fruit species.

In particular, I sought to determine whether increased frugivory in western as compared to mountain gorillas: 1) yielded a diet rich in easily-assimilated energy (i.e. total non-structural carbohydrates), 2) altered the nature of within-group female agonistic relationships and 3) affected rank-related skew in overall individual energy acquisition. To address the first aim, I asked a) whether nutritional contribution from total non-structural carbohydrates in the staple

diet of western gorillas was higher than in mountain gorillas, and if so b) whether this was brought about by higher total non-structural carbohydrate content of western gorilla fruits compared to mountain gorillas fruits. Although female agonistic relationships are well documented in mountain gorillas (Harcourt 1979a; Stewart and Harcourt 1987; Watts 1994; Watts 1996; Watts 2001; Watts 2003; Robbins et al. 2005; Harcourt and Stewart 2007; Robbins 2008), little is known about within-group social relationships among wild female western gorillas (Stokes 2004). To this end, I asked a) whether the majority of female aggression in western gorillas occurred in the context of feeding, b) whether the bulk of aggression was decided, c) whether rates of feeding aggression over fruit were higher in western gorillas than in mountain gorillas and whether this translated into d) a greater proportion of decided female dominance relationships and e) a steep and linear dominance hierarchy. Concerning the third aim, I asked a) whether females differed in their overall rate of energy intake and b) what factors explained variance in female energy intake throughout the year in western gorillas.

Ecological flexibility in gorilla diet and nutrition

My results revealed that western gorillas are consistent with some but not all predictions of the current socioecological model as they relate to effects of within-group contest competition (van Schaik 1989; Sterck et al. 1997). Environmental differences between tropical lowland forests of western gorillas and montane habitats of mountain gorillas were associated with broad-scale differences in the wet weight composition of diets and in the overall pattern of nutrient consumption. Western gorillas in this study (Mondika) consumed more fruit, less herb, and more dicotyledenous leaf by wet weight compared to two populations of mountain gorillas (Karisoke and Bwindi). These dietary changes were associated with increased nutritional contribution from

total non-structural carbohydrates and fiber and decreased contribution from crude protein in western gorillas (Chapter 2). My findings support the hypothesis that the nutrient composition of gorilla diets shows ecological flexibility and can vary according to the nutrient quality of foods and relative wet weight contributions from different food types. In contrast, Rothman and colleagues (2007) found that gorilla diets showed similar nutrient profiles despite differences in the nature and diversity of staple foods.

Differences in the nutrient composition of primate diets may have considerable life history implications. According to Janson and van Schaik's (1993) ecological risk aversion hypothesis, frugivorous primates should be expected to have slower life histories than folivorous primates (assuming similar body mass) because the temporal availability of fruit is highly variable and frugivores must buffer against energy shortages during periods of resource scarcity. Indeed, some primate studies support the ecological risk aversion hypothesis (Leigh 1994; Stoinski et al. 2013) while others refute it (Godfrey et al. 2004; Borries et al. 2011) or urge caution when comparing life history data of dubious quality (Borries et al. 2013).

Even so, comparisons of diet, nutrition, and life history schedules in closely related species living in different environments with different dietary regimes such as mountain and wild western gorillas offer the most suitable tests of the ecological risk aversion hypothesis (Stoinski et al. 2013). The herbaceous diet of mountain gorillas varies little throughout the year (Watts 1998; McNeilage 2001) and exceeds the protein requirements for animals of equivalent body mass (Rothman et al. 2008a; Rothman et al. 2011). In contrast, western gorilla diets are variable throughout the year (Nishihara 1995; Watts 1996; Remis 2003; Doran-Sheehy et al. 2009a; Masi et al. 2009), contained more fruit and less herb by wet weight intake (Chapter 2), and featured higher concentrations of total non-structural carbohydrate and neutral detergent fiber and less

crude protein (Chapter 2). Consistent with the ecological risk aversion hypothesis, mountain gorillas weaned their infants a full year earlier than wild western gorillas (Breuer et al. 2009; Stoinski et al. 2013), indicating faster developmental life histories in the more folivorous/herbivorous species with fewer fluctuations in seasonal resource availability and presumably less energetic risk compared to the more frugivorous species. The results of my dissertation help provide a nutritional link between increased frugivory and consumption of higher quality fruit species and slower developmental life history schedules in wild western gorillas than in mountain gorillas. However, additional studies of the nutritional composition of wild western gorilla diets from other social groups, in other years, and in different habitat types are needed to assess the full range of variation in gorilla nutrient consumption.

Effect of increased frugivory on female agonistic relationships

Ecological explanations for female social relationships and dispersal patterns in primates have traditionally focused on how variation in resource characteristics (i.e. distribution, patch size and productivity, and quality) determine the predominant form of feeding competition and resulting competitive regime, which in turn shapes the nature and strength of female agonistic relationships (van Schaik 1989; Sterck et al. 1997; Koenig 2002; Boinski et al. 2002). In chapter three, I used fruit as a proxy for high quality (and potentially) monopolizable foods in the absence of patch depletion data and tested four of the five premises of the socioecological model as they relate to the effects of contest competition on patterns of aggression and female agonistic relationships. Specifically, I examined the context and frequency of female aggression, the consistency of female dominance relationships on the basis of aggression, the steepness and

linearity of the female dominance hierarchy, and the frequency of female coalitions and male interventions in female conflicts.

Results from chapter three revealed an association between increased fruit consumption and increased rates of fruit-related aggression in western gorillas compared to Bwindi mountain gorillas. Although variation in rates of aggression among gorilla populations in different environments may be explained by ecological factors, the possibility of a phylogenetic basis to inter-specific differences in aggression rates cannot be ruled out. Based on recent molecular evidence it is estimated that western gorillas (*Gorilla gorilla*) diverged from eastern gorillas (*Gorilla beringei*) roughly 1.75 mya (Scally et al. 2012). Thus, ecological differences between western and eastern mountain gorilla habitats are confounded by the species' differing evolutionary histories over a time frame of about two million years. Additionally, I showed that a large proportion of aggression over food in western gorillas was associated with a higher proportion of decided aggression (overall and in the context of feeding) compared to mountain gorillas in both populations, suggesting that feeding bouts were interrupted in a higher percentage of instances in western gorillas than in mountain gorillas. Female dominance relationships were decided in many though not all (53 to 60 % of) pairs of female western gorillas (Chapter 3), which was consistent with the prediction of more directional asymmetry in western gorilla dyads compared to mountain gorilla dyads. A steep and linear female dominance hierarchy was indicated on the basis of aggression (Chapter 3), which adds to the variability in female dominance hierarchy characteristics seen in other gorilla populations (Watts 1994; Stokes 2004; Robbins 2008). In chapter three, I noted that females differed in overall competitive ability based on normalized David's scores (de Vries et al. 2006). However, for some females, there were much larger differences in competitive ability than with others, and some females showed

roughly the same level of competitive ability. Not surprisingly, I found that female coalitions were uncommon in western gorillas, occurring in only 2 % of aggressive events compared to a similarly low incidence of 4 % in mountain gorillas (Watts 1997). In addition, in western gorillas the male only rarely intervened in (ca. 5 % of) female conflicts. However, in contrast to mountain gorillas where males intervene to buffer differences in female competitive ability (Watts 1994; Watts 1996; Watts 2001), the western gorilla male intervened in direct support of the higher-ranking of the two females in most (81 % of) cases (Chapter 3).

In sum, my results demonstrate a shift in western gorillas toward increased feeding aggression, increased decidedness of female agonistic relationships, steep female dominance hierarchies based on aggression, and a different role of the male in moderating female conflicts than in mountain gorillas, which are thought to exhibit low levels of within-group contest and scramble feeding competition (Watts 1985; Watts 2003; Robbins et al. 2007; Harcourt and Stewart 2007). Differences in the nature of female social relationships between mountain and western gorillas were overall not as great as described in other comparative studies of closely related species occupying different environments such as Costa Rican, Surinamese, and Peruvian squirrel monkeys (Mitchell et al. 1991; Boinski 1999) and mountain and olive baboons (Barton et al. 1996). One plausible explanation for the social consequences seen in this study relate to small-to-moderate increases in within-group contest competition, however in the following section this explanation will be explored and challenged using data on individual energy intake.

Dominance and energy intake in western gorillas

Female rank is positively correlated with food intake (Whitten 1983; Janson 1985; van Noordwijk and van Schaik 1987; van Schaik and van Noordwijk 1988; Barton and Whiten 1993;

Saito 1996), energy intake (Vogel 2005), net energy gain (Whitten 1983; Koenig 2000; Schülke 2003), and birth rates, offspring survival, and female reproductive success (Silk et al. 1981; Borries et al. 1991; van Noordwijk and van Schaik 1999; Altmann and Alberts 2003a; Altmann and Alberts 2003b) in a number of cohesively foraging primates. There is less empirical evidence of a clear energetic or nutritional advantage to high female rank in primates with relaxed group cohesion or fission-fusion societies. However, in Gombe chimpanzees females of high dominance rank had faster rates of reproduction, higher infant survivorship, and faster maturing daughters compared to other females (Pusey et al. 1997), which was likely attributable to high-ranking females' use of higher quality core foraging areas (Murray et al. 2007). In Karisoke mountain gorillas, despite low levels of within-group contest competition (Watts 1985; Watts 1996; Sterck et al. 1997), high-ranking females had shorter surviving inter-birth intervals than low-ranking females (Robbins et al. 2007). It is possible that, given the significant displacement-based dominance hierarchy in Karisoke mountain gorillas (Watts 1994; Robbins et al. 2005), females of high and low rank status show subtle differences in dietary intake which then translate into differences in inter-birth intervals. If supported, this would be a case in which the categorical nature of the socioecological model obscures understanding (Clutton-Brock and Janson 2012). Theoretically, species with weak but non-zero potential for contest competition could have small but meaningful differences in female reproductive success based on small, rank-dependent differences in feeding success.

In chapter four I examined whether higher-ranking female western gorillas had higher overall energy intake than lower-ranking females using rank differences in energy intake as an indicator of increased within-group contest competition. My results showed that females in this western gorilla population did not differ in their overall energy intake on the basis of dominance

rank, despite presumed increases in within-group contest competition relative to mountain gorilla females (Chapter 4). I found a significant positive correlation between rank and energy intake in only one (January) month of the annual cycle and only three other months showed (non-significant) positive correlations between rank and energy intake (February; March; August). I could not rule out the possibility that the positive correlations occurred by chance (Chapter 4). Instead, variance in female energy intake throughout the year was positively predicted by the proportion of time spent feeding and proportion of feeding time devoted to fruit (Chapter 4). My results indicate that, for female western gorillas in one social group during one annual cycle, the strength of overall within-group contest competition was weak. Information on additional groups from different locations and in different years is needed to confirm the generalizability of these results to other western gorillas throughout tropical lowland forests in west-Central Africa. I stress the importance of examining rank-based energy intake in female western gorillas living in groups of different sizes over more than one annual cycle because of known inter-annual variation in fruit availability (Doran-Sheehy et al. 2009a). It would also be important to replicate the suggestive, but statistically weak, result from this study that positive effects of rank on energy intake may be present primarily in months of fruit scarcity.

It is likely that the assumption that a high amount of fruit feeding resembles a lot of monopolizable high quality food is wrong (see also, Koenig et al. 1998; Wheeler et al. 2013). It is possible that the relaxed group cohesion seen in western gorillas (Doran and McNeilage 2001) would have allowed females in our study group to spread out while foraging, thereby avoiding severe within-group contest competition at monopolizable food patches occupied by high-ranking group members. Theoretically, the capacity to increase group spread in the context of foraging should be much greater in western gorillas and other great apes compared to smaller-

bodied monkeys because of reduced predation pressure. A similar explanation has been hypothesized for why chimpanzees face reduced within-group feeding competition relative to some other primates despite feeding on high quality fruits (Wrangham et al. 1996). Females in this study have been reported to forage independently from other group members at distances of hundreds of meters from the dominant male (Salmi 2013), providing support for western gorillas' ability to avoid contest competition. However, when high-quality resource patches are scarce, low-ranking females who spatially avoid contest competition may often have to be content feeding on less-preferred resources, as was seen in the January sample of this study. Measures of resource dispersion and availability and group spread are needed to examine the ecological correlates of avoidance if this is a strategy employed by low-ranking females during certain months of the year.

Benefits of high rank in western gorillas

It is clear that increased frugivory (Chapter 2) in one wild western gorilla group at Mondika, when compared to mountain gorillas at Karisoke and Bwindi, was associated with increased aggression over fruit, more differentiated female dominance relationships, and a steep dominance hierarchy (Chapter 3). Yet, I found no rank-related differences in overall female energy intake. Thus, one question raised from a synthesis of results in my dissertation is what is the ultimate advantage of attaining and maintaining high rank in female western gorillas if not superior resource acquisition? In other primates with one-male multi-female social organizations and female dispersal, such as Thomas' langurs, mountain gorillas, and *Hamadryas* baboons, females form close bonds with the group male (Kummer 1967; Harcourt 1979b; Watts 1994; Steenbeek 1996; Watts 1996; Sterck 1997; Watts 2003) and depend critically on male services

for infanticide protection. Although special relationships between females and the male are likely to occur as well in western gorilla groups, there is growing evidence at Mondika that the group silverback favors higher-ranking females over others. High rank in female gorillas at Mondika influences female secondary transfer out of the group (Doran-Sheehy unpublished data), male mating effort (Doran-Sheehy et al. 2009b), and the direction of male support in female agonistic conflicts (Chapter 3). Future studies should expand on previous studies of female reproductive success in wild western gorillas (Stokes et al. 2003) by incorporating effects of male-female friendships, the relative quality of males, rank, and group size on female fitness parameters such as age at first reproduction, inter-birth intervals, and infant survival.

Conclusions

Overall, results of this research reveal that gorillas show considerable ecological flexibility in the composition of their diets, in nutrient intake, and in the nature of female agonistic relationships. This flexibility is consistent with ecological explanations for intra- and inter-specific variability in primate diets and female social relationships. The lack of rank-based differences in overall energy intake may indicate that within-group contest in western gorillas is relatively weak. Alternatively, my measures of female feeding rates averaged by food item may have obscured actual differences in female intake rates as seen in Bwindi mountain gorillas (Wright et al. 2014). Another possibility is that natural selection does not operate on time-averaged energy outcomes for the annual cycle, but instead plays a meaningful role during periods of preferred resource scarcity when individual energy intake is positively correlated with dominance rank. The significance of contest feeding competition on female reproductive success in wild western gorillas is not presently known and further research is needed to test this link.

Increased reliance on higher-quality fruits and greater dietary variability in western gorillas was associated with increased consumption of total non-structural carbohydrates and decreased consumption of protein, in addition to slower life history schedules compared to mountain gorillas (Breuer et al. 2009; Stoinski et al. 2013). Future work on female foraging strategies in gorillas should test for effects of varying resource characteristics on individual feeding time, feeding rates, patch depletion, feeding party size, group cohesion, and rates of aggression to reach an improved understanding of the ecological determinants of feeding competition in non-cohesive foragers like gorillas.

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